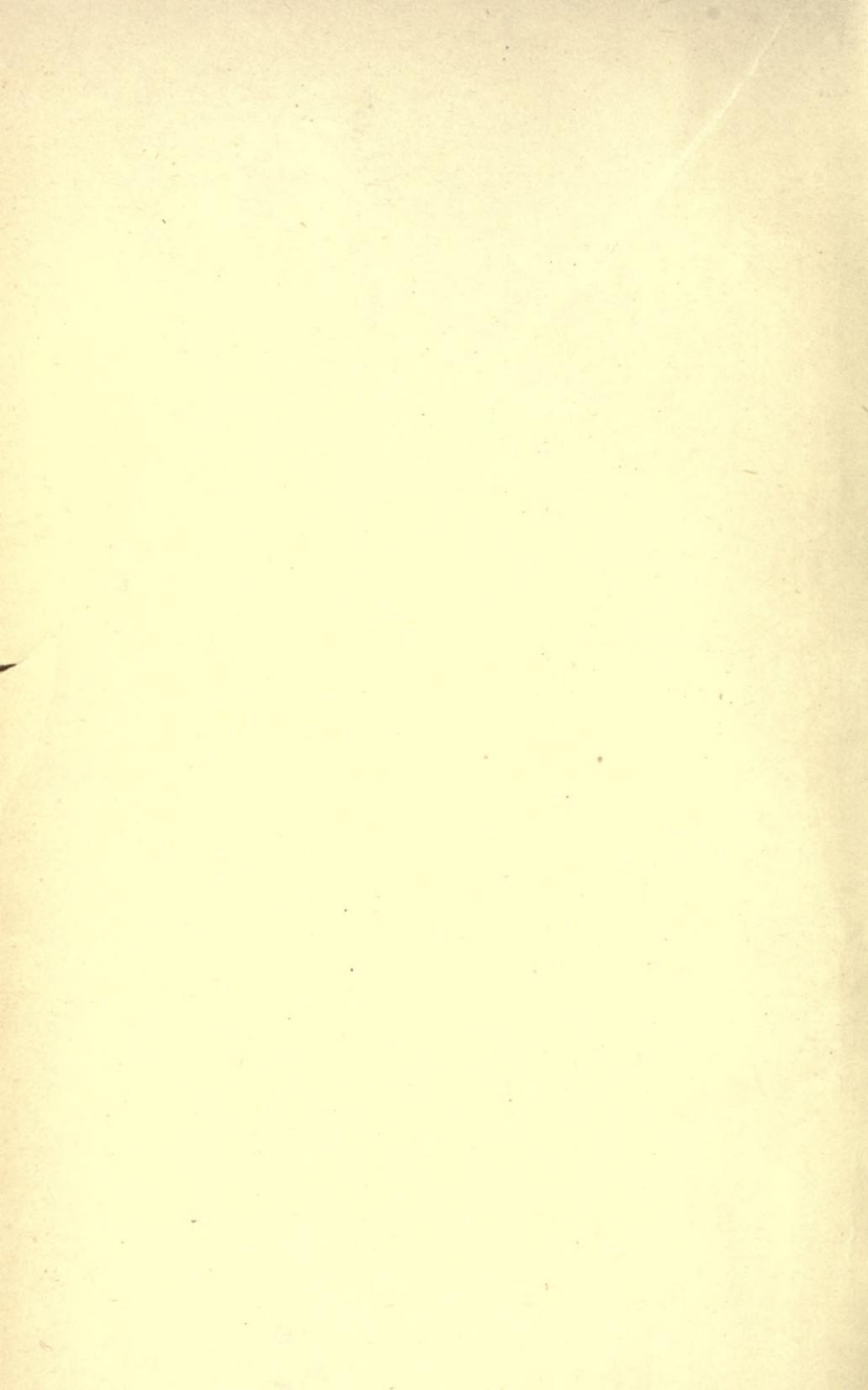




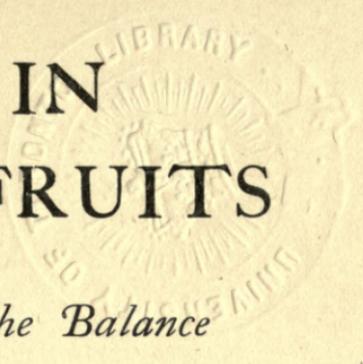
STUDIES
IN
SEEDS
AND
FRUITS
—
H. B. GUPPY



STUDIES IN SEEDS AND FRUITS

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STUDIES IN SEEDS AND FRUITS



An Investigation with the Balance

BY
HENRY BROUGHAM
H. B. GUPPY, M.B., F.R.S.E.

"The old is still the true."—AUSTIN DOBSON.

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1912

I DEDICATE THIS BOOK TO THOSE WHO
SO KINDLY APPRECIATED MY PREVIOUS
WORK AMONGST THE PLANTS. IN
GRATITUDE I HERE GIVE
THEM OF MY BEST

PREFACE

IN the preparation of this work my indebtedness lay in many directions. The circumstances of my life enabled me to devote all my time to it, a very important condition for extensive original investigation. Then, in connection with West Indian plants, with which these pages are principally concerned, there was always in my hand Grisebach's *Flora of the British West Indian Islands*, the only accessible general work on the plants of those regions. Most of the German botanical works consulted were in English dress; but amongst the exceptions was Nobbe's *Handbuch der Samenkunde*, a work essential for me to be familiar with, and I am deeply indebted to my wife for her assistance in mastering its contents.

Then, again, as I rambled about on the coasts and in the inland woods of the West Indian Islands, or sat quietly working in my study at home, or lay in my cabin during the voyages to and fro across the Atlantic, ideas came floating through my mind which often took solid form and developed into lines of investigation before unsuspected. Some of them may have been echoes of my reading. For instance, from a recent re-perusal of Professor F. W. Oliver's address to the Botanical Section of the British Association in 1906, I find that I have unwittingly supplied answers to more than one of his suggestive queries. But there are other ideas that cannot be explained in this fashion, and they also have solidified and stand out boldly in the following pages. Amongst the sources to which I owe much, they are not the least.

Whilst arranging the results of my observations, the difficulty of establishing a nexus between them soon became apparent. One thing led to another in an irregular manner, the new line of inquiry being often determined by some accidental indication, or by some inconsistency in the results of experiments. Perceiving that it would not be conducive to method to follow the order of inception of the several inquiries, I devised the plan of arranging the materials to be now described. The shrinking and swelling processes of seeds were first discussed until the question of permeability or impermeability was raised so frequently that the matter had to be dealt with before further progress could be made. In its turn, the subject of permeable and impermeable seeds was treated on its own ground until the question of their hygroscopicity demanded investigation. So also the matters relating to the proportional weight of parts of fruits, and to the connection between the seed-number and the fruit-weight, were discussed until the disturbing influences of the abortion of ovules and the failure of seeds became so obvious that an inquiry into their nature was necessitated.

Amongst the other difficult questions that presented themselves in this inquiry was that relating to the unit of weight most suitable for seeds and fruits. It was soon found, however, that the grain was by far the most fitting for my purpose, and it was accordingly adopted. The grain is not only one of the most ancient and one of the most extensively employed units of weight for small objects (such as precious stones), but it is Nature's primitive suggestion. Seeds of small size are in use as weights in the East at the present day; and other persons besides myself must have been at times so circumstanced that they had to extemporise a balance and employ grains of rice as weights. This choice has enabled me to avoid the multiplicity of terms inseparable from most systems. Whether it happens that 60,000 grains go to weigh down a green coco-nut, or that 6000 *Juncus* seeds go to weigh down a grain, no other term of weight need be used.

Though in a few instances the grains have been converted into grammes, the use of percentages in stating the results in the great majority of cases will enable the reader to be largely independent of the unit of weight employed.

My original plan was to include in this volume the results of my observations on the distribution of seeds by currents in the West Indian region, and through the agency of the Gulf Stream drift. However, this idea has been abandoned for at least two reasons. In the first place, such materials would have greatly added to the size of a book already large; and, in the second place, since the subject was concerned with quite another matter, it could very well be treated in a separate volume. Though much of the work done in this direction has been put into shape, it has been decided to defer its publication; and in the meantime I hope to considerably add to my facts relating to the occurrence of West Indian seed-drift on the Atlantic shores of Europe. This is the continuation of a study commenced by me in the Pacific about thirty years ago, and taken up from time to time in different parts of the tropics, many of the results being given in my book on *Plant-Dispersal* (1906), and in various papers enumerated in the list given on page xiii of that work.

I would take this opportunity to ask any reader who is interested in the occurrence of West Indian seeds on the west coast of Europe or on the neighbouring islands to communicate with me. Having studied the question during four winters in the home of the drift, in different parts of the West Indies, I wish to make as complete as possible the materials relating to this side of the Atlantic. These seeds are frequently stranded on the beaches of Europe, between the North Cape and the Straits of Gibraltar. Residents on the west coasts of Scandinavia, Scotland, Ireland, England (south-west), France, Spain, and Portugal, and on the off-lying island groups, must often come upon these stranded seeds. The great majority of the seeds thus picked up do not come into the hands of any person who has studied the subject. Some of those who read

these pages may be in a position to assist me in this inquiry, either by taking up the search themselves, or by lending me, for purposes of specific determination, any seeds in their possession, or by supplying information concerning collections of these seeds in the hands of private persons or in museums, or in giving me references to any literature (whether in the press or in scientific publications) dealing with the matter. Any materials left in my possession would subsequently, with the donor's permission, be distributed amongst the large museums.

H. B. GUPPY, M.B.

"ROSARIO," SALCOMBE,
SOUTH DEVON, *January 31, 1912.*

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STUDIES IN SEEDS AND FRUITS

CHAPTER I

THE HISTORY OF THE INVESTIGATION

THIS investigation commenced as a study of the rest-period of seeds ; but its course has often been determined by small indications, the balance and the oven, aided by a sharp knife and a pocket-lens, being the only means of research employed. From the beginning it was for me a leap in the dark, since although investigators far abler than myself have written on the subject, there was little that seemed to offer a clue. Needing some firm ground to stand upon with reference to fruit-maturation and as regards the behaviour of the ripening seed, and of the seed entering the rest-period, I turned to the most authoritative works at my disposal, those of Goebel and Pfeffer. From the pages of the *Organography of Plants* I learned that the biology of the ripening fruit has hitherto scarcely received attention (English edition, 1900-5, ii. 570-571) ; and when consulting the *Physiology of Plants* with reference to the assumption of impermeability by many seeds when they enter the rest-period, I learned that the means by which the power of resistance to drying is gained and the changes which cause its loss are quite unknown (English edition, 1903, ii. 253).

A leap in the dark.

I suppose the reason why many have not ventured in this field is that there seemed no near prospect of obtaining tangible and serviceable results. It has in truth been for me like an

exploring voyage in a little-known ocean where the lead rarely reaches the ocean's floor and "two thousand fathoms and no bottom" is a frequent record. Just as during my sojourn in the Pacific, the study of seed-buoyancy led me finally to discuss the history of the whole flora of those islands, so this work has been developed by slow degrees from my original observations on the vivipary of plants in that region. The possibility of all seeds being able to germinate on the plant presented itself to me whilst observing on the Hawaiian lava-plains the behaviour of the seeds of *Guilandina bonducella* in the green pod; and this led me to the study of the rest-period of seeds. But at first, to employ another simile, it was like a plunge into the depths of a primeval forest. My path branched off in a hundred different ways, tracks crossing and re-crossing and often leaving me in some tangled jungle. Instead of simplicity I found complexity, my inquiries taking me in all kinds of unexpected directions, the difficulty lying in the choice and in knowing when to retrace my steps. However, ultimately I emerged from the forest at a place far distant from where I entered, and have now the story of my experiences to tell.

Perhaps I shall best explain the discursive character of this work and the variety of subjects handled, if I state briefly the various stages of my investigations. When observing the maturation and germination of the seeds of *Guilandina bonducella* in 1897 in Hawaii (*Observations of a Naturalist in the Pacific*, ii. 191), I noted that in germinating these stone-like seeds assumed again the appearance of immaturity. The soft, moist seed from the green unopened pod and the soft, swollen seed on the eve of germination were both of them two or three times the size of the normal resting seed, and might at first sight be mistaken for each other. Surely, I argued, it would be possible, in the case of the seeds of this and other leguminous plants, by subjecting the pod on the plant to warm, humid conditions, to dispense with the rest-period altogether, and to bring about the germination on the plant of

Suggested
by previous
studies of
vivipary in
the Pacific.

The first
clue.

the large, soft, seemingly immature seeds before the drying and shrinking process that ushers in the rest-period begins.

However, nearly ten years passed by before I saw my way to attacking the problem that first presented itself almost as in a dream during my sojourn in Hawaii. Here again it was from the same plant (*Guilandina bonducella*) that I obtained my clue. Whilst observing in December 1906 this plant in immature fruit on the beach of St Croix (Danish West Indies), it occurred to me that there was at least one indirect way of approaching the problem other than by carrying out an experiment more visionary than practicable in its nature. So I placed a number of the soft unripe seeds in wet sand, believing that under such moist conditions they would not go through the usual shrinking and hardening process. The experiment was completed at Black River, Jamaica; and after five weeks I found that the seeds had retained their original size and consistence. The shrinking process had thus been deferred; whilst in the case of seeds gathered at the same time and allowed to dry in the air the seed had been reduced by shrinking to about a third of its original weight.

Just at this time, whilst studying the floating seed-drift of the Black River, I noticed that the shrinking process was consistently shirked by some of the river-side plants, the seeds, after falling into the water, rapidly passing on into the germinating state whilst still afloat. They were not viviparous plants, but possessed seeds with soft coverings which would not protect the embryo against injurious desiccation, the result being that unless the fallen seed found itself in moist conditions and germinated quickly, its chance of reproducing the plant was gone. Perhaps the most interesting of these plants were *Crudya spicata* and *Moronobea coccinea*, the one leguminous, the other guttiferous. The first is known as the Kakoon (Cacoon) tree, from the resemblance of its seeds to those of *Entada scandens*, a plant bearing the same name. The second is the Hog-gum tree.

The indications of river seed-drift in Jamaica.

It was, however, an observation on the seeds of *Abrus*

precatorius that gave direction and method to my inquiries. Noticing that the large, soft, unripe seeds of the green unopened pod were three times the size and double the weight of the normally contracted hard seeds of the dehiscent pod, I found that a large, soft, unripe seed weighing 3 grains lost $1\frac{1}{2}$ grains of water when drying and entering the resting state. This, I argued, would be the water that the resting seed would take up when swelling for germination; and it thus appeared that in preparing for germination, a seed was merely resuming its original unripe condition. But it was to the phenomena of the shrinking process that my opportunities at first restricted my attention during the early part of 1907 in Jamaica. Observations on the seeds of *Cæsalpinia sepiaria*, *Canavalia ensiformis*, *C. gladiata*, and *C. obtusifolia*, led me to distinguish a critical period in the shrinking process which roughly coincided with the shrivelling of the cord or funicle, and the severing of the biological connection.

When the soft, unripe, though full-sized seed was detached before the cord began to shrivel, it lost 70 or 75 per cent. of its weight in the drying and shrinking process; but if the detachment was effected after the cord had commenced to wither, but before any drying of the seed was evident, then the subsequent loss of weight was only about 50 per cent. The result in the first case was a shrivelled seed; in the second case a normal resting seed. Now I assumed that the difference between the two losses in the drying stage, viz. 20 or 25 per cent., represented the water retained by the resting seed for the support of the embryo, and I termed it "the water of inclusion." In forming this inference I was also influenced by the results of simultaneous observations on the seeds of other plants, such as those of the Bastard Tamarind (*Pithecolobium flicifolium*); but I need not here particularise them further.

My attention became then directed more especially to the observation of the shrinkage of the soft, unripe, or uncontracted seeds of two leguminous climbers, *Entada scandens* and *Mucuna urens*, very favourable opportunities being afforded

Other indications.

Working hypotheses.

at Moneague in the interior of Jamaica. In March 1907 I there studied the maturation of the seed on the living plant and collected material which not only gave me employment at the time, but has occupied me at various intervals ever since. The results then obtained gave support to the theory of shrinkage above noted, and when I returned to England in May I adopted the water-of-inclusion theory.

I then set to work to procure the germination of seeds of *Entada*, *Mucuna*, *Canavalia*, *Abrus*, etc., which had assumed the typical resting state after being gathered in the moist, soft condition, with their funicles beginning to shrivel; and the results confirmed the view suggested by the earlier observations that the resting seed in preparing for germination takes up the water lost in the previous shrinking stage. In other words, the swollen seed on the eve of germination resumed its condition of before the rest-period. The work was then continued on these lines, guided more by opportunities than by method. It was then argued that if the water absorbed for germination is the water previously lost in the drying process, it does not necessarily involve germination, meaning thereby the commencing growth of the embryo. It was held that if the above view was correct a swollen seed dried when on the eve of germination ought to return to its original resting weight and ought to retain its germinative powers. Both these inferences were established by the results of several experiments discussed in the next chapter; and I finally adopted "the reciprocal theory," as it was termed, which is to the effect that the water taken up for germination is the water lost in the previous shrinkage process.

The theory of germination thus held good; but it was very different when one came to confirm by experiment the water-of-inclusion view, which was really a theory concerned with the embryo's life in the resting seed. It is there suggested, as already pointed out, that some of the water which the shrivelled seed has lost through being prematurely detached is retained in the normally contracted resting seed

The reciprocal theory of germination.

The water of the resting seed.

for the benefit of the embryo. From this point of view the water-contents of seeds might be thus characterised :—

A. The water lost in the normal shrinking process and regained for germination	}	50 per cent.
B. The water which the seed shrinking excessively loses and the seed shrinking normally retains }		
C. The water which the normal resting seed loses in the oven in addition to the water A and B }		15 "
Waterless residue		15 "
		<hr/>
		100 "

Whilst A would be the water of germination, B would be the water of inclusion or the water of the rest-period, and C would be the water of combination, only to be driven off by exposure to a temperature of 100° C.

It follows from the above view that all resting seeds should possess impervious coats which would secure the retention of the water of inclusion for the use of the embryo, and that the result of puncturing the resting seed or baring it of its coats would be a considerable loss of weight. It is also implied that the abnormally shrunken seed would lose less water in the oven than the normal resting seed.

To make a long story short, I may remark that all the implications failed when put to the test. Many seeds proved to have pervious coats. They, as a rule, preserved the same weight when deprived of the protection of their coats by baring or puncturing. Lastly, the abnormally shrunken seeds lost about as much water in the oven as the normal resting seed.

So my hypothesis, relating to a special supply of water for the use of the embryo in the resting seed, collapsed. But whilst putting it to the proof I had accumulated a large number of results of experiments which are utilised in other connections in the next chapter, and I chanced upon other suggestive lines of inquiry. After determining the water-percentage of seeds in the oven, I used to throw away the sample. But on one occasion a sample of the broken-up

seeds of *Guilandina bonducella* was unintentionally left overnight in the pan of the balance. Out of curiosity I noticed its weight and found that it was 2 per cent. heavier than when originally placed in the oven. In other words, a sample of 100 grains, which had been reduced in weight by exposure to a temperature of 100° C. to 92 grains, on the following morning weighed 102 grains. This result was startling, and quite a new road of investigation was opened up, occupying much of my time for three years and supplying materials for several of the chapters of this work. Under the stimulus of this discovery I made at the time a few speculative comments in my notebook, which proved to be the starting point of a theory of cosmic adaptation to which Chapter XX is devoted. Here again the seeds of *Guilandina bonducella* have been a source of inspiration, and I soon got to realise that I owed much to these interesting seeds.

A clue to a new line of inquiry.

But in the meanwhile my horizon had been greatly extended. With the old theory gone it was evident that I could no longer treat the seed independently of the fruit, and that I could no longer ignore the facts that the seed had coverings, that the embryo in the resting seed was in all stages of development, and that the reserve of food within the seed presented great variations in amount as well as in disposition. The investigation promised to branch out in a multitude of ways, provokingly divergent in their direction. However, I continued the method of following indications and was soon hard at work again with the balance and the oven.

The widening of the horizon of the inquiry.

Since the seed-coats had played a variety of parts in the experiments, one of the first of the new inquiries begun was concerned with the seed-coat relation, meaning thereby its relative weight as part of the entire seed. Great variety in this respect soon displayed itself. At the same time I began to compare the seed-coat relation of the resting seed with that of the soft, unripe seed and of the seed swollen for germination. Now commenced the separate treatment of the coats and kernel in the oven experiments, when I was surprised to

The seed-coat relation.

On the way
to the con-
struction of
the régime of
the shrinking
and swelling
seed.

find that the water-percentage for the coats was often greater than for the kernel. Before long it was realised that materials were gathering for a complete statement, as far as the indications of the balance and the oven went, of the part played by water in the economy of the seed from its immaturity through its rest-period to the germinating stage. I was in fact on my way to the construction of the seed's régime in passing from the unripe to the resting state and thence on to the germinating condition.

Whilst engaged in this inquiry I took advantage of my oven-experiments for the determination of the water-contents of seeds to investigate further the curious fact that certain seeds after being subjected in a broken condition to a temperature of 100° C., being thus deprived of their free water, not only regained all the lost water from the air, but in a few days were markedly heavier than in the entire state. This was found to be common with leguminous seeds possessing impervious coverings. The unexpected results of an experiment on the seeds of *Entada scandens*, which belong to this type, threw fresh light on the matter. Separate samples of the coats and kernel were subjected to the oven-test, when the first experienced a loss of weight of about 15 per cent., and the second of about 10 per cent. They were then left exposed for five days on a table, together with samples of the coats and kernel which had not been heated. It was then found that in all cases, whether with the heated or unheated materials, the samples were considerably heavier than before the experiment, the weight of the coats in both cases being increased 2 or 3 per cent., and that of the kernels 3 to 5 per cent. There was, therefore, an inherent tendency in both the coats and the kernel when separated from each other to increase their weight by absorbing water from the air, a tendency unimpaired by a previous loss of all the free water through exposure to a temperature of 100° C. In other words, the seed in the broken condition held more water than in the entire state, and whether or not exposed to the heat-test,

the ultimate result was the same. Such was the commencement of a long series of experiments which has extended off and on over three years. In some of the early experiments I tested the capacity for resorption possessed after heating by leaves, wood, slices of fruits, etc., and also by hydrated minerals, such as opal and chlorite.

Another line of inquiry first taken up at this time was the determination of the relative weight of the embryo in albuminous seeds. An investigation somewhat crudely begun soon branched off in many directions, the seeds of palms figuring largely in the results. Almost at the commencement of my work I had started experiments on the effect of time on the weight of seeds. They were carefully weighed and placed in paper packets, the intention being to extend the experiments over years. At this time I was feeling my way in many small inquiries, striking out blindly very often in my efforts to obtain further clues. Thus I took with me to Jamaica in the winter 1907-8 several seeds with the object of determining their changes of weight under different climatic conditions, the result being given in Chapter VII.

Other lines
of inquiry.

These investigations began in October 1906, and during the first twelve months I mainly ignored the fruit; but not altogether, since during the summer I had been periodically observing some capsules of *Scilla nutans* to ascertain the effect of cutting a window in the walls of the young fruit on the maturation of the seeds. The experiment was not deterrent and the changes not important. In a word, the seeds of the Bluebell had behaved like those of a Gymnosperm. About the same time Lubimenko was carrying out a similar series of experiments on leguminous pods.

The author's
attention
now directed
to the fruit.

Now began some observations on the dehiscence and drying of the capsules of *Iris Pseudacorus* and of *Æsculus Hippocastanum* (Horse-chestnut). I experimented with the idea that dehiscence was the result of drying, a notion that guided many subsequent experiments, though a year passed before my error was discovered.

The winter 1907-8 spent in Jamaica was chiefly occupied in working as opportunity offered on the lines before indicated. I repeated several of the experiments made in England on the resorption of water from the air by seeds in the broken condition, so as to be assured that it was a capacity unconnected with climatic causes. At this time I began my observations on the Coco-nut (*Cocos nucifera*), ascertaining the proportional weight of all the parts—the husk, the shell, the albumen, and the embryo—and also determining their water-contents.

My work in
Jamaica.

The maturation and drying of the fruits of numerous other plants also occupied my attention, such as those of *Anona*, *Bauhinia*, *Citrus decumana* (Shaddock), *Datura*, *Entada*, *Ipomaea*, Mahogany (*Swietenia*), *Sapota*, etc. I was surprised to find that the ripe capsule, the ripe legume, and the ripe berry often lost much the same amount of water when allowed to dry spontaneously, fleshy drupes like those of *Prunus* (tested in England) behaving in the same fashion. Then I reflected that fleshy fruits (drupes and berries) corresponded to the full-grown living legume and capsule in the moist, unopened condition, and that if we wish to find the correlative of these dehiscent fruits in the dry, opened state, we must look for it in the shrivelled currant and the dried-up apple. This raised the whole question of special adaptation in connection with seed dispersal. It was argued that if we can discern no evidence of adaptation in the shrivelled berry as regards seed distribution, we should look for none in the drying capsule and pod, and that the apparent display of method in the last-named is purely accidental.

To enter more into the details of my work during my second winter in Jamaica would be to anticipate much that will be found in the succeeding chapters. I may, however, say that one branch of inquiry which was more fully developed was the hygroscopic behaviour of seeds, and that my study of the maturation of the fruits of *Momordica*

furnished me with some new ideas on the subject of the sequence in the genesis of the berry and capsule, two types of fruits often associated. With the observations on *Momordica* my active work in Jamaica came to an end. However, whilst spending the last few days on the summit of Mount Diavolo, rambling in the forests and increasing my seed materials for future work in England, the theory of cosmic adaptation before alluded to was further elaborated.

During the spring and summer of 1908 I was occupied in extending my observations on the rest-period of seeds, on the swelling antecedent to germination, on the relative weight of the embryo in albuminous seeds, and on various other subjects. In May I began a series of observations on the fruiting and seeding of the Ivy (*Hedera Helix*), which have been extended to the spring of 1911. The result has been to establish the growth of the embryo within the seed throughout the winter months, and the not infrequent germination on the plant (vivipary) in the spring. Here much assistance has been received from collections of fruits made at intervals during a winter by my sister, Mrs H. Mortimer. In the late summer and early autumn my systematic observations on the maturation, dehiscence, and drying of fruits were resumed. The fruits included those of *Iris fetidissima*, *Quercus Robur* (Oak), *Arum maculatum*, *Tamus communis*, and several other plants. In most cases the inquiry was continued during the next two or three years, the final result in the instance of the Oak being to establish a slight but normal tendency to vivipary or germination on the tree.

Perhaps the most important outcome of these observations was the clue to the homology of fruits supplied by my observation of the shrinkage of seeds within the moist berry of *Berberis*. This afforded a clue for the comparison of fruits in their various stages, which was subsequently strengthened by data supplied by the seeds of *Arum*, *Tamus*, and *Passiflora*, and ultimately enabled me to trace the homologies in the

My work in
England.

A clue to the
homology of
fruits.

ripening and drying stages of different types of fruits, such as the legume, the capsule, and the berry, by fixing on a stage common to all. The result was to further undermine the prevailing notion of special adaptation to seed dispersal, and to show that the mechanism of a dehiscing capsule or legume, however adaptive it may appear, does not count for more in nature than the shrivelling of a berry.

A sojourn in
Grenada,
Tobago, and
Trinidad.

The winter 1908-9 was spent again in the West Indies, mainly in Grenada and Tobago, but including a sojourn of two or three weeks in Trinidad. It was at Port of Spain that I made the acquaintance of Mr Hart, the late superintendent of the Botanic Gardens, and I was indebted to the courtesy of Mr Evans, temporarily in charge, for the opportunity of obtaining an abundant supply of ripe palm fruits of different kinds. Mr Broadway of the Botanic Station in Tobago kindly gave me valuable information respecting Grenada, and subsequently assisted me by replying by letter to numerous queries I had put to him. To Mr Anstead of the Botanic Station in Grenada I was very deeply indebted for, so to speak, giving me the run of the gardens and for other aid. The fruits and seeds of palms occupied much of my attention in Grenada; but I made also several special studies, including one of the fruits of *Barringtonia speciosa* (an introduced plant). It was in Tobago that I made my first acquaintance with the "Twist Coco-nut," where the kernel lies loose within the hard shell.

But one of the most important lines taken up during this winter was the study of the connection between moniliform legumes and the abortion of ovules, which opened up an interesting field of inquiry. The pods of *Erythrina corallodendron* supplied me with my first clue. This raised the question of the influence of the abortion of ovules and of the failure of young seeds on the form, size, and weight of the fruit; and in this connection I made an extensive series of observations on the pods of *Albizzia Lebbek*, *Entada polystachya*, and *Leucæna glauca*. As often happened in other

cases, this led to another inquiry into the relation between the number of seeds and the size and weight of the fruit, which ultimately supplied me with materials for a special chapter.

Whilst in Grenada I spent some weeks at the Grand Etang in the mountainous interior of the island. My attention here was occupied with many things in the surrounding forests; but I was particularly interested in studying the habit of growth and the maturation of the fruit and seeds of *Dioclea reflexa*, a leguminous climber, the seeds of which are amongst those stranded by the Gulf Stream on the western shores of Europe. The method of preparation of the seed for its Trans-Atlantic voyage and the opportunities it possessed of starting on its way were points of special interest for me.

To give an idea of my mode of work in the West Indies I will describe my work-room at St George's, Grenada. . . . Hanging from nails on the walls to dry were the ripe fruits of *Cassia fistula*, *Entada polystachya*, and *Hura crepitans* (the Sandbox tree). On the window sill exposed to the sun were the opening fruits of *Ravenala madagascariensis*, displaying the beautiful blue arils of the seeds and completing the process of dehiscence which they had commenced on the tree. On the sill of another window were the large square fruits of *Barringtonia speciosa* in various stages of drying, all of which, together with the fruits above mentioned, were methodically weighed from time to time. On the table where I wrote were placed at one end my balance and at the other end my copper oven for the determination of the water-contents of seeds and fruits. Close beside me lay a saucer containing the seeds of *Dioclea reflexa* from the green pod, which were silently illustrating the coloration process of leguminous seeds. In other saucers around me lay a variety of seeds, all of them either under observation or destined for future experiment, such as the seeds of *Barringtonia*, *Entada*, *Enterolobium*, *Monstera*, and *Eleis*.

My work-room in Grenada.

In a large press were two extensive series of pods of

Albizzia Lebbek and *Leucæna glauca*, arranged according to the number of seeds, and from which I obtained my principal material for investigating the relation between the number of seeds and the size and weight of the fruit. In the same press were two small paper trays containing the bared seeds of *Cæsalpinia Sappan*, *Erythrina corallodendron*, and *Elæis guineensis*, which, having been exposed to a temperature of 212° F. for two hours, were now regaining from the air the moisture lost in the oven. But perhaps the most interesting things around me were a number of seeds of *Barringtonia speciosa* which had been cut up with the hope of discovering the missing cotyledons. Lying about the room were many West Indian fruits, such as those of *Saccoglottis amazonica*, *Carapa guianensis*, and *Mauritia setigera*, all from Trinidad; whilst a box under the table contained my collection of seed-drift from the Trinidad and Tobago beaches, much of which had been brought down by the Orinoco from the interior of the neighbouring continent.

In England,
1909-1910.

In the spring of 1909 I brought back to England abundant material for further research in the various lines already instituted. During the summer the observations on the abortion of ovules and the failure of young seeds were continued, and I began to pay systematic attention to the coloration of seeds, a subject about which many notes had been previously made. At the same time I was arranging my notes and working out the general results, during which many "lacunæ" presented themselves; and it was with the filling up of these gaps, together with the working up of results, that most of the following twelve months were occupied. I may add that large seed-collections were at my disposal for this purpose.

The Turks
Islands.

At the close of 1910 I went to Turks Islands, which form geographically the southernmost portion of the Bahamas, and remained there three months. This locality was selected as the most suitable one in the West Indies for the study of oceanic seed-drift, or, in other words, for observing the dispersal

of seeds by currents, a subject which I had been following up in various parts of the world since it first attracted my attention amongst the coral islets of the Solomon Islands in the early eighties, and one which I had constantly kept in view during my previous three winters in the West Indies. I had made collections in Jamaica, Tobago, and Trinidad, the large quantities of Orinoco drift washed up on the southern beaches of Trinidad proving full of interest. So I took up my abode in Grand Turk, and from there visited all the cays of the group, making a special study of the littoral plants and especially investigating the abundant stranded seed-drift, hardly any of which belongs to plants that have established themselves in those islands, or in fact in the Bahamian region generally.

Whilst at Grand Turk I was fortunate enough to meet Dr Millspaugh, who was just completing the botanical survey of the Bahamian flora which Dr Britton, himself, and other botanists from the United States had been six years engaged in. The Turks Islands are the farthest south, and it might have appeared as if I had come in to spoil the finish of a great undertaking. However, our special interests lay far apart, and I could not for a moment lay claim to a fraction of the intimate knowledge possessed by Dr Millspaugh of the plants of this region. I was the astonished spectator of the application of his great experience to the flora of the little island of Grand Turk. All the knowledge of years acquired through the length and breadth of the Bahamas was brought to bear within the narrow limits of the flora of this small island. It was a lesson that I shall not readily forget. Dr Millspaugh very kindly lent me the manuscript of the *Flora of the Bahamas* by Dr Britton and himself; and in return I gave him a collection of seed-drift obtained from the beaches of the group, which is now lodged in the Field Museum of Natural History, Chicago. When the American botanists publish their work they will enrich their science with the most complete account of a flora hitherto made in the West Indian region.

The
botanical
survey of the
Bahamas by
botanists of
the United
States.

This brings to an end my record of work and travel. During the preparation of this book many other "lacunæ," as well as new lines of inquiry, have presented themselves. The first I have been compelled to largely ignore, whilst the new openings for investigation have been promptly blocked up. But little has been said of my study of the rest-period of seeds in this account of my work. As a matter of fact, however, it has formed the pivot of my inquiries from the beginning to the end. It started me on my work, and it is towards the clearing up of the problem concerned in its mystery that many lines of my inquiries now converge.

The work-
ing-up of my
materials.

Looking back at all the data collected in this investigation, I am puzzled to account for their bulk. So often on returning home from my excursions it seemed that I had only made one or two observations worth recording during the day. Yet much of the work has been done by the seeds and fruits themselves, whilst I have stood by to register results. Whilst I was engaged in weighing, or in some experiment, a score of seeds and fruits were silently at work around me. Amongst my seeds I have led a busy life, but no one has been so busy as the seed itself. The labour came when all the results had to be sifted, tabulated, and digested. The arrangement of the materials indeed occupied a good deal of serious thought and extended over a considerable time. It proved very difficult to avoid two dangers: the first that of going over old ground; the second the assuming in an argument in an early part of the work what could only be demonstrated in a later page. Accordingly I finally hit upon the method of first dealing with the shrinking and swelling of seeds until the question of the permeability or impermeability of their coats blocked the way and demanded a response. This enabled me to open up the whole matter of these qualities in seeds, and to establish a nexus in the general arrangement of the work.

A serious
word.

And now for a serious word in concluding this chapter. The plan of sending forth treatises without a trace of the personality of the worker is to me repellent. Knowledge in

itself has but few attractions for me. That knowledge which brings one into touch with the life around one and enables the observer and the observed to tell their common story is the only thing that charms. I should feel no interest in inquiries that led one to the confines of habitable space and left one looking out on a dreary, cold, grey universe of nothingness. I would instead get quickly home to my cosy terrestrial surroundings and revel in thoughts that were comforting and consoling.

Yet the fancy must always play a part if we wish to profit by and to make a real advance in any investigation. It would be easy to sustain the view that mere digging for facts is like digging into the ground. Under such conditions one does not see much beyond the length of one's nose. It is doubtful whether the progress of knowledge thus effected resolves itself into much more than the splitting up of phenomena, or into a process of differentiation that can only end in a relative zero. On the other hand, if at times we leave the solid ground of fact and rise into the air on the wings of fancy, we can at all events greatly extend our range of mental vision, and can mark down points for investigation which never would have come under our notice whilst adopting the mole's method of inquiry. It is the man in the air that gives the directions, and the man on the ground that does the work. By limiting our field of inquiry and excluding the play of fancy we are groping about as blindly as an army without its air-men. The dreamers figure in my mind as the leaders of the world.

CHAPTER II

THE THREE CONDITIONS OF THE SEED

The three conditions of the seed.

WE are all familiar with the three conditions presented by the large, soft pre-resting seed, the contracted, hard resting seed, and the soft, swollen seed on the eve of germination. Yet to each of them we are apt to apply an epithet which is never altogether true and rarely altogether wrong. Thus we often speak of the pre-resting seed as immature, of the resting seed as mature, and of the swelling seed as germinating. In these connections it is necessary to remember that, as a rule, the embryo is fully developed in the soft, swollen pre-resting seed, and is quite ready, as shown in a later page, to proceed with germination, should the shrinking process be averted. If, then, the embryo is "mature" in the pre-resting seed, such an epithet can have no distinctive value for the resting seed.

So again, when we speak of the germinating seed, we have to decide whether we mean the swollen seed on the eve of germination, or whether we refer to the seed with the tip of the radicle already protruding through the coats. Botanists, like Nobbe, Pfeffer, Jost, and others, lay stress on the fact that absorption of water by the resting seed is not actual germination, but merely a preparation for that process; whilst gardeners are familiar with the circumstance that seeds may swell up and not germinate. Strictly speaking, the germinating condition with the radicular tip showing is a fourth stage. It is a stage of growth and activity within the

seed, and cannot be compared with the three previous stages (characterised by a passive vitality), which may be fitly termed the shrinking, resting, and swelling stages. The germinating stage may never be reached, since the absorption of water that brings about the swelling of the resting seed is more a mechanical than a vital process, and may or may not terminate in the growth of the embryo, which is the essential feature of germination.

The shrinking stage is characterised by loss of water, the swelling stage by absorption of water, and the intervening resting stage by a suspension, more or less complete, of the drying process and by a greater or less state of passivity on the part of the embryo. It is with these three stages that we are now concerned, that of germination not coming within the field of our inquiry. The shrinking of the pre-resting seed and the swelling of the resting seed are the two processes to be now discussed. It is the shrinking process that ushers in the rest-period, and it is the swelling process that prepares the seed for germination. In the first case there is water-loss, in the second, water-gain; and it may safely be assumed that as a general rule we are here concerned mainly with these processes, the proofs of which are discussed later on in this chapter.

Here the balance becomes the instrument of investigation; and it is to the changes in weight in the different processes that appeal is chiefly made. We deal at first with the entire seed, the independent behaviour of seed-coats and kernel being separately discussed in Chapter IX. The weight of the resting seed is taken as one, whilst the maximum weights of the pre-resting seed before shrinkage begins and of the swollen seed on the eve of germination are expressed in ratios. Thus, to take one of the very largest of leguminous seeds, that of *Entada scandens*: a seed which weighed 1004 grains in the soft, swollen condition weighed 408 grains in the contracted resting state; and subsequently, when on the eve of germination, it increased

The shrinking and swelling stages are concerned with water-loss and water-gain.

Method of inquiry.

its weight to 1012 grains by water-absorption. We thus get the result :—

Large, soft, pre-resting seed.	Resting seed.	Swollen seed on eve of germination.
1004 grains.	408 grains.	1012 grains.

which expressed in ratios becomes :

Shrinking ratio.	Resting seed.	Swelling ratio.
2.46	1	2.48

Modes of determining the shrinking and swelling ratios.

The ideal method of carrying out such observations would naturally be, as was done in the instance just given, to note the shrinkage and swelling of a single seed, that is, to take its maximum weight in the green fruit, to weigh it again after prolonged air-drying, and to weigh it once more when on the eve of germination. This involves the separation of the pre-resting seed from the parent plant; and although one can choose the time when the cord or funicle is beginning to shrivel and the vital connections are being severed, still it is open to the objection that a seed thus detached does not dry under normal conditions. However, checks can often be found by comparing the state of the coats of a resting seed thus produced with that of a typical resting seed; whilst any marked divergence from the average can be detected by a comparison of the swelling ratios of the two seeds. With seeds typically impermeable, a resting seed thus artificially obtained often lacks the impermeability of the outer coverings; and its shrinkage, as indicated by the change in weight, is not so great as with the seed that has properly contracted on the plant.

On the other hand, typical permeable seeds when dried under these conditions frequently shrink too much. Nevertheless, normal results were at times obtained, some of which are mentioned below; whilst the behaviour of the imperfectly shrunken seeds has offered a fruitful field of investigation.

But there is another plan, and that is by comparing the average shrinkage of a number of detached pre-resting seeds with the average swelling of a number of resting seeds prepar-

ing for germination. This method is more practicable and has been frequently employed, and, although open to the same objection as regards the premature separation of the seeds from the parent plant, it is easy, by the use of normal seeds as a check, to exclude those where the shrinkage has been irregular.

A third method employed at times, especially for the shrinkage, has been to compare the average weight of a number of full-sized pre-resting seeds or of seeds swollen for germination with the average weight of a resting seed. This is exposed to the objection that seeds vary much in weight, an objection losing some of its force if a large number of seeds are used.

With reference to the determination of the maximum weight of the swelling seed, it would appear difficult to ascertain where simple absorption ends and germination, or active growth within the seed, begins. In practice, however, this difficulty does not often arise, and it can usually be met by frequently weighing the swelling seed up to the beginning of germination, an approximate estimate being alone expected.

By way of opening the subject I will first deal with my experiments on single seeds or sets of seeds, where the history has been followed for each seed from its soft, swollen pre-resting condition through the rest-period on to the swelling stage terminating in germination. I possess such a continuous series of observations for the seeds of four leguminous and one malvaceous species. As given in the tables subjoined, these data afford an early indication of a principle which will figure prominently in subsequent pages, that the water lost in shrinking is regained in swelling for germination. Thus, if a full-sized pre-resting seed weighing 100 grains shrinks to 40 grains during its drying, and after a rest-period of some months regains its original weight of 100 grains when swelling for germination, we have data directly indicating such a principle. There is much in these tables that will be elucidated as the work proceeds; but I may here point out that the behaviour of the imperfectly shrunken seeds of *Guilandina bonducella* there

Observations on the shrinking and swelling ratios of single seeds or sets of seeds indicate that the water lost in shrinking is regained in swelling for germination.

noted lends a double support to this view, since it indicates that if less than the normal amount of water is lost in the shrinking process, less is also required in swelling for germination. In Table A the histories of single seeds, and in Table B the history of a group of seeds, are followed in all three stages, the pre-resting, the resting, and the swollen stage preparatory for germination.

A.—SHOWING THE WEIGHTS OF THE SAME SEED IN ITS UNRIPE OR PRE-RESTING CONDITION, IN ITS RESTING STAGE, AND ON THE EVE OF GERMINATION.

Name of plant.	Weight in grains.			Shrinking and swelling ratios.			Duration of the resting stage.
	Unripe.	Resting.	Swollen.	Shr.	Rest.	Sw.	
Entada scandens A .	969	371	930	2'62	1	2'51	3 months.
" " B .	1004	408	1012	2'46	1	2'48	4 " "
" " C .	954	380	985	2'51	1	2'59	3½ " "
Dioclea reflexa .	239	111	212	2'15	1	1'91	2½ " "
Poinciana regia .	24'3	10'5	25'3	2'31	1	2'41	4½ " "

B.—SHOWING THE TOTAL WEIGHTS OF A NUMBER OF SEEDS OF THE SAME SPECIES IN THE SAME THREE STAGES.

Guilandina bonducella (4 seeds).	416'0	176'0	449'0	2'37 (3'20)	1 1	2'55 (3'08)	4½ months.
Thespesia populnea (11 seeds).	60'7	34'9	62'7	1'74	1	1'80	4 " "

Note.—All the seeds in these experiments germinated. Those of *Guilandina bonducella* did not complete the shrinking process, becoming permeable but "germinable" seeds. The ratios obtained independently for the normal impermeable seeds are in this case given in brackets.

The same reciprocal relation between the shrinking and swelling processes is established by independent observations on a number of seeds.

The general indications afforded by observing individual seeds from the pre-resting stage to germination are confirmed and extended by the large amount of additional data given in the two tables subjoined. In Table A are arranged all my results on the shrinking and swelling ratios of seeds belonging to about ninety-six species, of which all but those in the supplementary list of palm seeds, etc., belong to the present discussion. They have for the most part been obtained

independently from different seeds or sets of seeds of the same species, since the opportunities of making a successful series of observations on individual seeds were rare. In Table B will be found a number of swelling ratios for other seeds as determined by the data supplied by Hoffmann and Nobbe. As supplementing my own results they are extremely valuable, since they supply some of the conspicuous deficiencies in Table A, and enable one to extend the field of inquiry in a tentative fashion over a large portion of the seed-bearing plant-world. It should of course be remembered that even with the best of observers and the best of conditions such results can only be approximations; and it must not be forgotten that we are concerned here not merely with one process, but with all those changes concerned with the transition from the pre-resting stage to the eve of the germinating condition. The results as a whole are to be regarded here as supporting the general contention, based on the study of individual seeds, that the seed in swelling for germination is as a rule returning to the pre-resting or so-called unripe condition, that it gains in swelling what it lost in shrinking, and that the relation of the swelling to the shrinking seed is mainly reciprocal, the resting stage figuring as an interruption in the embryo's development in response to the pressure of external conditions.

Before discussing these data, one may remark that there is little that is novel in the enunciation of this principle. Gardeners must often act on the tacit assumption of its reality, and scientific investigators have gone far to establish it. In our case it is particularly necessary to possess a clear conception of the mutual relation of the shrinking and swelling processes, since without the establishment of some preliminary general principle we should be unable to study with profit the mechanism of these processes as exhibited in the separate behaviour of the seed's coats and its kernel (see Chapter IX).

This principle was so fully expected and accepted by Dr Nobbe that he was satisfied with only a few experiments

Dr Nobbe's
proof.

for its demonstration. In his *Handbuch der Samenkunde*, published in 1876, he shows that in the case of the seeds of the Common Bean (*Faba vulgaris*) the water lost in the shrinking process was gained back in the swelling stage. In the act of swelling, he says, the original volume of the "fresh" (or pre-resting) seed is restored (p. 71). Two of these fresh seeds were allowed to go through the shrinking process, the minimum size being reached in about ten days. Measurements were taken; and it was ultimately found that one of the shrunken seeds when placed in water regained its original dimensions in about four days, whilst the other kept in a chamber saturated with water-vapour regained but little of its original size after five weeks.

TABLE A.—SHRINKING AND SWELLING RATIOS OF SEEDS (GUPPY).

Note.—The ratios represent the relation in weight between the resting seed and the pre-resting and swelling seeds, the resting seed being taken as 1. Thus if a seed weighed 25 grains before shrinking, 10 grains when resting, and 24 grains when swollen for germination, its formula would be 2·5 1 2·4, the shrinking ratio being indicated on the left, and the swelling ratio on the right.

	Family.	Average weight of a resting seed in grains.	Ratios.		Permeable, impermeable, or variable.
			Shr.	Sw.	
<i>Abrus precatorius</i> . . .	Leguminosæ	1·5	2·15	1 2·25	Variable.
<i>Acacia Farnesiana</i> . . .	"	2·0	2·13	1 2·00	"
<i>Adenanthera pavonina</i> . . .	"	4·7		1 2·42	Impermeable.
<i>Æsculus Hippocastanum</i> (Horse-chestnut) . . .	Hippocastaneæ	130·0	2·17	1	Permeable.
<i>Albizzia Lebbek</i> . . .	Leguminosæ	2·3		1 2·27	Variable.
<i>Allium ursinum</i> . . .	Liliaceæ	0·1	2·00	1	Permeable.
<i>Andira inermis</i> . . .	Leguminosæ	25·0	2·09	1	"
<i>Anona muricata</i> . . .	Anonaceæ	6·0	1·40	1 1·43	"
" <i>palustris</i> . . .	"	4·0	1·45	1	"
<i>Aquilegia (specie)</i> . . .	Ranunculaceæ	0·03	1·62	1	Variable.
<i>Arenaria peploides</i> . . .	Caryophyllaceæ	0·25	1·85	1	"
<i>Artocarpus incisa</i> (Bread-fruit) . . .	Artocarpeæ	45·0	2·22	1	Permeable.
<i>Arum maculatum</i> . . .	Aroideæ	0·5	1·63	1	"
<i>Barringtonia speciosa</i> . . .	Myrtaceæ	380·0	2·78	1	"
<i>Bauhinia sp.</i> . . .	Leguminosæ	4·0	2·10	1 2·20	Variable.
<i>Berberis sp.</i> . . .	Berberideæ	0·12	1·92	1	Permeable.
<i>Bignonia sp.</i> . . .	Bignoniaceæ	5·0	2·30	1	"

TABLE A.—*continued.*

	Family.	Average weight of a resting seed in grains.	Ratios.		Permeable, impermeable, or variable.	
			Shr.	Sw.		
<i>Monstera pertusa</i>	Aroideæ	0·8	2'44	1	Permeable.	
<i>Montrichardia arborescens</i>	"	35'0	2'40	1	"	
<i>Mucuna urens</i>	Leguminosæ	90'0	1'80	1	Impermeable.	
<i>Opuntia Tuna</i>	Cactææ	1'0	1'90	1	Permeable.	
<i>Phaseolus multiflorus</i> (Scarlet-runner)	Leguminosæ	18'0	2'50	1	1'98	"
<i>Phaseolus vulgaris</i> (French Bean)	"	12'0	1	1'84	"	
* <i>Pisum sativum</i> (Pea)	"	6'0	2'80	1	1'91	"
<i>Pithecolobium filicifolium</i>	"	13'0	1'58	1	"	
<i>Poinciana regia</i>	"	10'0	2'31	1	2'37	Variable.
<i>Primula veris</i> (Primrose)	Primulaceæ	0'012	2'36	1	Permeable.	
<i>Pyrus Malus</i> (Apple)	Rosaceæ	0'40	1'90	1	"	
<i>Quercus Robur</i> (Oak)	Cupuliferæ	25'0	2'50	1	"	
<i>Ravenala madagascariensis</i>	Musaceæ	5'0	1'60	1	"	
<i>Ribes grossularia</i> (Goose-berry)	Ribesiaceæ	0'09	1'63	1	"	
<i>Ricinus communis</i> (Castor Oil)	Euphorbiaceæ	3'5	1	1'33	"	
<i>Scilla nutans</i>	Liliaceæ	0'1	1'60	1	"	
<i>Stellaria Holostea</i>	Caryophyllaceæ	0'45	1'82	1	2'10	"
<i>Swietenia Mahogani</i>	Meliaceæ	3'7	3'78	1	"	
<i>Tamarindus indica</i>	Leguminosæ	20'0	1	2'15	"	
<i>Tamus communis</i>	Dioscorideæ	0'25	1'75	1	"	
<i>Theobroma Cacao</i> (Cocoa)	Buttneriaceæ	20'0	1'37	1	"	
<i>Thespesia populnea</i>	Malvaceæ	3'0	1'87	1	1'82	Variable.
<i>Ulex europæus</i>	Leguminosæ	0'11	2'30	1	Impermeable.	
<i>Vicia sativa</i>	"	0'31	2'26	1	Permeable.	
" <i>sepium</i>	"	0'35	1'90	1	Variable.	
<i>Vigna luteola</i>	"	0'70	2'45	1	2'7	Impermeable.

SUPPLEMENTARY LIST (see Note 20 of Appendix).

<i>Prunus communis</i> (Sloe)	Rosaceæ	1'00	1'89	1	The question of permeability does not here arise. In all cases the seed proper is here referred to.
<i>Acrocomia lasiospatha</i>	Palmaceæ	30'0	1'47	1	
<i>Areca Catechu</i>	"	40'0	1'72	1	
<i>Cocos nucifera</i> (Coco-nut)	"	4600'0	1'89	1	
" <i>plumosa</i>	"	6'0	1'59	1	
<i>Hyophorbe Verschafftii</i>	"	5'0	1'15	1	
<i>Mauritia setigera</i>	"	300'0	1'75	1	
<i>Oreodoxa regia</i>	"	5'0	1'23	1	
<i>Sparganium ramosum</i>	Pandanaceæ	0'06	2'00	1	

* See Note 1 of Appendix. The seeds were abnormally shrivelled. As with *Faba vulgaris* (Broad Bean) and *Phaseolus multiflorus* (Scarlet-runner), the seeds of *Pisum sativum* (Pea) shrink excessively if detached from the pod. It is therefore not possible to get good results in these cases.

THE THREE CONDITIONS OF THE SEED 27

TABLE B.—SWELLING RATIOS OF SEEDS (HOFFMANN AND NOBBE).

Swelling ratios of seeds adapted from the results obtained by Hoffmann and Nobbe, and given in the latter's *Handbuch der Samenkunde*, p. 119, etc. (The weight of the resting seed is here taken as 1, as in the previous table.)

		Hoffmann.	Nobbe.	Page references, etc.
Triticum vulgare (Wheat)	Gramineæ	1'455	1'600	p. 119.
Hordeum vulgare (Barley)	"	1'482	...	"
Secale cereale (Rye)	"	1'577	...	"
Avena sativa (Oats)	"	1'598	...	"
Zea Mays (Maize)	"	1'440	1'398	"
Panicum miliaceum (Millet)	"	1'250	...	"
Fagopyrum esculentum (Buck-wheat)	Polygonaceæ	1'469	...	"
Ervum lens (Lentils)	Leguminosæ	1'934	...	"
Pisum sativum (Peas)	"	2'068	{ (a) 1'960 } { (b) 1'710 }	pp. 119, 122.
Phaseolus sp. (Weisse Bohnen, White Beans)	"	1'921	...	P. multiflorus?
Phaseolus vulgaris	"	...	{ (a) 2'175 } { (b) 2'007 }	pp. 119, 123, 124.
Faba vulgaris (Broad Beans)	"	2'040	2'570	pp. 109, 119.
Vicia, Lathyrus (Vetches)	"	1'754	...	p. 119.
Medicago sp. sp. (Lucern)	"	1'560	1'878	p. 120.
Trifolium repens (White Clover)	"	2'267	1'890	"
" pratense (Red Clover)	"	2'175	2'053	"
Papaver sp. sp. (Mohn, Poppy)	Papaveraceæ	1'910	...	P. somniferum, etc.
Brassica Napus varieties (Raps)	Cruciferæ	1'510	1'483	pp. 80, 96, 120, 418, 431.
Raphanus sativus chinensis (Oelrettig)	"	1'080	1'595	pp. 36, 120.
Camelina sp. sp. (Leindotter, Cameline)	"	1'600	...	pp. 120, 359.
Cannabis sativa (Hemp)	Cannabineæ	1'439	...	pp. 90, 120.
Helianthus annuus (Sunflower)	Compositæ	1'565	...	pp. 120, 518.
(Weisse Rübe)	...	1'625	1'518	p. 120.
(Zuckerrübe)	...	2'205	...	"
Pinus austriaca	Coniferae	...	1'358	"

Note.—According to Siewert, quoted on p. 120, the Lupines (*Lupinus*) have a swelling ratio of 2'00 to 2'30.

With regard to Table B, it is to be observed that the original swelling results were stated as percentages of the weight of the resting seed. These have been converted into the ratios employed for my own results in Table A, where the shrinking and swelling processes are combined in one simple formula, the resting seed being taken as 1. To have treated

the swelling process as a thing apart would have been to ignore its all-important reciprocal relation to the shrinking process. This conversion is easy. Thus, whilst Nobbe states the swelling capacity of Wheat at 60 per cent., and Hoffmann puts that of Broad Bean (*Faba vulgaris*) at 104 per cent., I should state them as 1.60 and 2.04 respectively, the resting seed being 1.00.

Value of the
results in
Tables A
and B.

Although there is a distinction to be drawn, as will be subsequently pointed out, between the water required for germination and the water necessary to saturate a seed, seeds under ordinary swelling experiments are apt to strike a rough average of their own by germinating, so that such experiments frequently prove to be germination experiments, in which one has to fix a somewhat arbitrary limit indicating where swelling ends and germination begins. This was in fact an almost invariable rule in my own experiments; but by placing the seed in its earliest swelling stage in damp moss, excessive estimates were probably avoided. I do not gather that either Hoffmann or Nobbe attached much weight to the distinction between the swelling needed for germination and the swelling involved in saturation. Indeed, the latter expressly states (pp. 119, 120) that the kernels require as a rule to be thoroughly soaked before germination begins. In his carefully guarded recorded experiments the seeds were either immersed in water or kept moist by pouring water over them, methods that seem likely to produce excessive estimates. Yet, except in the case of *Faba vulgaris*, his results as a rule come near to those obtained by Hoffmann for the same species; and in spite of the difference in our methods my estimates for *Pisum sativum* (Pea), *Phaseolus vulgaris* (French Bean), and *Phaseolus multiflorus* (Scarlet-runner), are not far separated from those of Nobbe. This will be seen in the comparison made in Note 1 of the Appendix. As I have said before, the seeds assert themselves in ordinary experiments, and, disregarding divergent conditions, strike out a rough average result for all. For these reasons, therefore, we may, I think, claim that the

results given in Tables A and B for the swelling ratios are fairly representative of the relative values of the swelling processes which precede germination in a state of nature.

It will have been inferred that if the seed in swelling for germination takes up the water lost in shrinking, the processes must be essentially mechanical in their nature. That the swelling of a seed is essentially a mechanical process was established by Dr Nobbe in a variety of experiments. Thus, he found that Clover seeds swelled with much the same readiness in ordinary pure water as in water that had been previously either oxygenated, or carbonated, or chlorinated (pp. 102, 103); whilst he showed that the absorbing capacity is largely independent of the retention of the germinating powers, since seeds of Lady's-fingers (*Anthyllis vulneraria*), with a low germinative value (8 per cent.), swelled almost as freely as seeds of which nearly all (86 per cent.) were able to germinate (p. 114). The swelling of a seed, as he asserts on p. 101, is merely a mechanical process preparatory for germination.

In the reciprocal character of the shrinking and swelling processes is involved their essentially mechanical nature.

In the course of my own observations with the balance, there presented themselves a number of other proofs of the mechanical and reciprocal character of the shrinking and swelling processes. These are merely summarised or illustrated in the remarks immediately following, references being there made to where a detailed treatment of the points raised will be found.

That the increase in weight of a seed in preparing for germination is essentially due to absorption of water is indicated :

Additional proofs of the mechanical nature of the swelling process.

- (1) By the fact that when a seed on the eve of germination is dried in air at the ordinary temperature it returns approximately to its original weight as a resting seed ;
- (2) By the circumstance that the weight-relations between the kernel and its coats and between the embryo (in albuminous seeds) and the other parts of the seed

are much the same in the seed that has been dried after swelling for germination as they are in the resting seed ;

- (3) In the fitness of the embryo in many pre-resting seeds to pass on at once to germination without the intervention of the resting stage.

The results of a number of experiments on leguminous seeds indicate that when a seed on the eve of germination is dried under ordinary air conditions it returns approximately to its original weight. In illustration there are given below five examples selected from the table in Note 2A of the Appendix, where numerous other results, all pointing to the same conclusion, will be found, together with a discussion of the general nature of such experiments. All the results refer to seeds that subsequently germinated.

EXAMPLES OF THE EFFECT OF DRYING UNDER ORDINARY AIR CONDITIONS ON LEGUMINOUS SEEDS THAT ARE READY TO GERMINATE (taken from Note 2 of the Appendix).

	Permeable or impermeable.	Weight in grains.			Gain (+) or loss (-)
		Resting seed.	Swollen for germi- nation.	After drying.	
Guilandina bonducella .	Impermeable	33'35	97'30	35'35	+ 6'0 per cent.
Entada scandens . . .	"	312'50	728'00	318'70	+ 2'0 "
Poinciana regia . . .	Variable	8'70	19'50	8'70	0'0 "
Phaseolus vulgaris (French Bean) . . .	Permeable	13'50	24'60	13'35	- 1'1 "
Faba vulgaris (Broad Bean) . . .	"	41'50	86'30	40'60	- 2'2 "

Note.—A plant with both permeable and impermeable seeds is characterised as "variable."

Although these samples support the view of the mechanical nature of the swelling process, they present curious divergencies in their behaviour when dried ; and the same may be said of the other results incorporated in the table in Note 2A. It appears, therefore, that as compared with their weight in the

First, that a seed on the eve of germination returns approximately to its original weight.

resting state some seeds on being dried in air after reaching the point of germination are heavier, others are lighter, and others remain unchanged. Various disturbing causes that would be likely to come into play in the course of the experiment here suggest themselves ; but they can usually be eliminated ; and, as shown in Note 2A, none can account for the great contrast in the behaviour of the seeds of *Guilandina bonducella* and *Faba vulgaris*, where in the one case there is a gain of about 6 per cent., and in the other a loss of 2 per cent.

However, as will be seen in the table, as well as in the illustrations given above, these marked differences are displayed by two distinct types of seeds, the impermeable as represented by *Guilandina bonducella*, and the permeable as exemplified by *Faba vulgaris*. A good deal of this contrast, therefore, lies behind the distinction between permeable and impermeable seeds ; and its significance will become evident only after a detailed consideration of those two types of seeds.

The second additional proof that the swelling of a seed for germination is essentially concerned with absorption of water might seem to be included in the first ; but there we were concerned with the seed in its entirety, whilst here we are dealing with its parts. The proof lies in showing that the absolute weight of parts that obtains in the resting seed is in the main preserved in the seed that has been dried after swelling for germination. Four illustrations supplied by leguminous seeds are here given ; but for full details on this subject reference must be made to Note 3 of the Appendix. I am here giving the results of observations on single seeds, and these are compared with the average weights of the parts in resting seeds of about the same size. The parts of the swollen seed were separated in the wet state and allowed to dry in an ordinary room. The small changes in weight that actually occur have a significance which is alluded to in a later page ; but they are not such as to materially affect the general conclusion to be drawn from the comparisons. The first two

Second, that the weight-relations of coats, kernel, albumen, and embryo are much the same in the seed dried after swelling for germination as they are in the resting seed.

seeds are exalbuminous, and here one is concerned only with the coats and the kernel. The last two are albuminous, and we have, therefore, in their cases to distinguish between the albumen and the embryo.

COMPARISON OF THE WEIGHTS OF THE COATS, KERNEL, AND EMBRYO (IN TWO CASES) IN RESTING LEGUMINOUS SEEDS, AND IN THE SAME SEEDS WHEN DRIED AFTER SWELLING FOR GERMINATION.

	Resting seed average.	Swollen seed.	Dried swollen seed.
<i>Mucuna urens</i> (exalbuminous) { coats kernel	23.7 grains	34.2 grains	23.1 grains
	64.4 ,,	136.1 ,,	66.9 ,,
	88.1 ,,	170.3 ,,	90.0 ,,
<i>Faba vulgaris</i> , Broad Bean (exalbuminous) { coats kernel	5.6 ,,	11.2 ,,	5.7 ,,
	34.4 ,,	68.8 ,,	33.3 ,,
	40.0 ,,	80.0 ,,	39.0 ,,
<i>Poinciana regia</i> (albuminous) { coats albumen embryo	4.95 ,,	9.43 ,,	4.60 ,,
	2.35 ,,	7.36 ,,	2.90 ,,
	2.70 ,,	6.21 ,,	2.50 ,,
	10.00 ,,	23.00 ,,	10.00 ,,
<i>Cassia marginata</i> (albuminous) { coats albumen embryo	2.84 ,,	5.90 ,,	2.70 ,,
	5.69 ,,	12.70 ,,	5.65 ,,
	1.27 ,,	2.80 ,,	1.23 ,,
	9.80 ,,	21.40 ,,	9.58 ,,

Third, that the embryo in many pre-resting seeds is able to pass on at once to germination.

Nature often supplies evidence of the readiness of seeds to "jump" the rest-period, the shrinking and swelling processes being then dispensed with. This is what we would expect if the shrinking of the soft pre-resting seed and the swelling of the hardened resting seed are essentially concerned with the loss and absorption of water. But in thus appealing to the potential vivipary of seeds we do so only in a very general sense, since numerous other influences may come into play. Though typically the resting stage represents a complete interruption in the embryo's development, this is not always so. A treatment of this complicated subject will be found in a later chapter; and it is there shown that in the case of

the seeds of plants like *Arenaria peploides*, *Vicia sepium*, *Iris Pseudacorus*, etc., which under normal circumstances enter into the typical resting state, it is possible, by keeping the soft, uncontracted pre-resting seed in warm, moist conditions, to induce germination, thus dispensing altogether with the shrinking and resting stages.

Before making further reference to the ratios for the shrinking and swelling of seeds, it should be pointed out that as a rule neither the full-grown, uncontracted pre-resting seeds nor the resting seeds swollen and ready for germination are in a state of saturation. Both markedly increase their weight when placed in water. The distinction between the amount of water required for germination and the larger amount needed for saturation is dealt with in a later page of this chapter. Here I will more particularly allude to the behaviour of the soft pre-resting seed in this respect. According to the principle that the swelling seed gains what the shrinking seed loses, we should infer that the behaviour of the large pre-resting seed and of the swollen seed on the eve of germination would be the same. This proves to be the case.

When in Jamaica, I found that full-sized soft seeds from the moist green pods of *Guilandina bonducella* gained about 20 per cent. in weight when placed in water; whilst, in the failures of my germination experiments, when the seeds were kept in wet moss, the weight of the swollen seed was often correspondingly in excess of the normal weight for germination. So in England with seeds of *Faba vulgaris* (Broad Bean) and *Phaseolus multiflorus* (Scarlet-runner), I obtained similar results. Here, full-grown soft seeds from the green pod, that is to say, seeds that had not yet begun to shrink, added at least 10 per cent. to their weight after lying in water for half a day. Then, again, resting seeds of *Faba vulgaris*, that under ordinary conditions would have germinated when their weight had increased by 90 or 100 per cent., did not germinate at all when allowed to remain in water, but kept adding to their weight by

Neither the large, soft pre-resting seeds nor the seeds swollen for germination are in a state of saturation.

absorbing more water, until they had reached their saturation point of about 120 per cent.

A closer consideration of the shrinking and swelling ratios.

We are now in a position to consider more closely the shrinking and swelling ratios before tabulated. There are dealt with in these tables the results of observations on the seeds of more than 100 plants, four-fifths of which, as given in Table A, are from my own observations, whilst the rest, as included in Table B, are from the observations of Hoffmann and Nobbe. They belong to 38 families and comprise about 80 genera, of which rather over one-third are leguminous. In three or four cases only, viz. *Pisum sativum*, *Faba vulgaris*, *Phaseolus vulgaris*, and perhaps *P. multiflorus*, are the same plants referred to in both tables.

In the list containing my own results, seeds alone are dealt with, seed-like indehiscent fruits being excluded; but in Table B we find also the "grains" of Cereals and a few seed-like indehiscent fruits, such as those of Buckwheat; but I do not apprehend that the swelling ratios will be very materially affected. Dr Nobbe himself did not regard this disturbing cause as concerning the validity of his comparison (p. 112); and from my own observations on fruits to be subsequently discussed I would infer that, at all events with the grains of Cereals, which comprise most of the seed-like fruits in Table B, the effect of the coverings would be rather to lessen than to increase the contrast which evidently exists between the swelling capacities of the seeds of Cereals and the seeds of other plants.

The views of Dr Nobbe.

Dr Nobbe sums up very briefly the results obtained by Hoffmann and himself concerning the swelling capacities of seeds (p. 120). Leguminous seeds, he infers, possess the highest capacity for absorbing water, whilst the lowest is possessed by oily and resinous seeds and by the grains of Cereals. This inference receives a general support from the results in Table A, and it will be sufficient at present to take the two extreme cases in illustration, the seeds of *Ricinus communis* absorbing one-third of their weight of water before

germination, whilst those of the leguminous *Guilandina bonducella* treble their weight. But this cannot take us very far. A host of questions present themselves as we run our eyes down the lists; and when we endeavour to answer them off-hand, a long vista of undetermined influences opens up. It would be easy to discover differences and to formulate distinctions; but they would have little or no meaning now; and it would be futile at present to base any general contrast, such as between families or between genera, on these data. (As already remarked, indehiscent fruits of the type found in palms and in genera like *Prunus* and *Sparganium* do not come within the limits of this discussion, but are referred to in Note 20 of the Appendix.)

We have yet to appreciate the value and to estimate the significance of such distinctions. Behind the varying behaviour of the shrinking and the swelling seed lie the seed's life-history and the cumulative effect of a multitude of inter-relations as between the seed and the embryo, between the kernel and its coverings, between the coverings and the fruit, and, through the fruit, between the seed and the parent and between the plant and its environment. It is, therefore, obvious that we can only with some security ignore the past when we have reason to believe that the seeds are akin in their history; and that is why it will be wise at present to mainly confine our discussion of principles to the Leguminosæ. But even here it will soon be evident that the risks increase as the affinities grow less, and the safest road will often lie in the study of the varying behaviour of seeds of the same species.

Proceeding on these lines, we will inquire into the constancy of these ratios in the same species, a necessary preliminary consideration, since such estimates would lose much of their value for comparative purposes if the normal range is great. But few of the "shrinking" results admit of being stated in this fashion, as it was my wont in most cases to weigh

The difficulties of the subject.

The constancy of the shrinking and swelling ratios in the same species.

a number of seeds together. Only the very large seeds were treated individually; and I here give the shrinking ratios for three full-sized pre-resting seeds of *Entada scandens* (all of which subsequently germinated), the weight of the resting seed being taken as 1. They were 2.46, 2.51, and 2.62.

My method of determining the swelling ratios was better fitted for ascertaining their range in seeds of the same species, and the sample of results given in the table below is sufficient to bring out their relative constancy.

Species.	Family.	Number of seeds tested.	Range of the swelling ratios.	Average ratio.
<i>Adenanthera pavonina</i> . . .	Leguminosæ	10	2.30 2.60	2.42
<i>Cassia grandis</i>	"	5	2.04 2.22	2.13
<i>Entada scandens</i>	"	12	2.21 2.59	2.42
<i>Faba vulgaris</i> (Broad Bean) . . .	"	4	1.95 2.08	2.01
<i>Guilandina bonducella</i>	"	10	2.80 3.26	3.08
<i>Mucuna urens</i>	"	11	1.93 2.12	2.05
<i>Poinciana regia</i>	"	13	2.24 2.44	2.32
<i>Canna indica</i>	Cannaceæ	8	1.43 1.52	1.48

The great contrast between the shrinking and swelling ratios in different species.

The next point to notice is the great contrast which the seeds of different plants display in their combined shrinking and swelling capacity. Relatively to their weight some seeds shrink and swell three or four times as much as others. We have seen that as a general rule the water lost in the shrinking is regained in the swelling, the one counterbalancing the other, so that it would be legitimate to estimate the missing ratio where only one value has been found. It will, however, be more convenient at first in dealing with the great range of the capacities to speak only of the swelling ratio, remembering of course its reciprocal character.

In the tables the swelling capacity is stated as a ratio of the weight of the resting seed taken as 1, the reason being that the swelling is only one-half of a reciprocal process which is centred in the resting seed. To avoid, therefore, the in-

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convenience of stating the values of the shrinking and swelling in different terms, a simple reciprocal ratio was invented, as described in a previous page. Thus, to take the seeds of *Canna indica*, where the pre-resting seed loses 66 per cent. of its weight in entering the resting stage, and where the resting seed adds 50 per cent. to its weight in swelling for germination, the use of percentages for the two results would be clumsy and inconvenient. But stated in this manner :

Pre-resting seed.	Resting seed.	Swelling seed.
1·5	1·0	1·5

we at once get a clear view of the problem.

Now, however, when we are dealing particularly with the swelling capacity, the usual method of stating the increase as a percentage of the weight of the resting seed will be adopted. The conversion of the ratio into a percentage is simple enough, the swelling ratio of 1·5 for the seeds of *Canna indica* being equivalent to an increase of weight of 50 per cent. We see accordingly that with many Leguminosæ, where the seed swollen for germination is more than double the weight of the resting seed, the increase amounts to more than 100 per cent. Thus with *Abrus precatorius*, where the swelling ratio, taking the resting seed as 1, is 2·05, the actual increase in weight is 105 per cent.

Looking at the extremes of the range of the swelling capacity of seeds in general, we find amongst the hundred and odd plants in the tables two groups that we can handle fairly well, one where the absorbing capacity is not over 60 per cent., the other where it is at least twice as much, reaching 120 per cent. and over. In the first or "minimum" group are to be included a number of plants in Table B, such as all the Cereals, species of the cruciferous genera *Brassica* and *Camelina*, *Cannabis sativa*, *Pinus austriaca*, and one or two others, together with several in Table A of the genera *Anona*, *Canna*, *Citrus*, *Datura*, *Ricinus*, *Theobroma* (Cacao), etc., belonging in both cases to a variety of families, but,

The employment of percentages in dealing solely with the swelling capacities.

The range of the swelling capacity, (a) as represented by extreme groups,

if we except the species of *Pithecolobium*, in no instance to the Leguminosæ.

On the other hand, of the seeds of plants to be placed in the "maximum" group, where the increase of weight is 120 per cent. or more, quite two-thirds are leguminous; and of these we may cite *Adenantha pavonina*, *Canavalia obtusifolia*, *Cassia fistula*, and species of *Entada*, *Enterolobium*, *Erythrina*, *Guilandina*, *Leucæna*, *Poinciana*, etc. Belonging to a variety of other families are the seeds of *Barringtonia speciosa*, *Bignonia*, *Ipomæa pes-capræ*, *Primula*, *Swietenia* (Mahogany), etc., which are for the most part placed here provisionally, since only occasionally, as with the species of *Ipomæa*, has the germinative capacity been tested for individual seeds of which the shrinking has been observed. Several of these probably belong to a type of seeds where the shrinking of detached seeds under experiment is considerably in excess of what takes place in nature. If we were able to interrogate nature more closely, we should probably find that the "maximum" group would be almost entirely leguminous, thus justifying the original view of Nobbe, which is referred to a few pages back.

(b) by individual species.

We can now turn from the range of extreme groups to that of different species. Here we can cite as extreme cases:

- (a) On the "minimum" side, the seeds of *Ricinus communis*, which require to absorb only 33 per cent. of their weight in order to germinate, and the grains of Millet (*Panicum miliaceum*), which only increase their weight by 25 per cent. when swelling by water-absorption;
- (b) On the "maximum" side, the different leguminous seeds that increase their weight from 150 to rather over 200 per cent. in taking up water for germination, such as *Canavalia obtusifolia*, *Entada scandens*, *Guilandina bonducella*, and *Leucæna glauca*.

There is this much to be said concerning all cases where the amount of water absorbed for germination is very small,

let us say below 20 per cent. of the weight of the resting seed, that such seeds are on the borderland of vivipary, where they dispense with shrinking and swelling altogether. This consideration links itself with some curious reflections that are dealt with subsequently. It is possible that we may have here an explanation of the very low swelling capacity ascribed by Hoffmann to a species of *Raphanus* (*Oelrettig*), viz. 8 per cent., which is equivalent to a swelling ratio of 1.08.

However, the ground will have to be cleared in many directions before we can expect to discover the significance of such contrasts in the swelling capacities as presented in the tables. A tentative use of the method of exclusion may perhaps assist us in getting into the right road; and we will now endeavour to ascertain if there is any connection between these contrasts and certain conspicuous differences in the seeds. In the first place, there is the distinction in size. This can be at once dismissed, since the ordinary variation in the swelling capacity becomes almost a negligible quantity when we reflect on the great differences in size and weight between seeds. Thus the difference in weight between a seed of *Primula veris* ($\frac{1}{100}$ th of a grain) and a seed of *Entada scandens* (400 grains) is as between 1 and 40,000; yet the difference in their swelling ratios would only be as between 2.3 and 2.5.

Then, again, it is possible that the distinction between albuminous and exalbuminous seeds may supply a clue to the variation in swelling. Exalbuminous seeds are most characteristic of the Leguminosæ; but plants of the same family with albuminous seeds are fairly represented in the tables. The albuminous leguminous seeds there included have the embryo more or less fully developed, the large, flat cotyledons being nearly as long and as broad as the kernel. We are therefore employing seeds where the resting period has been imposed at much the same stage of development of the embryo. It will be seen from the comparison made below that such differences do not explain the great variation in the swelling capacity displayed by seeds of leguminous plants.

The causes of the great variation in the swelling capacity.

(a) Distinctions in size and weight.

(b) Albuminous and exalbuminous seeds.

COMPARISON OF THE SWELLING CAPACITIES OF ALBUMINOUS AND EX-ALBUMINOUS SEEDS OF SPECIES OF LEGUMINOSÆ, THE RESTING SEED BEING TAKEN AS 1.

Albuminous.	Exalbuminous.
Bauhinia sp. 2'20	Cæsalpinia sepiaria 2'20
Cassia fistula 2'52	Erythrina indica 2'49
„ grandis 2'11	Tamarindus indica 2'15
„ marginata 2'10	Abrus precatorius 2'05
Poinciana regia 2'37	Entada polystachya 2'29

(c) Differences in the proportional weight of the seed-coats.

Since the proportional weight of the seed-coats varies greatly between different species, a subject discussed in Chapter IX, it is possible that this may determine the variation in the swelling capacity. A cursory reference to the results there tabulated will make it apparent that this is not the case. This is sufficiently indicated by the comparison made below, from which it is to be inferred that in leguminous seeds with similar swelling capacities, the coverings may constitute as little as 24 per cent., and as much as 61 per cent. of the entire weight.

COMPARISON BETWEEN THE SWELLING CAPACITIES OF THE SEEDS OF FOUR LEGUMINOUS PLANTS AND THEIR SEED-COAT RATIOS.

	Swelling ratio.	Seed-coat ratio, the weight of entire seed taken as 100.
Acacia Farnesiana	2'0	60'8
Bauhinia sp.	2'1	23'5
Cæsalpinia sepiaria	2'2	61'4
Mucuna urens	2'0	26'3

(d) The seeds of berries and legumes.

A noticeable feature in Table A is the small shrinking ratio of the seeds of moist or pulpy indehiscent fruits of the berry type. I was rarely successful in getting them to germinate; but in the successful cases of *Anona muricata* (the Soursop) and of *Citrus decumana* (the Shaddock), it will be seen that the swelling ratio is similarly small, and no doubt this rule

generally applies. That there is a real distinction between the seeds of berries and pods in this respect is shown in the comparison made below ; but it will not be possible here to do more than allude to it in passing. It will be futile to attempt to discuss it until the relations between fruits and seeds have been studied, a subject treated with detail in a subsequent chapter.

COMPARISON OF THE SHRINKING AND SWELLING RATIOS (THE RESTING SEED BEING TAKEN AS 1) OF THE SEEDS OF BERRIES OR BERRY-LIKE FRUITS WITH THOSE OF THE SEEDS OF LEGUMES.

Berries.			Legumes.		
	Shr.	Sw.		Shr.	Sw.
Anona muricata (Soursop)	1'40	1 1'43	Abrus precatorius . . .	2'15	1 2'05
„ palustris . . .	1'45	1	Bauhinia sp.	2'10	1 2'20
Arum maculatum . . .	1'63	1	Cæsalpinia sepiaria . . .	2'25	1 2'20
Citrus decumana (Shaddock)	1'65	1 1'60	Entada scandens . . .	2'51	1 2'47
Lonicera Periclymenum (Honeysuckle)	1'72	1	Faba vulgaris (Broad Bean)	2'30	1 2'00
Ribes grossularia (Gooseberry)	1'63	1	Guilandina bonducella	3'20	1 3'08
Tamus communis . . .	1'75	1	Phaseolus multiflorus (Scarlet-runner)		1 1'90
Theobroma Cacao (Cocoa)	1'37	1	Ulex europæus	2'30	1
Chrysophyllum Cainito (Star Apple)	1'45	1	Vicia sativa	2'26	1

Only very moist baccate fruits are here named, the seeds of relatively dry berries losing rather more in the shrinking process, such as those of *Hedera Helix* (Ivy) and *Berberis*, where the shrinking ratios are 2'00 and 1'92 respectively. Bearing this in mind, it would appear from the foregoing comparison that whilst the seed of a moist berry when the fruit dries up loses on the average about a third of its weight, the unripe seed of the leguminous green pod during the shrinking process loses as a rule rather more, and sometimes much more than half its weight on entering the resting state.

Yet considerations such as these do not carry us very far in dealing with the problem of the varying swelling ratios of seeds, since it is apparent from Table B that there are whole groups of plants with dry-looking fruits, such as the Cereals

There is much that these distinctions will not explain.

and the Cruciferæ, where the seeds possess swelling ratios quite as low as those of baccate fruits, and to these groups may be added often plants with capsular fruits. There would, therefore, seem to be some common influence that brings not only the seed of the berry, but the seed of the cruciferous pod, of the capsule, and of dry-looking indehiscent fruits, into contrast with the seed of the legume.

An appeal to
unusual
deviations in
the swelling
capacity of
seeds of the
same species.

We will now appeal to the varying behaviour of seeds within the limits of a species, with the hope of discerning in their differences some clue to the origin of the greater contrasts between the seeds of plants that stand apart from each other. We have before seen that the ordinary range of the swelling ratios in the same plant is small ; and inquiry has led me to believe that we shall not profit much by the study of small differences. At times, however, there are deviations that lie quite outside the usual range of the swelling ratios. The cases of excessive swelling, which are probably just as apt to occur in nature as they are in our experiments, are often readily explained by the unusual prolongation of the swelling period in normal seeds, which allows the seed to take up more water than is actually needed. Both permeable and impermeable seeds are liable at times to absorb much more freely than is usual. Under such conditions germination usually fails ; but occasionally it takes place, and we obtain swelling ratios far in excess of the average. Then, again, we have cases of excessive swelling, also ending at times in germination, where there has been abnormal shrinking in the drying of the moist pre-resting seed ; and since the exceptional loss of water has to be made up in the preparation for germination, according to the compensatory relation between the shrinking and swelling processes before established, we find this expressed in the increase of the swelling ratio. In these cases we are concerned only with permeable seeds, as will be explained in a later page.

On the other hand, we have instances of swelling ratios considerably below the average and equally outside the ordinary

range. This happens in the case of impermeable seeds where the shrinking process has been incomplete, and considerably less water is required for germination than in the instance of the typical resting seed.

I will first take those cases of excessive swelling displayed at times by normal seeds, and will begin with permeable seeds, to which indeed earlier investigators seem to have mainly confined their inquiries. Dr Nobbe inferred that as a rule seeds require to be well soaked for germination, and that those cases where complete soaking is not necessary are exceptional (pp. 118, 119). But he remarked that the minimum amount of water needed to start the germinating process was a subject for future inquiry (p. 120). It is, in fact, in this direction that later investigators have worked, and it is now possible to distinguish between

First, to the excessive swelling displayed at times by normal seeds.

(a) By permeable seeds.

- (a) The minimum amount of water required for starting germination,
- (b) The average amount that seeds absorb under natural conditions in swelling for germination,
- (c) The amount of water required for saturation.

The quantity of water that a seed absorbs before germinating under natural conditions, or in ordinary germination experiments, is considerably above the minimum amount needed, and markedly below the amount requisite for the seed's saturation. A rough indication that leguminous seeds germinate before they are saturated is found in the fact that normally seeds germinate long before they rupture their coats, which is the sign of the seeds being thoroughly soaked with water. (I refer to ruptures taking place away from the hilum.) Minimum results can, of course, be only obtained in the laboratory. By an ingenious course of experiments, referred to in Note 4 of the Appendix, Victor Jodin established a "germinative minimum" for Peas (*Pisum sativum*), and in his paper he quotes similar estimates made by Van Tieghem for "Fèves" (I suppose, Broad Beans, *Faba vulgaris*). The results, which are stated in different fashions by the various investi-

gators, have all been converted into percentages of the weight of the resting seed carrying its normal water-contents.

COMPARISON OF THE MINIMUM AMOUNT OF WATER REQUISITE FOR GERMINATION, AND OF THE AVERAGE QUANTITY ABSORBED UNDER NATURAL GERMINATING CONDITIONS, WITH THE MAXIMUM AMOUNT THAT A SEED CAN TAKE UP, *i.e.* THE AMOUNT NEEDED FOR SATURATION. (Stated as percentages of the weight of the normal resting seed.)

	<i>Pisum sativum.</i>	<i>Faba vulgaris.</i>
Minimum for germination .	67 J ; 71 N	74 T.
Average for germination .	91 G ; 107 H ; 96 N	95 G ; 104 H
Maximum (for saturation) .	110 G	120 G ; 118 T

G=Guppy. H=Hoffmann. J=Jodin. N=Nobbe. T=Van Tieghem.

I have endeavoured here to give the general run of the results. The critical results are of course those made by the same investigator on the same set of seeds. Thus we notice particularly in the case of "Fèves" (assumed above to be *Faba vulgaris*) Van Tieghem's estimate of 74 per cent. as the minimum amount of water required for germination and 118 per cent. as the maximum amount that a seed can absorb. So again my own results for *Faba vulgaris* (Broad Beans) were very definite, 95 per cent. being the average for germination and 120 per cent. the amount needed for saturation. The general indications above afforded for seeds of the types of the Pea (*Pisum*) and the Bean (*Faba*) clearly show that whilst the minimum amount of water required for germination is about 70 per cent. of the weight of the resting seed, a considerably larger quantity of water is needed for saturation, *viz.* 110 to 120 per cent. Between these two extremes lie the average amounts of water required for germination under ordinary conditions, as determined from the observations of Hoffmann, Nobbe, and myself.

The seeds of *Pisum sativum* and *Faba vulgaris* are typical permeable seeds. Similar indications were presented in many of my experiments on impermeable seeds of the same family.

(b) by impermeable seeds.

THE THREE CONDITIONS OF THE SEED 45

Thus, a seed of *Entada scandens* weighing 400 grains in the resting state will be ready to germinate under normal conditions when it has increased its weight by water-absorption to from 950 to 1000 grains. But if the conditions are unfavourable and it fails to germinate, it will continue absorbing water until it reaches a condition of saturation, when its weight will be about 1150 or 1160 grains. Thus :

	Water required stated as a percentage of the weight of the resting seed.		Swelling ratios, taking the resting seed as 1.	
	For germination.	For saturation.	For germination.	For saturation.
<i>Entada scandens</i> . . .	140 to 150 %	190 %	2'4 to 2'5	2'9

In other experiments seeds often continued to absorb water long after they had failed to germinate. They may occasionally germinate when the swelling ratio has far exceeded the normal limits, but only in an imperfect and belated fashion. One or two more instances will serve to illustrate these points. A seed of *Albizzia Lebbek*, 2 grains in weight, only requires to increase its weight to 4.5 grains in order to germinate ; but when it has failed to germinate it will continue absorbing water without rupturing its coat until nearly 6 grains in weight, the limits of the normal swelling ratio, 2.25, being long passed. So, again, a permeable seed of *Entada polystachya*, weighing 7 grains, germinates usually after its weight has been increased by the absorption of water to about 16 grains, its swelling ratio being 2.3 ; but when it fails it continues to swell and reaches a weight of 21 grains and over, thus tripling its original weight to no purpose. Convolvulaceous seeds, possessing in the resting stage a hard, dry albumen, are especially liable to take up more water than is needed for germination. In its transition into the mucilaginous state, the albumen absorbs a very large amount of water. The normal swelling ratio for a seed of *Ipomœa pes-capræ* is about 2.5, but seeds may germinate tardily

after their weight has been increased threefold, and seeds that fail to germinate sometimes acquire $3\frac{1}{2}$ times their original weight.

When we come to deal with the hygroscopicity of seeds we shall be able to state precisely the lower value of the seed's hydratation, that is to say, below the minimum required for germination. This is the "hygroscopic maximum" (see Chapter VII).

Coming to the second kind of excessive swelling, we deal here with seeds abnormally shrunken, when the excess of water absorbed in the swelling process compensates for the excess lost in the shrinking stage. But it should be noted that we are not here concerned with seeds so much shrunken that they have lost their vitality, a fate that may befall permeable and impermeable seeds alike, but with seeds that still retain their germinating powers. Thus it comes about that permeable seeds alone illustrate this type of excessive absorption, since defective shrinking acts in different ways on the swelling capacity of seeds, according to their permeable or impermeable character in the resting state. If permeable, the shrinking is too great, and the swelling is also excessive. If impermeable, the shrinking is deficient and the swelling ratio is much reduced. This is in accord with the compensatory principle before established, that what the shrinking seed loses the swelling seed gains. But it is important to notice that we are here again brought face to face with the distinction between permeable and impermeable seeds.

Permeable seeds that are allowed to dry when detached from the plant in the full-sized moist condition generally shrink too much; and as a rule they fail to germinate, absorbing much more water in proportion to their weight than in the case of the normal resting seed. Greatly shrivelled seeds are, as is manifest, imperfectly developed, so that they scarcely call for our attention. However, to illustrate this subject, I give below my observations on the seeds of *Canavalia ensiformis* in three conditions: excessively shrivelled, moderately shrivelled, and normal.

Second, to the excessive swelling of abnormally shrunken permeable seeds.

COMPARISON OF THE SHRINKING AND SWELLING RATIOS OF THE SEEDS OF *CANAVALIA ENSIFORMIS* UNDER DIFFERENT CONDITIONS.

Condition of seed.	Weight in grains.			Ratios, taking the resting seed as 1.		Germinative capacity.
	Pre-resting.	Resting.	Swollen.	Shr.	Sw.	
Excessively shrivelled . . .	44'1	15'0	39'0	2'94	1 2'60	Lost.
Moderately „ . . .	60'0	25'5	59'7	2'36	1 2'34	Usually retained.
Normally contracted . . .	48'3	23'3	46'6	2'07	1 2'00	Normal.

Those cases where seeds of the same species at times display much diminished swelling capacities, as expressed in swelling ratios considerably below the average and outside the ordinary range of variation, now claim our attention. Such cases are peculiar to impermeable seeds, and occur when the shrinking process is incomplete, less water being required for germination, since less than the normal amount is lost in the shrinkage. This is a point of considerable importance, and one on which much of my work has been concentrated, since it supplies the key to one of the principal positions maintained in these pages. We get here our first glimpse at the significance of impermeability, and we perceive how it comes about that both permeable and impermeable seeds may be found in the same species.

Very interesting indications in this direction are supplied by the seeds of *Guilandina bonducella*, and I will briefly state the general results of numerous observations made in Jamaica. When we open the full-grown green pods of this plant we find two kinds of soft green pre-resting seeds :

- (a) Yellowish green soft seeds, about 100 grains in weight and 25 to 27 millimetres in diameter, which represent the maximum development in size and weight of the pre-resting seed before the shrinking process commences.

Third, to the great diminution of the swelling capacity caused by the deficient shrinkage of impermeable seeds as illustrated,

(a) by *Guilandina bonducella*,

- (*b*) Dark olive-green soft seeds, rather firmer than those above, 94 or 95 grains in weight, 23 to 25 mm. in diameter, and representing the pre-resting seed in the earliest stage of shrinking.

If we open other pods that are commencing to wither we find the seeds in various stages of contraction ; and finally we come upon the dried-up brown dehiscing pod containing hard, grey impermeable seeds very much smaller than those of the *a* and *b* stages, and weighing 33 or 34 grains.

Such is Nature's method, provided we do not interfere with it. But if we remove from the green unopened pod seeds in the *a* and *b* stages and allow them to dry on the table, we get the following results. The fully formed pre-resting seed of the *a* stage shrinks excessively, and when that process is complete we find a greatly shrivelled seed, weighing 27 or 28 grains, which takes up water readily, yet fails to germinate. But if we take one of the olive-green *b* seeds, where shrinking has already commenced, and allow it to dry on the table under the same conditions, we notice that instead of shrinking excessively its shrinkage as compared with that of the normal resting seed is deficient, and that instead of weighing about 33 grains, as it would have done if it had been left undisturbed in the pod, its final weight is as much as 42 grains. Such a seed, though permeable and hygroscopic, retains its germinative capacity.

Now comes the critical part of the experiment. If we put the greatly shrivelled *a* seed in the conditions for germinating, we find that whilst it swells excessively by absorbing water and increases its weight by about 230 per cent., it fails to germinate. On the other hand, the *b* seed, which has shrunk deficiently, absorbs water easily, increases its weight by about 150 per cent., and germinates healthily. Very different is the behaviour of the normal resting seed. Its impervious outer coat has to be filed through before it can take up water for germination ; and before that stage is reached it increases its weight by about 200 per cent.

But the important point as indicated in the results tabulated

below is that the two germinable seeds, the permeable, deficiently shrunken seed and the normal, impermeable seed, when swelling for germination, take up much the same amount of water that they surrendered in the shrinking process. In other words, the needs for germination are satisfied by the seed's regaining the water previously lost, the permeable seed taking least and the impermeable seed most. This is well brought out in the ratios given in the table; and thus we see how, without impairing the germinative powers, deficient shrinkage leads to decrease in the swelling capacity and to the loss of impermeability.

TABLE SHOWING THE DIFFERENT EFFECTS OF EXCESSIVE, DEFICIENT, AND NORMAL SHRINKAGE ON SEEDS THAT ARE TYPICALLY IMPERMEABLE IN THE RESTING STATE, AS ILLUSTRATED BY THE RESULTS OF EXPERIMENTS ON THE SEEDS OF *GUILANDINA BONDUCELLA*.

Condition of the resting seed.	History of the seed.	Weight in grains of the pre-resting, resting, and swollen seed.			Shrinking and swelling ratios, the resting seed as 1.		Effect on the seed.
		Pre-resting.	Resting.	Swollen for germination.	Shr.	w.	
A. Excessively shrunken	Detached from the green pod before shrinking had begun	100	28.5	92	3.50	1 3.30	Permeable and hygroscopic, germinative powers lost.
B. Deficiently shrunken	Detached from the green pod in the early stage of shrinking	100	42.0	105	2.38	1 2.50	Permeable and hygroscopic, germinative powers retained.
C. Normally contracted	Shrinking process carried out in the pod on the plant	100	33.3	100	3.00	1 3.00	Impermeable and normal in all respects.

The shrinking ratio for the normal resting seed was mainly obtained by comparing the average weights of seeds in different stages of contraction on the same plant.

The weight of the resting seed averages nearly 40 grains; but for convenience in stating the ratios the weight of 33 grains is employed in the table and in the text.

The important lesson of the seeds of *Guilandina bonducella* in this matter is that decrease in the swelling capacity is

associated with the loss of impermeability, and that these results are primarily due to the deficient shrinkage of the pre-resting seed. In my experiments other impermeable seeds behaved like those of *Guilandina bonducella*. When they had lost their impervious character they swelled less and in consequence required less water for germination. The loss of impermeability was in fact associated with marked diminution in the swelling ratios. A good example of this result was afforded in the case of the seeds of *Dioclea reflexa*, gathered by me in the woods of the Grand Etang in Grenada, their mode of occurrence being described in Chapter V. Here the origin of the loss of impermeability could be readily traced, and the permeable seeds were easily recognised by their larger size, darker hue, softer coverings, and by other indications of deficient shrinkage. The outcome of a number of observations was as follows:—

(b) by *Dioclea reflexa*,

The permeable seeds of *Dioclea reflexa* in swelling for germination increase their weight by about 80 per cent; whilst the impermeable seeds just double their weight. This difference is not so great as in other impermeable seeds, since the seed-coverings act somewhat irregularly, as described in Chapter IX.

If the share taken by the coats in the swelling process is eliminated, the contrast between the swelling capacities of these two types of seeds is made more evident, the kernel of the permeable seed showing an increase of weight of about 80 per cent., and that of the impermeable seed of about 130 per cent. The swelling mechanism of these seeds is discussed in Chapter IX.

The behaviour of the seeds of *Guilandina bonducella* and *Dioclea reflexa* must be typical of many other leguminous seeds with impervious coats. Any influence that impedes the shrinking of the soft seed of the green pod tends to prevent the acquirement of impermeability. One may cite in this connection the seeds of *Cæsalpinia sepiaria* and *Cæsalpinia Sappan*, which are often impermeable when allowed to ripen on the plant, but permeable if they have been prematurely detached from the pod, as described in Chapter V.

Sometimes these deviations from the normal behaviour of a seed become fixed ; and Nature then facilitates our inquiries by presenting in the same species two types of seeds which are distinguished not only in size and colour, but also by their different degrees of impermeability. Such seeds have also two corresponding degrees of swelling capacity, the permeable seeds requiring much less water than the impermeable seeds.

Entada polystachya, as observed by me in Grenada, is a case of this kind. Here we find two types of seeds differing from each other in almost all the critical points that distinguish permeable and impermeable seeds, and equally capable of reproducing the plant. As indicated in the table below, they differ in colour, size, and weight, as well as in their swelling capacity, the permeable seed increasing its weight by about 124 per cent. before germination, whilst the impermeable seed requires more water and adds 150 per cent. to its weight.

(c) *Entada polystachya*, which displays the same principle in its two types of seeds.

COMPARISON OF THE TWO TYPES OF SEEDS PRODUCED BY ENTADA POLYSTACHYA

Type.	Colour.	Length and breadth.	Resting weight.	Shrinking and swelling.				
				Weight in grains.			Ratios.	
				Unripe.	Rest-ing.	Swollen.	Shr.	Sw.
A. Large and permeable	Yellowish brown	15 x 12 mm.	6.6 grs.	14.8	6.6	14.8	2.24	1 2.24
B. Small and impermeable	Dark brown	13 x 11 mm.	5.0 grs.	12.5	5.0	12.5	2.50	1 2.50

Different hypotheses present themselves in explanation of this relation between the swelling capacity and the permeability of a seed. For example, it may be suggested that it is merely a matter concerned with the water-contents or hydration of a seed, a view that would accept, without explaining, the implication of these experiments, that impermeable seeds contain less water than permeable seeds. To form an opinion now would be to prejudge a matter which will prove to be far more

The question of permeability and impermeability blocks the way.

complex than it at first appears. This question of the ability or inability of seeds to absorb water through their coats has been constantly arising in this chapter in connection with other seed-capacities; and in the particular subject we have just been considering it is manifestly impossible to make further progress until we investigate the nature of the differences associated with the distinction between a permeable and an impermeable seed. At present, therefore, the question of permeability and impermeability blocks the way. We will accordingly proceed to its discussion in the next three chapters.

SUMMARY

(1) We deal here with the three conditions presented by the large, soft pre-resting seed, the hardened, contracted resting seed, and the soft, swollen seed about to germinate (p. 18).

(2) This involves the study of the shrinking and swelling of the seed, processes which are in the main concerned with water-loss and water-gain (p. 19).

(3) The balance is the instrument of this investigation, and the modes of thus determining the shrinking and swelling ratios are described (p. 20).

(4) The indications of the single seed, when its history has been followed in all three conditions, prove that the water lost in shrinking is regained in swelling for germination, and that the swollen seed represents the return to the pre-resting or so-called unripe state (p. 21).

(5) The same reciprocal relation between the shrinking and swelling processes is established by independent observations of the three conditions on a large number of different seeds (p. 22).

(6) The principle that the water lost in the shrinking process is gained back in the swelling stage was accepted by Dr Nobbe in his *Handbuch der Samenkunde*, 1876 (p. 23).

(7) Tables of the shrinking and swelling ratios are given, the first containing the results of the author's observations, the second those of Hoffmann and Nobbe (pp. 24-27).

(8) It is then pointed out that the essentially mechanical nature of the shrinking and swelling processes is involved in their reciprocal character (p. 29).

(9) Additional proofs of the mechanical nature of the swelling process are indicated as follows:—

(a) By the fact that when a seed on the eve of germination is dried, it returns approximately to its original weight as a resting seed. The results of a number of experiments on leguminous seeds are given, and it is shown that seeds fall short of or exceed the original weight according as they were in the first place permeable or impermeable (p. 30);

(b) By the fact that the weight-relations of coats, kernel, albumen, and embryo are much the same in the seed dried after swelling for germination as they are in the resting seed; illustrated by examples (p. 31);

(c) In the ability of the embryo in many pre-resting seeds to pass at once to germination without the intervention of the resting stage, such embryos being potentially viviparous (p. 32).

(10) Neither the large, soft pre-resting seeds nor the seeds swollen for germination are in a condition of saturation (p. 33).

(11) The shrinking and swelling ratios are then more closely considered (p. 34).

(12) The views of Dr Nobbe (p. 34).

(13) The difficulties of the subject, and the necessity of confining the discussion of principles to one family, namely, the Leguminosæ (p. 35).

(14) The constancy of the shrinking and swelling ratios of normal resting seeds of the same species is then shown (p. 35).

(15) But the contrast, as exemplified by the swelling ratios, is great between different species, whether in groups or in individuals. Thus, the Cereals with a swelling capacity of not over 60 per cent., and the Leguminosæ with a capacity ranging between 90 and 200 per cent., represent the minimum and maximum groups. That leguminous seeds possess the highest capacity for absorbing water when preparing for germination was stated long since by Nobbe. The contrast between individual species is displayed by the seeds of *Ricinus communis* and of *Guilandina bonducella*, the first adding only one-third to their weight, and the last trebling their weight when swelling for germination. Seeds that possess a very low swelling capacity, for instance, below 20 per cent., are probably on the borderland of vivipary (pp. 36–38).

(16) The reasons of the great range in the swelling capacities of different seeds are then considered, that is to say, why the seeds of some plants absorb much water and others very little in swelling for germination. After endeavouring to ascertain whether there is any connection between this great variation, and certain conspicuous differences in

seeds, such as distinctions in size and weight (p. 39), the albuminous or exalbuminous character of seeds (p. 39), differences in the proportional weight of the seed-coats (p. 40), the difference in the types of fruits, as between berries and legumes (p. 41), etc., it is inferred that there is much which these distinctions will not explain (p. 41).

(17) Appeal is then made to the unusual deviations in the swelling capacity of seeds of the same species, with the hope of finding a clue to the origin of the great contrasts in this respect presented by the seeds of different plants (p. 42).

(18) In the first place, cases of excessive swelling in normal resting seeds are discussed, both of the permeable and impermeable types; and it is pointed out that it is possible to distinguish between

- (a) The minimum amount of water required for germination as shown in laboratory experiments;
- (b) The average amount of water that under natural conditions seeds absorb when swelling for germination;
- (c) The maximum amount of water that seeds can absorb to produce saturation, the seed continuing to take up water long after it has failed to germinate (pp. 43-45).

(19) In the next place, reference is made to the case of excessive swelling in abnormally shrunken resting seeds where the absorbing process is compensatory, the unusual loss of water in the shrinking process being thus supplied. But such seeds, whether in the normal condition permeable or impermeable, have lost their germinative powers, and as such have no concern for us here. Seeds that shrivel much, absorb much, but do not as a rule propagate the species. This is usually the fate of seeds that are removed from the green pod in the soft, full-grown pre-resting state before shrinking has begun. But with impermeable seeds it sometimes happens that such seeds shrink less when allowed to go through the shrinking process detached from the plant than when left undisturbed in the pod. If we wait until shrinking has just begun before detaching the seed from the plant, this deficiency in the shrinkage is the rule. Such seeds retain their germinative powers, but their shrinking has been deficient; and, according to the compensatory principle that what the shrinking seed loses the swelling seed gains, their capacity of absorbing water for germination is proportionately reduced. They are larger and heavier than the normal impermeable seeds, and take up water easily (p. 46).

(20) When, therefore, we come to appeal to cases of unusual diminution of the swelling capacity in resting seeds, we find that examples are only supplied by abnormal impermeable seeds. Here the shrinking process is incomplete, and in consequence less water is required for germination than in the normal resting seed. This unexpected contrast between the behaviour of permeable and impermeable seeds when

they are detached in the soft pre-resting state from the green pod, and allowed to go through the shrinking process removed from the parent, brings us face to face with the significance of the impermeability of seeds. A great deal lies behind the fact that under such conditions with a permeable seed the shrinking is too great and the subsequent swelling for germination excessive, whilst with an impermeable seed the shrinking may be deficient and the swelling ratio much reduced (p. 47).

(21) Illustrations of the behaviour of impermeable seeds in this respect are afforded by those of *Guilandina bonducella* and *Dioclea reflexa*, where deficient shrinkage of the large, moist pre-resting seeds leads to a corresponding decrease in the normal swelling capacity and to the loss of impermeability; and by those of *Entada polystachya*, which displays in its two types of normal seeds, permeable and impermeable, a small shrinking capacity and a small swelling ratio for the first, and a large shrinking capacity and a large swelling ratio for the second (pp. 47-51).

(22) Experiments on seeds of the impermeable type in their soft pre-resting condition therefore indicate that a diminution of the shrinkage prevents the acquirement of impermeability and at the same time lessens the amount of water required for germination. This strange relation between the amount of water a seed absorbs in preparing for germination and the permeability or impermeability of the seed-coverings renders necessary an investigation of the distinctive characters associated with these two types of seeds. The question of permeability and impermeability, therefore, blocks the way (p. 52).

CHAPTER III

THE IMPERMEABILITY OF SEEDS AND ITS SIGNIFICANCE .

THE impermeability of seeds has occupied the attention of many able investigators, but usually in connection with some other character. They have not, however, always been in agreement as to the meaning to be attached to the term "impermeable," a fundamental difference which is reflected in their occasionally inconsistent conclusions. In this work a seed is regarded as impermeable only when it is able to resist the penetration of water during an immersion of weeks or months.

Nature supplies abundant evidence of the impermeable character of certain seeds in the floating drift of ponds and rivers and of the ocean currents ; and many inquirers in their observations and experiments on seed-buoyancy have dealt indirectly with this subject ; but as it would be out of place to allude to their results here, I would refer the reader for a detailed treatment of the matter to my book on *Plant Dispersal*. It should, however, be remarked that impermeability may be equally a quality of the seed that sinks and of the seed that floats, its connection with buoyancy being only of an indirect character.

I will at once proceed to deal with some of the aspects of the subject, on which recent investigations have thrown light. The frequency of impermeability in the case of seeds of certain families, especially among the Leguminosæ, was established by Nobbe a generation ago in the pages of his work on

The frequency of impermeability.

seeds, *Handbuch der Samenkunde*; and he it was who pointed out that even with plants where all the seeds seemed to be permeable, there might be a small residuum of 2 or 3 per cent. that continued to resist the penetration of water even after some months' immersion (pp. 112, 113). But this botanist made no special study of the subject, except in so far as it was in relation to other seed-characters.

It is to a recent Italian investigator, Dr Guiseppe Gola, that we are indebted for an extensive series of studies of the nature and prevalence of this quality. His memoir, which is entitled *Ricerche sulla biologia e sulla fisiologia de Semi a tegumento impermeabile*, and which was published by the Royal Academy of Sciences of Turin in 1905, will come as a surprise to many who, like myself, were unaware that impermeable seeds are so frequently to be met with in the plant-world. Although not able to follow him in all his conclusions, I have found in his data the materials for a solid foundation on which to begin in these pages a discussion of the subject of impermeability.

After ascertaining by a preliminary inquiry that this character was exhibited most markedly by the seeds of Leguminosæ and then by those of Cistaceæ and Malvaceæ, Dr Gola decided to limit his researches to those three families. His method was well adapted to test the capacity of seeds in this respect, since they were kept immersed in water for periods of between thirty and eighty days. When swelling occurred, it took place generally in from three to five days, and less usually in about ten days. Impermeable seeds remained unaffected at the end of the trials. The seeds of about 300 species of plants were exposed to this test, of which about 260 (belonging to 45 genera) were leguminous, whilst nearly 30 belonged to the Cistaceæ, and 10 were malvaceous. Temperate genera greatly predominate in his list of results, not merely numerically, but also in the number of species tested. Including the Acacias, we may here mention the genera *Astragalus*, *Cytisus*, *Genista*, *Lathyrus*, *Lotus*, *Medicago*, *Melilotus*,

Its investi-
gation by
Dr Gola.

Trifolium, *Vicia*, etc. As a rule between 50 and 100 seeds of each species were experimented on, and the percentage of permeable seeds is recorded in a special table.

On tabulating the results given by Dr Gola for the Leguminosæ and Cistaceæ in the manner shown below, I was surprised to learn how common it was to find permeable and impermeable seeds in the same species.

TABULATION OF THE RESULTS FOR THE LEGUMINOSÆ AND CISTACEÆ GIVEN BY DR GOLA IN HIS TABLE SHOWING THE PERCENTAGE OF PERMEABLE SEEDS IN THE SAME SPECIES.

	Number of species.	Species with no seeds permeable.		Species with all seeds permeable.		Species with both permeable and impermeable seeds.	
		Number.	Per-centage.	Number.	Per-centage.	Number.	Per-centage.
Leguminosæ .	260	17	7	40	15	203	78
Cistaceæ . .	27	0	0	0	0	27	100

Permeable and impermeable seeds commonly found in the same species.

We see here that 78 per cent. of the species of Leguminosæ possessed both permeable and impermeable seeds, those with all seeds impermeable or with all seeds permeable amounting to 7 and 15 per cent. respectively. The proportions of each kind of seed in a species were in most cases fairly constant, the results for two different samples being as a rule not far apart. Within the limits of a genus the species exhibited great contrasts in their proportions of permeable and impermeable seeds. Almost all the leguminous genera that are best represented in Dr Gola's table show variations ranging between the two extremes: (a) of species with all seeds permeable, and (b) of species with all or nearly all seeds impermeable, none containing exclusively species possessing one type of seed. Not one of the leguminous genera which are here represented by ten or more species could be designated as exclusively characterised by permeable or impermeable seeds.

All are variable or "mixed" in this respect. It would thus appear from the results of the investigations of Dr Gola that impermeability with the Leguminosæ is not usually a distinction between species, and hardly ever between genera.

But although the leguminous genera best represented in the table of Dr Gola are "mixed" in the sense that not one of them can be described as exclusively possessing species with one type of seed, they may differ in degree considerably from each other. The average proportions of permeable and impermeable seeds for the species of the three genera, *Acacia*, *Astragalus*, and *Lathyrus*, are given below; and from the tabulated results it appears that in order of impermeability *Acacia* stands first, with an average of 83 per cent. for a species, and *Lathyrus* last, with an average of 20 per cent.

Impermeability not a generic character, though more characteristic of some genera than of others.

AVERAGE NUMBER OF PERMEABLE AND IMPERMEABLE SEEDS IN THE SPECIES OF THREE LEGUMINOUS GENERA. (Tabulated from data given in Dr Gola's Memoir.)

	Number of species tested.	Average percentage for a species.	
		Permeable seeds.	Impermeable seeds.
<i>Acacia</i> . . .	20	17	83
<i>Astragalus</i> . . .	43	35	65
<i>Lathyrus</i> . . .	20	80	20

In the same way, with regard to species of Leguminosæ, it would seem that although as a rule, that is in 80 per cent. of the plants, we cannot employ the presence or absence of impermeability in the seeds as a specific distinction, yet species differ very much in the proportion of impermeable seeds that they possess.

Such, then, are the preliminary conceptions with reference to impermeability that one forms from the data obtained by Dr Gola. These conceptions will be considerably extended

as one follows the trend of still more recent investigations. However, I pass over for a time the results of the brilliant researches of Paul Becquerel, carried out in the laboratory of the Sorbonne between 1904 and 1907, because in as far as they deal with matters discussed in these pages they are primarily concerned with the impermeability of seeds to air, and will be more appropriately referred to in the chapter on the hygroscopicity of seeds.

The re-
searches of
Becquerel.

Mr Crocker
on the asso-
ciation of im-
permeability
with the
longevity of
seeds.

In following the history of the investigation of this subject from the data at my disposal, the next advance on solid ground seems to be that supplied by the results obtained by Mr Crocker. If Dr Gola opened our eyes as to the frequency of impermeability in the seed-world, Mr. Crocker has done much to enlighten us as to its biological significance. In different papers published in the *Botanical Gazette* (University of Chicago Press, 1906-9) he expresses the opinion that "delayed germination," or, as we might term it, "seed-longevity," is more generally due to seed-coat characters "limiting or entirely excluding water or oxygen-supply" than to embryo characters or the "so-called dormancy of protoplasm." His results go far to establish the view put forward by Nobbe and Hänlein in 1877, and quoted by him, that "delayed germination is due in many cases to the impermeability of the seed-coat to water." One of his papers ("Rôle of Seed-coats in Delayed Germination," October 1906) is concerned especially with this point; but he repeats the general conclusion formed, as above given, in a later paper ("Germination of Seeds of Water-plants," November 1907), and in a short article in the same publication in January 1909. It may be remarked before concluding this reference that Mr Crocker regards impermeability to water as much more conducive to seed-longevity than imperviousness to oxygen (*ibid.*, October 1906); and this is the point that is of most interest to us in the present stage of this discussion. "The coats that exclude water" (he writes) "are undoubtedly much better adapted to securing a long delay."

It is to Professor Ewart of the University of Melbourne that we are indebted for a most important contribution to our knowledge of seed-longevity and of the impermeability of the seed-coverings. If the author had had the leisure to extend the explanatory portion of his memoir, it would have ranked as one of the most extensive records of investigations concerned with seeds since De Candolle published his *Géographie botanique* rather over half a century ago. Dr Gola and Mr Crocker, as far as the dates of publication are concerned, were his predecessors in the field ; but it would be probably more correct to say that they were contemporaries in their labours. Professor Ewart, like Dr Gola, discusses the distribution of impermeability in seeds, and, like Mr Crocker, he considers the relation between longevity and impermeability. But on this point the two investigators in America and Australia seem to diverge widely, Mr Crocker holding that "delayed germination is generally related to seed-coat characters rather than to the so-called dormancy of protoplasm," whilst Professor Ewart considers that longevity depends not on the seed-coats, but on the staying power of the protoplasm. The difference, however, is more apparent than real, since Professor Ewart evidently regards the impermeable covering as an adaptation for ensuring the long life of the seed in the soil ; and at all events it would seem likely there is enough common ground on which to base a theory that would reconcile both the views.

In this memoir on "The Longevity of Seeds," which was published in the *Proceedings of the Royal Society of Victoria* for 1908, he deals with the seeds of about 2500 species of plants. In addition to the results of his own work, which involved the employment of nearly 3000 tests, Professor Ewart incorporates in his table, which in itself occupies 176 pages, all the previous records relating to the subject that he could find. Yet, in spite of the great importance of this contribution to knowledge, one is conscious of missing much in the 22 pages that are alone devoted to the summarising of results,

The investigations of
Prof. Ewart.

since a very large amount of interesting, if subsidiary, matter finds no expression either in the table or in the text.

The relation between impermeability and longevity.

Professor Ewart arrives at the conclusion that "macrobiotic" seeds (as he terms seeds that may last from 15 to over 100 years) are characterised by "more or less impermeable coats, and are restricted to a few natural orders, of which the Leguminosæ greatly surpass all others, whilst Malvaceæ and Myrtaceæ come next in importance." The general trend of the curves, he remarks, indicates that the extreme duration of vitality, probable for any known seed, lies between 150 and 250 years. The number of species in the list of plants characterised by macrobiotic seeds amounts to 180, which is less than 1 per cent. of the total number of species experimented upon; and of these about 75 per cent. are leguminous. Sixty per cent. or 30 out of the 50 species of *Acacia* included in the general table possess these long-lived seeds; and since impermeability and longevity are so closely associated in this genus, we may recall here the high average of impermeability assigned above to seeds of species of *Acacia* from data supplied in Dr Gola's tabulated results. There is naturally no attempt here to deal with the general question of impermeability, except in its relation to longevity; and the method of stating the results in the table rarely allows me to draw such inferences for myself with security. Still, some general principles of much importance are indicated in the text and in the table; and they may be here alluded to.

Impermeability as an adaptation to soil-conditions.

In the first place, as was previously implied by Mr Crocker, the impermeability of seeds to water exhibits itself as an adaptation for ensuring the long life of the seed in the soil. It is not essential for securing the longevity of seeds in air. Professor Ewart points out that some seeds with readily permeable coats, such as those of species of *Phaseolus* and *Triticum*, may retain their vitality for many years in dry air. This being the case, it follows that the experiments, based as they chiefly are on seeds that have been kept in dry air for a varying number of years, are mainly concerned with the

longevity of seeds under those conditions. The question whether impermeable seeds will preserve their vitality longer in the soil seems to be as yet unanswered. Although, as quoted in this paper, Duvel has shown that in the case of ordinary seeds the advantage lies with seeds dried in air, he did not determine this point for the hard seeds that did not germinate in his experiments, apparently, as Professor Ewart observes, because he did not employ methods that would fully test their germinative capacity. Commenting on the results of the extensive experiments of Duvel and Waldron to determine the length of time weed-seeds must be buried in order to lose their vitality, Crocker points out that "vitality tests of this kind, that neglect the effect of the seed-coats, are tests of the condition of the seed-coats rather than tests of the real vitality of the embryos themselves" (*Botanical Gazette*, October 1906). In this connection the testimony of Professor Pammel of Iowa is significant. As concerning the seeds of a number of weeds, he found that the percentage of seeds germinating was lower and the dormant period longer if the seeds were kept during the winter in paper packages than if they were placed in sand and exposed to the climatic conditions of an ordinary winter (*Brit. Assoc.*, 1909, "Nature," October 28, 1909).

The question whether impermeable seeds will preserve their vitality longer in the soil than in the air.

It is nevertheless evident from the Australian observations that even the most resistant of seeds tend to lose their impermeability in the course of years when kept in dry air. With the loss of this quality the seed is not necessarily deprived of its power of retaining its vitality for a longer period, since typically permeable seeds, as has been already remarked, may preserve their germinative capacities for many years. It, however, is deprived of the power of prolonging its existence in the soil; and in consequence it either germinates or dies. How long a seed with impermeable coverings could remain alive when buried deeply in the soil, it would be extremely difficult to determine with accuracy. But it is apparent from Professor Ewart's own observations that under the conditions of undisturbed primeval forest in Australia they might lie buried in the

soil for very long periods without losing their impermeability. Under such conditions he found that all *Acacia* seeds found below the surface possessed impermeable coats and required special treatment to produce swelling and germination.

Whether or not the seeds always retain their vitality when they preserve their impermeability is another matter, since longevity, as Professor Ewart observes, may not depend primarily on the impermeability of the seed-coats, but on a peculiar inherent property of the protoplasm, the duration of which under the soil is secured by the impermeable coverings. Seed-longevity would seem therefore to be determined by two independent eventualities, the limit of the impermeability of the coats and the limit of the staying power of the protoplasm of the kernel or embryo; and the question arises as to which lasts the longest. Amongst the results of Professor Ewart's experiments it is easy to find cases where impermeability has survived its utility; but it would be hazardous to assert that this is the usual course of events under the soil. This method of stating the problem seems to be the best way of reconciling the views of Mr Crocker in America and Professor Ewart in Australia.

An important outcome of these two series of investigations is that the issues can be narrowed, thus permitting one to distinguish between the extrinsic and the intrinsic in the results of experiments. Results applicable to the behaviour of the seed in air are in a sense extrinsic, since such are not the usual conditions under which Nature tests its longevity. Those that can be brought into some kind of relation with the seed as it occurs naturally in the soil are likely to be the most instructive. Two questions, it would seem, have shaped themselves whilst considering these results.

The first is: Under which conditions would an impermeable seed retain its vitality longest, in the air or in the soil? The second is: Which has the greatest staying power, the impermeability of the seed-coats, or the germinative capacity of the kernel? Notwithstanding the evidence before us, the answer to both of them is indeterminate.

Seed-longevity determined by the limit of the impermeability of the coats and by the limit of the staying power of the embryo.

The two chief issues raised by the investigations of Mr Crocker and Prof. Ewart.

There are, however, one or two points to which further reference might be made. Thus, to take the first query, it may be replied that even in the case of the most impermeable seeds the effect of being kept in the dry air of a room for many years would be undoubtedly to favour the development of small cracks in the outer covering, thus converting them by degrees into permeable seeds. My observations on the seeds of *Entada scandens* (Chapter X) will go to show how this could be brought about. We can thus perceive how much less likely it is that impermeable seeds exposed without protection to the weather could withstand year after year the alternating conditions of heat and cold, of sun and shade, of drought and humidity, which in one form or another they would experience whatever their situation. In an elaborate series of experiments, in which he reproduced the extreme changes between moist and dry conditions and between heat and cold in various shapes, such as an ordinary climate would present, Dr Gola found that the seeds lost their impermeability. To come to a matter of my own observation, it is doubtful whether any of the numerous impermeable seeds washed up on tropical beaches could withstand for many years exposure to the sun and rain. All of them would show sooner or later signs of wear and tear in the injuries to the outer coats.

On the other hand, buried in the soil, the seed would be more or less safeguarded against the risks to which a seed lying on the ground would be exposed. But the degree of protection would vary with the depth below the surface, so that the seed deepest down, as shown by Duvel, Crocker, and Ewart, would have the longer life. At the same time new dangers might arise; but on the whole it seems likely that under such favouring conditions as characterise the typical Australian forests, the buried seed might retain its impermeability for much longer periods than when kept dry in cupboards or in botanical museums.

But this raises again the second question whether the germinative capacity would be similarly retained. Of this it

may be said that we shall probably be never quite secure in our interpretation of Nature's experiments in this direction. But this insecurity does not invalidate the testimony altogether; and it scarcely seems prudent to ignore altogether the accumulation of evidence respecting the high antiquity of "germinable" seeds found in ancient graves or when an old soil is disturbed.

With regard to the little value of negative evidence in such an inquiry, I point out in the next chapter that we can never be certain that the failure is due to the incapacity of the germinative powers and not to the method employed. Both Crocker and Ewart are emphatic on the point that it would require more evidence than was deemed necessary by the earlier investigators to convince us that the cause of the failure to respond by germination to the call of their experiments lay always with the seeds. I venture to think, and here I am supported by a considerable amount of evidence given in the succeeding chapters, that the truest test of the potential vitality of an impermeable seed is to be found in the constancy of its weight under all ordinary conditions and under the influence of time. If a seed with sound coats gained nothing in weight after weeks of immersion in water, made no response to the varying hygrometric changes of the atmosphere, and preserved the same weight for a number of years, I would presume its germinative soundness, whatever its previous history or whatever its attested antiquity.

Not the least important part of Professor Ewart's memoir is the account given by Miss White in an appendix of the results of her investigation of the structure of coats of impermeable seeds. After making a microscopical examination of the coats of nearly seventy species of impermeable seeds which had been the subject of Professor Ewart's inquiry, she formed the following conclusion:—"As a general rule in small and medium-sized seeds the cuticle is well developed, and represents the impermeable part of the seed-coat; whilst in the case of large seeds, such as those of *Adansonia Gregorii*, *Mucuna gigantea*, *Wistaria Maideniana*, and *Guilandina bonducella*, the

The little value of negative evidence.

The seat of impermeability.

cuticle is extremely unimportant and inconspicuous. In these seeds the extreme resistance which they exhibit appears to be located in the palisade cells." . . . The circumstance that the seat of the chief resistance to the penetration of water may lie in large seeds in the deeper tissues may explain how Dr Gola comes to consider that this is the rule for impermeable seeds. Miss White's investigations, however, establish the fact that the seat of impermeability lies for most seeds in the structureless cuticle, a conclusion previously indicated, but on less extended grounds, by the inquiries of Nobbe and by those of Bergtheil and Day.

SUMMARY

(1) The frequency of impermeability in seeds of certain families, especially of the Leguminosæ, which was first indicated by Nobbe a generation ago, has within the last few years been established by Gola, an Italian investigator. His results bring out the facts that, though more typical of some genera than of others, impermeability is not a generic character, and that it is rarely even a specific character, since both permeable and impermeable seeds are commonly found in the same species (p. 57).

(2) Another of the inferences of Nobbe that delayed germination is due in many cases to the impermeability of the seed-coverings to water has been confirmed and extended by the recent researches of Crocker in America. After this point, questions affecting seed-impermeability usually resolve themselves into matters concerning seed-longevity. Crocker rejects the idea that a seed's long life is as a rule to be attributed to embryo characters or to the dormancy of protoplasm (p. 60).

(3) However, Ewart in Australia, after very extensive researches, arrived at the conclusion that the longevity of seeds depends not on their coverings, but on the persistence of the protoplasmic constitution of the embryo or kernel; and he views impermeability of the coats as an adaptation for ensuring the long life of the seed under soil-conditions (p. 61).

(4) Of the 2500 species (more or less) with which Ewart deals, either directly or through the observations of others, rather less than 1 per cent. are long-lived seeds that will retain their germinative capacity from fifteen to one hundred years and over. Of these "macrobiotic"

seeds all possess more or less impermeable coats, and three-fourths are leguminous (p. 62).

(5) It is suggested in this chapter that seed-longevity should be regarded as determined by two factors, represented in the impermeability of the coats and in the persistence of the protoplasmic constitution of the embryo-kernel (p. 63).

(6) It is also suggested that, accepting impermeability as an adaptation to soil-conditions, we should leave to the future investigator these two points to determine: (a) whether the impermeable seed would retain its germinative capacity longer in the soil than in the air; (b) as to the relative durability of the impermeability of the seed-coats and the germinative capacity (p. 64).

(7) Recent investigators lay stress on the fact that negative results obtained by earlier investigators in testing the persistence of the germinative powers of hard seeds were more probably due to their inacquaintance with the right methods of procuring germination than to failure on the part of the seeds (p. 66).

(8) Whilst considering that a combination of the theories of Crocker and Ewart would present the best working hypothesis, the author is inclined to the view that the most practical tests of the potential vitality of an impermeable seed are to be found in the constancy of its weight under all ordinary conditions and in the lapse of years. He would presume the germinative capacity of such a seed, whatever its antiquity, provided, as has just been implied, that its coats are sound, that it absorbs no water, and that it makes no response by alterations in its weight to the varying hygrometric states of the air. The author also does not regard it as prudent to ignore altogether the accumulation of evidence respecting the great age of "germinable" seeds found in ancient graves or when an old soil is disturbed (p. 66).

(9) Lastly, the opinion of Nobbe and of later investigators that the seat of impermeability lies in the outer coverings of the seed has been confirmed by the results of the recent researches of Miss J. White, who places it in the case of small seeds in the cuticle and with large seeds often in the outer palisade cells (p. 66).

CHAPTER IV

PERMEABLE AND IMPERMEABLE SEEDS

THE observations and experiments on the results of which the four following chapters are based cover the period of 1906 to 1911. They were practically completed, and the greater part of the results elaborated and written out, before the works of other investigators had been consulted. In this condition they have been in the main reproduced in these pages, as I thought it best that they should tell their own story, my original purpose having been to make an independent study of the impermeability of seeds without being influenced by the ideas of others. That has been done; but in the final summing up of my own results I have been guided in the estimate of their value and in the drawing of my conclusions by the results obtained and the opinions formed by other inquirers.

In order to introduce the subject and to give method to the arrangement of the results of a large number of observations and experiments, I will take the very divergent behaviour, as revealed by the balance, of the seeds of two leguminous plants, *Guilandina bonducella* and *Canavalia ensiformis*. The first named has a very hard grey seed of the size and form of a marble, weighing usually about 40 grains, and possessing very thick coats. The second has a thin-skinned white seed, about 20 millimetres long, weighing 20 to 25 grains, and typical of a large number of leguminous plants. (See Note 5 of the Appendix.)

Comparison
of the seeds
of *Guilandina*
bonducella
and *Canavalia*
ensiformis,

(a) as regards their permeability,

On placing these two seeds in water we obtain very different results. That of *Guilandina bonducella* absorbs no water and preserves its original weight after an immersion of many months or even years. On the other hand, the seed of *Canavalia ensiformis* begins to swell in a few hours, and within twenty-four hours has doubled its weight. One seed, therefore, is impermeable or waterproof, whilst the other is permeable. But this difference in behaviour is associated with a difference in other qualities. If we weigh the seeds daily for a week or two, employing a quartz pebble as a standard of comparison, we observe that the seed of *Guilandina bonducella* behaves exactly like the pebble and keeps its weight to within a small fraction of a grain. The seed of *Canavalia ensiformis*, on the contrary, varies considerably in response to the daily changes in the atmospheric humidity, the amplitude of its variations amounting to 2 or 3 per cent. of its average weight. One seed, therefore, behaves hygroscopically, and the other does not. As might have been expected, it is the impermeable seed of *Guilandina bonducella* that is non-hygroscopic, whilst with the seed of *Canavalia ensiformis* permeability and hygroscopicity go together. When extending the weighing observations over twelve months, we find the same features of difference displayed. Whilst the *Guilandina* seed maintains its weight unchanged, the *Canavalia* seed continues to exhibit the same hygroscopic variations. If we were to represent these results in a diagram, we should denote the behaviour of the seed of *Canavalia ensiformis* and that of the *Guilandina* seed by a horizontal line. The line of the last named would be even, but that of the *Canavalia* seed would display numerous zig-zag irregularities, marking the hygroscopic responses of the seed. It is essential to understand that we are here dealing with seeds that have completed their spontaneous drying in air. Where the shrinking and drying process is unfinished quite other influences come into play.

(b) as regards their hygroscopicity.

Up to this point we have been dealing with the seed in its coats. But if we remove these coverings we find another singular contrast in the behaviour of these two seeds. In the instance of *Canavalia ensiformis* we discover that it makes no essential difference whether we employ the seed in its coverings, or puncture it through its coats, or deprive it of them altogether. In any case the same average weight is maintained, the baring of the kernel or puncturing of the coats merely resulting in a small increase of the hygroscopic range. Whatever may be the function of the coats of a permeable seed, they do not prevent it from responding from day to day to the variations in the atmospheric humidity, though they may regulate the process. This would seem to be true of the large majority of similar seeds, and it follows naturally from the permeable character and the hygrometric behaviour of the seed-coverings. (See Note 6 of the Appendix.)

The influence of the seed-coats on the changes in the seed's weight,

(a) in the case of a permeable seed,

In the table below I have given the results of simultaneous observations on the bared, punctured, and entire seeds of *Canavalia ensiformis* collected from the plant at the same time. The table explains itself, except that one may add that the hygroscopic or hygrometric variation is the range of the changes in weight exhibited in the course of two or three weeks stated as a percentage of the total weight.

COMPARISON OF THE BEHAVIOUR OF THE SEEDS OF CANAVALIA ENSIFORMIS WHEN BARED, PUNCTURED, AND ENTIRE.

Condition of seed.	Hygroscopic variation.	Loss of weight in two years.
Entire in its coats	2.5 per cent.	Nil.
Punctured through its coats	3.0 " "	" "
Bared of its coats	4.0-4.5 per cent.	" "

If we repeat these experiments with the seeds of *Guilandina bonducella*, and either remove the hard, impermeable, shell-like coats or pierce them with a file, we obtain results of quite a

(b) in the case of an impermeable seed.

different nature. A sample of the bared kernels weighing 100 grains immediately after the removal of their shells will be found after a period of four or five days to have increased its weight to 111 or 112 grains. The gain in weight begins as soon as the hard coats are removed; and thus my materials became sensibly heavier whilst in preparation for the balance. In one case, for instance, a sample of 500 grains weighed 503 grains after an hour occupied in preparing it for an experiment. This increase in weight is maintained, although in a diminished degree, for a long period. In fact, the bared kernel never returns to the weight it possessed when enclosed in its impermeable coverings. As is shown in the table below, after a period of a year and more, it is still 3 or 4 per cent. in excess of its original weight.

RESULTS OF THE EXPOSURE TO AIR OF THE BARED KERNELS OF
GUILANDINA BONDUCELLA. (WEIGHT IN GRAINS OF SIX KERNELS
AT VARIOUS PERIODS.)

Immedi- ately after being bared of their shells.	After 5 days.	After 20 days.	After 3 months.	After 6 months.	After 16 months.	After 20 months.	After 26 months.
100	113'4	111'0	107'3	107'0	103'0	103'3	104'4

The explanation, of course, is simple. The kernel when bared, being in a state of ultra-dryness, supplies its deficiency by absorbing water from the air. In so doing it has changed its nature and now responds to the hygrometric variations of the weather, behaving in fact like the kernel of a permeable seed. We have here, then, the disclosure of another striking character distinguishing impermeable seeds, such as those of *Guilandina bonducella*, from permeable seeds, like those of *Canavalia ensiformis*.

This curious quality has been exhibited in varying degrees

The dis-
closure of
the ultra-
dryness of
impermeable
seeds.

by the bared kernels of nearly all impermeable seeds that have been subjected to this test. The dry friable kernels when coarsely broken up contrast greatly in their appearance with the relatively moist and compact materials of permeable seeds; and hence it could be presumed without further inquiry that absorption of water-vapour from the air is the cause of the subsequent increase in weight. But this capacity in seeds of becoming considerably heavier when exposed to the air than when locked up in their impermeable coats pre-supposes a condition of ultra-dryness within the seed itself. We should thus expect that the seeds of *Guilandina bonducella*, as types of impermeable seeds, would contain much less water than typical permeable seeds, such as those of *Canavalia ensiformis*.

We have accordingly to appeal to the evidence of the oven in order to interpret the indications of the balance; and in the table now to be given are to be found the results of exposing these two kinds of seeds to a temperature of 100° to 105° C. for a period of from one and a half to two hours.

An appeal to the evidence of the oven.

WATER-CONTENTS OF A TYPICAL PERMEABLE AND A TYPICAL IMPERMEABLE LEGUMINOUS SEED AS ASCERTAINED BY EXPOSURE TO A TEMPERATURE OF 100° TO 105° C. FOR 1½ TO 2 HOURS.

	Character of seed.	Number of experiments.	Average water-contents.	Range of result.
<i>Canavalia ensiformis</i> .	Permeable	4	16 per cent.	14 to 18 per cent.
<i>Guilandina bonducella</i> .	Impermeable	5	8 ,,	6 to 10 ,,

Note.—These results represent the combined water-contents of kernel and coats. have omitted decimal fractional parts, as these values are dealt with in later chapters.

These results establish the ultra-dryness of the seed of *Guilandina bonducella* enclosed in its impermeable coverings; and we recognise in the absorption of water-vapour from the air by the bared seed an attempt to assume the condition of a permeable seed. As far as their water-contents are concerned,

permeable hygroscopic seeds are, relatively speaking, in a state of saturation, or perhaps it would be more correct to say in a state of equilibrium, with regard to the moisture of the air. On the other hand, impermeable seeds like those of *Guilandina bonducella* stand in no such relation to the atmosphere, and preserve their abnormally dry condition independently of any atmospheric changes. When, by the removal of their coverings, such seeds have been deprived of their power of resisting the permeation of water, either as vapour or as liquid, they rapidly supply their deficiency by absorbing it from the air. Roughly speaking, the amount of water regained from the air by the bared seed of *Guilandina bonducella* represents the deficiency in its water-contents, as compared with the bared seed of *Canavalia ensiformis*, or, in other words, the price of its impermeability.

As regards their water-contents and other characters diagnostic of permeable seeds, the seeds of *Canavalia ensiformis* may be placed with our edible leguminous seeds, such as Peas, Broad Beans, Scarlet-runners (*Pisum sativum*, *Faba vulgaris*, *Phaseolus multiflorus*), which usually contain 15 or 16 per cent. of water. But the low percentage of water in the seeds of *Guilandina bonducella* appears quite abnormal when compared with the data given in the ordinary tables of the analyses of seeds used as food, though representative of impermeable seeds. Rice, Maize, Wheat, and other cereal grains, for the most part permeable, contain from 12 to 15 per cent. of water, whilst the flour yielded by them holds 11 or 12 per cent.

Up to this point the indications appear to be sufficiently plain, though the subject gives promise of much complexity. But now comes another curious fact. Whilst the coats of a permeable seed like that of *Canavalia ensiformis* behave hygroscopically when removed from the seed, neither increasing nor decreasing their previous average weight, it is very different with the impermeable seed.

The detached shell-like coverings of the seed of *Guilandina bonducella* possess the same quality of ultra-dryness and display the same absorptive capacity in air as the bared kernel, though to a less degree. They exhibit the relation between the water-contents which we might have expected, the larger water-percentage of the seed-coverings being associated with a smaller absorptive capacity in the air as compared with the kernel. These qualities are well brought out in the tabulated results given below of an experiment in Grenada in which the shell and the kernel of several seeds were equally divided in each case between two samples, so that the air exposure and oven-tests were applied to truly mixed samples. It may here be added that, as in the case of the kernels, the detached shell retains its excess for a long period, though in a diminishing ratio. In one experiment, after a lapse of twenty-one months it still weighed 6 per cent. heavier than when first removed.

The shell or covering of the seed of *Guilandina bonducella* has the same quality of ultra-dryness and the same absorptive capacity as the kernel.

COMPARISON OF THE ABSORPTIVE CAPACITIES IN AIR WITH THE WATER-CONTENTS OF FRESHLY BARED KERNELS AND OF THE DETACHED SEED-SHELLS OR COVERINGS OF *GUILANDINA BONDUCELLA*, THE SAMPLES BEING TRULY MIXED, AS ABOVE DESCRIBED.

	Gain in weight after exposure to the air for 4 days.	Original water-contents as determined in the oven.
Seed-shells . . .	12'0 per cent.	7'6 per cent.
Kernels . . .	16'2 ,,	4'2 ,,

We are thus brought face to face with the curious circumstance that if we break open one of the seeds of *Guilandina bonducella* and allow it to remain in this condition for a few days it will increase its weight on the average by 11 or 12 per cent. It is essential to break through the seed-shell, it being immaterial whether the shell is in a few or in many pieces, or whether the kernel is left whole or in fragments.

The same result is produced by puncturing or filing through the shell, though, as shown in the results tabulated below, the change is much more gradual. Here the total increase of weight is the result of the combined absorptive capacities of the kernel and its coverings.

The same effect is produced by puncturing or filing through the shell, though, as shown in the results tabulated below, the change is much more gradual. Here the total increase of weight is the result of the combined absorptive capacities of the kernel and its coverings.

RESULTS OF FILING INTO THE SHELL OR HARD COVERING OF THE SEEDS OF *GUILANDINA BONDUCELLA*, STATED AS A PERCENTAGE OF THE ORIGINAL WEIGHT OF THE SEEDS (34 TO 35 GRAINS).

	Original weight.	After 2½ weeks.	5½ weeks.	2 months.	4½ months.	12 months.	16 months.	18 months.	21 months.	24 months.
*A seed with shell intact	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0
†A seed filed halfthrough its shell	100·0	105·8	108·2	108·5	110·4	106·6	106·9	108·3	108·0	107·2
†A seed with kernel exposed by filing	100·0	106·9	109·1	109·2	111·0	107·0	107·3	108·8	108·5	107·8

* The seed with shell intact, weighing originally 35·06 grains, varied only between 35·04 and 35·08 grains during the period.

† After the experiment both germinated readily in 4 to 5 days, and produced healthy plants.

By comparing the changes which these seeds experienced in the first three or four months we find :—

- (a) That the seed with shell intact varied only at the rate of $\frac{1}{1000}$ of its weight during these twenty-four months, a result probably instrumental and too small to be noted in the table ;
- (b) That the seed with shell filed halfway through gained 10·4 per cent. in weight ;
- (c) That the seed with its kernel exposed by filing through into the seed-cavity gained 11 per cent.

I shall have to return again to this subject when further discussing these matters in Chapter VI ; but some additional remarks may here be made.

In the first place, the only impervious portion of the seed-shell is the outer skin and the hardened tissue immediately beneath it, but little effect being produced by merely filing the cuticle. If we file through this outer impervious portion, it makes but little difference in the subsequent behaviour of the seed whether we expose the kernel or file only half through the shell.

In the next place, it should be noted that whilst the freshly bared seed gains its maximum weight by imbibing moisture from the air in a few days, the filed seeds occupy some months in reaching their greatest weight. They then remain at about the same average weight and behave like permeable seeds in their response to the hygro-metric variations of the atmosphere. But the most noteworthy feature in the behaviour of these filed seeds is that they retain their germinative capacity after two years in this condition.

In the third place, the behaviour of the filed impermeable seeds of *Guilandina bonducella* may be contrasted with that of the permeable seeds of *Canavalia ensiformis*, where, as before described, the effect of puncturing the seed-coverings is merely to increase to some degree the hygroscopic variation.

Such, then, is the contrast in the behaviour between permeable and impermeable seeds as described in the case of two type seeds in the previous pages. The principal differences are there outlined to a sufficient extent for this introductory notice of my observations on this subject. But there still remain some interesting features in the absorptive capacity of impermeable seeds to be noticed and some general reflections to be made before this chapter is brought to a close.

An accident led me to the discovery of another singular quality of impermeable seeds, one that probably could have been foreseen, had the successive stages of this inquiry followed the order adopted in this chapter. However, it was this

Exposure to a temperature of 100° C. does not prevent a bared impermeable seed from increasing its original weight by absorbing water-vapour from the air.

accident that first disclosed to me the ultra-dryness of impermeable seeds. After weighing a sample of kernels of *Guilandina bonducella* which had just been exposed in the oven for a short time to a high temperature and had lost 8 per cent. of its weight, I unwittingly left it over-night in the pan of the balance, and was surprised to find that it was between 1 and 2 per cent. heavier than before it was placed in the oven. During the night it had regained all the water driven off by heat and something more.

The results of numerous oven-experiments on this and other impermeable seeds go to make it evident that the capacity of such a seed to considerably increase its weight when exposed in a broken condition to the air is but little affected by first subjecting the material to a temperature of 100° to 105° C. for an hour or two. If, to take an actual case, a seed on being broken up increased its weight after three or four days' ordinary exposure on my table from 100 to 113 grains, it made but little ultimate difference whether or not its weight had first been reduced to 93 grains through the loss of water in the oven. I will here appeal again to the behaviour of the seeds of *Guilandina bonducella*, reserving for a subsequent chapter the detailed treatment of this matter as regards other impermeable seeds.

There are given below the results of two actual experiments, the first in Jamaica and the second in Grenada, on the effect of exposure to a temperature of 100° to 105° C. on the absorptive capacity in air of the broken seeds of this plant. In the second experiment the seed-coats were separated from the kernels, thus enabling one to differentiate between the bared seed and its coverings in this respect. Since the seeds in this case were equally divided between the samples, we are able to compare the absorptive behaviour in air of truly mixed materials under these different conditions. We thus perceive that in the slight influence of exposure to high temperatures on their absorptive capacities both the

Both the kernel and the coats of an impermeable seed retain their absorptive capacities in air after exposure to a temperature of 100° C.

PERMEABLE AND IMPERMEABLE SEEDS 79

kernel and its coverings behave in a similar manner. (For convenience I have also added under C the average result of all my experiments.)

EFFECT ON THE ABSORPTIVE CAPACITY IN AIR OF EXPOSURE TO A TEMPERATURE OF 100° TO 105° C. FOR 1½ TO 2 HOURS IN THE CASE OF BROKEN SEEDS OF GUILANDINA BONDUCELLA. (Results stated in percentages.)

A	Three broken seeds, kernels and coats mixed together, originally weighing 125 grains.			
	Original weight.	Weight after the oven test.	Subsequent weight after four days in air.	
	100	93·6	115·3	
B	Seed-coats and kernels treated separately, the true mixing of the samples being secured by dividing the seeds between them. Three seeds weighing 106 grains were used.			
	Materials.	Original weight.	Condition of experiment.	Subsequent weight after four days in air.
	Coats . . .	100	Reduced to 92·4 after exposure in oven to 100-105° C.	113·3
	„ . . .	100	Not heated	112·0
	Kernels . . .	100	Reduced to 95·8 after exposure in oven to 100-105° C.	115·5
„ . . .	100	Not heated	116·2	
C	Average results of all experiments on the absorptive capacity in air with and without previous exposure to a temperature of 100-105° C. in the case of the kernel and coats together.			
	Original weight.	Absorptive capacity in air.		
		Average of eleven experiments without heat.	Average of five experiments with previous exposure in oven.	
100	111·5	112·0		

An impermeable seed's capacity of absorbing moisture from the air in the broken state varies inversely with the water-contents.

That the absorptive capacity of the impermeable seed, that is to say, its power of absorbing water from the air in the broken condition, varies inversely with the water-contents was implied a few pages back. A small water-percentage and a large absorptive capacity go together, and *vice versa*. This is brought out in the tabulated results given below for *Guilandina bonducella*. These experiments were carried out in different places and under varying hygrometric conditions, so that only a general result is to be expected. Better examples of the principle that the impermeable seed when broken up takes up water from the air in proportion to its ultra-dryness are given in Chapter VI.

RESULTS OF THREE EXPERIMENTS ON THE SEEDS OF GUILANDINA BONDUCELLA, SHOWING THAT WITH IMPERMEABLE SEEDS THE SEED WHICH ADDS MOST TO ITS WEIGHT IN THE BROKEN CONDITION BY ABSORBING WATER-VAPOUR FROM THE AIR IS THE SEED WITH THE SMALLEST WATER-CONTENTS. (Stated in percentages, the samples varying between 50 and 130 grains.)

Original weight.	Reduced weight in oven.	Water-percentage.	Subsequent weight after exposure to air for four days.
100	89.9	10.1	105.2
100	93.8	6.2	114.2
100	93.6	6.4	115.3

The behaviour of the permeable seed under the oven test.

When we contrast the behaviour under the oven test of a permeable and an impermeable seed we obtain very different results. The seed of *Canavalia ensiformis*, after being subjected to the same oven test in the broken state, regains in a few days most of its lost water from the air; and after a week or two reaches its original weight affected only by the ordinary hygroscopic variation of 2 or 3 per cent. For example, a sample of seeds weighing 100 grains would be reduced in the oven to about 85 grains. After standing for four or five days its weight would be about 98 grains, and in a few more days it would attain its original weight, varying according to the

hygrometric condition of the atmosphere between 99 and 101 grains.

Enough has been said in this connection of the singular ultra-dryness of impermeable seeds. Though illustrated here only by the seeds of *Guilandina bonducella*, this capacity is described in the case of several other impermeable seeds in Chapter VI. This quality depends for its maintenance entirely on the impervious character of the outer part of the seed-coverings. There is nothing impermeable in this seed but the skin and the portion of the layer immediately beneath it. Let it be pierced only by a pin-prick, and sooner or later the seed takes up water from the air and ultimately behaves like a permeable seed, soon decaying as it lies in the soil, unless the conditions for germination arise. Let, however, the outer covering remain intact, and the embryo within may remain for long periods in a state of suspended vitality. But the impermeability of the coverings is not the only conspicuous quality associated with ultra-dryness. We have already seen that in the case of the seed of *Guilandina bonducella*, although both the coverings and the kernel share this character, it is to the kernel that it more especially belongs. In the sample examined, whilst the water-contents of the seed-coverings amounted to 7.6 per cent., in the kernel they were only 4.2 per cent. In Chapter VI it will be shown that this excess of water in the seed-coats as compared with the kernel is a typical character of impermeable seeds, a character that distinguishes them from permeable seeds of the same order, the coats of which as a rule possess a rather smaller water-percentage than the kernel.

It is to be doubted if any seeds are better fitted to preserve their germinating power for ages when buried in dry soil than the seeds of *Guilandina bonducella*. Professor Ewart, who employs the synonym of *Cæsalpinia bonducella* for this seed, places it amongst his group of "macrobiotic" seeds that would last from fifteen to over a hundred years under favourable conditions. I fancy that some very old seeds were once tested at Kew, but cannot put my finger on the reference. However,

Ultra-dryness maintained by the impermeability of the seed-coats and associated with a larger water-percentage in the coats than in the kernel.

Professor Ewart gives the result of an experiment where, out of twenty-four seeds fifteen years old, five germinated. I only tested their keeping capacity in the case of two seeds collected by me ten and eleven years previously in Fiji, and found that both germinated readily and produced healthy plants.

Negative results not to be exclusively relied on in testing the longevity of impermeable seeds.

Negative results in the germination of old impermeable seeds should not be exclusively relied upon, since they may arise more from a failure in the conditions of the experiment than from a failure in the seed. For instance, it is not at all easy, one might almost say it is impossible, to exactly reproduce the processes of nature in a soil-experiment. The initial step, when we place in warm, moist conditions an impermeable seed that has been lying dry for years in the air of a room is a distinct departure from the natural process; and, as Professor Ewart shows in the case of an experiment on "fifty-year" old seeds under what he describes as "optimal" conditions, there may be no results. Yet if the seeds that still remain intact and impermeable after such a soil-experiment are placed in a germination chamber, after the impermeable cuticle has been removed by sand-papering, about half on the average will germinate. In such a case every seed having been made permeable must either germinate or die. But we are not, I venture to think, justified in presuming that the seeds which failed to germinate in the second experiment had necessarily lost their vitality. The inference we should be apt to draw from the first soil-experiment that the seeds had lost their germinative powers would be disproved, as Professor Ewart observes in recounting the experiments, by the test in the germinating chamber; and it is equally possible that our second inference might be erroneous if we assumed that the failures in the germinating chamber are all to be attributed to the lost powers of the seed and not to some failure in the conditions.

Artificial methods, such as sand-papering, filing, scraping, the use of an acid, etc., are generally necessary in experiments to procure the germination of impermeable seeds, the seed being rendered permeable by being deprived of its cuticle;

but in my own experiments, where scraping or filing was generally adopted, I attached but little importance to the occasional negative results. Every seed of average weight that possessed completely sound coverings, that displayed no increase in weight whilst immersed in water for weeks, and that behaved like a quartz-pebble in response to the hygrometric changes of the air, was for me a germinable seed, whatever its age. An ineffectual result I regarded as merely reflecting on my method, provided that the seed originally possessed the qualities named.

The final proof seems to me to lie almost outside the reach of the direct experimental method. Nature would probably follow a very slow and graduated process in procuring the germination of ancient seeds; and it is not easy to see how we are to imitate such a process, and yet be confident that our failures lie in the seeds and not in the conditions of our experiment. In default of this there is still open to us the plan of testing the duration of the three chief qualities of an impermeable seed: the soundness of the coats, the impervious character of its outer covering, and its practically non-hygroscopic behaviour. The indirect method would appear to give most promise in the investigation of the longevity of impermeable seeds.

Yet occasionally some strain of weakness due to a defect in the shrinking process offers to the opposing external conditions their opportunity, and the seed that appeared able to survive for very long periods begins to fail. The indications of the change are exceedingly interesting. They have already been noticed on p. 76 in this chapter in the description of the results of filing into seeds of *Guilandina bonducella*, and they will be again noticed in the account of a similar experiment on the seeds of *Entada scandens* in Chapter VI. During several months the filed seeds gradually increased in weight, until, in the case of the first-named, they had increased by 10 or 11 per cent., and in that of *Entada scandens* 2 or 3 per cent., assuming ultimately the condition of permeable

Suggested test of longevity in the duration of the external qualities of impermeable seeds.

seeds and behaving hygroscopically. Such is the change that impermeable seeds undergo in the air when their coats are injured ; but this is the natural end of all such seeds in the soil. It is the loss of their impermeability, according to Professor Ewart, that brings the resting life of *Acacia* seeds in the surface-soil of the Australian forests to a close, leaving no choice between germination and death. The earlier seeds to swell in his experiments were, as he observes, mostly dead.

Similar indications were at times presented in my long weighing experiments on impermeable seeds. In Chapter X, which is devoted to the fate of seeds as indicated by the balance, I refer to the gradual increase of weight, extending over a year or more, of seeds of *Entada scandens* and *Guilandina bonducella* that displayed slight defects in their coats.

One may perhaps be permitted to slacken for a while the reins that control the fancy whilst reflecting on the mysterious development of this condition of ultra-dryness in impermeable seeds in association with the completely suspended vitality of the embryo. If, when we come to discuss this subject in its general bearings in a later chapter, it loses a little of its mystery, we shall still, I venture to think, regard the impermeable seed as one of Nature's indications of the direction in which speculation should be aimed in discussing the extra-terrestrial or cosmic aspects of plant-life. If such a seed as is presented to us now will not withstand the strain of the ages, it suggests to us in more ways than one the type of plant-organism that might withstand the test. It seems to show us how a plant in a state of suspended vitality might tide over great periods of time not only on this planet, but on others where different conditions prevail.

Such a seed appears to be almost unconditioned when contrasted with a permeable seed, which is very much in touch with its surroundings, and responds closely in its changes of weight to the varying hygrometric states of the atmosphere. The life of the embryo of a permeable seed

The ultra-dry impermeable seed and its cosmic suggestiveness.

depends largely on the conditions in which the seed is placed, and it is ever threatened by many dangers, against which the embryo of an impermeable seed is fully protected. It is immaterial to the young plant enclosed in the hard shell of a seed of *Guilandina bonducella* whether the seed lies exposed to the sun on a desert or is submerged in a swamp. As compared, then, with the permeable seed, the impermeable seed seems to present to us a relatively unconditioned existence of its embryo.

Whilst indulging in such speculations it is pertinent to ask which was the prior state of the seed, the permeable or the impermeable. To this it may be replied that if in past ages seeds had no rest-period, the matured seed passing on at once to germination, the development of the impermeable state would be of later origin. But the seed-stage may be conceived as the permanent state of plant-life under certain iron-bound conditions, such as may prevail on other planets, and such as may have originally prevailed on the earth. In such a case the seed-stage would represent the plant's response to the rigid control of contracted life-conditions, whilst the vegetative growth would represent in the production of stem and foliage the plant's response to the expanding conditions of existence. Under such circumstances the impermeable seed would be the older state.

As the plant-world exists at present, though impermeability has the appearance of necessity, impermeable seeds have to become permeable in order to germinate. It can, however, be easily shown, and this will be done in a later chapter, that in plants possessing both types of seeds the impermeable state is the goal sought in the seed's development, and that the permeable seeds have their origin in checks to the shrinking process. With such plants the impermeable seed, when beginning to swell for germination, resumes the appearance of the permeable seed. May it not be that impermeability is a cosmic character which, in response to the expanding terrestrial conditions, has largely given place to permeability?

Which is the oldest, the permeable or the impermeable seed?

It would indeed appear that this is an ancient attribute of seeds which they are now in process of discarding.

A consideration that gives additional force to this line of thought is that one of the greatest foes to the development of impermeability in seeds is mould or mildew. These minute fungi, when they establish themselves in the tender skin of the soft, so-called unripe seed, either bring about the death of the embryo before the resting stage is reached, or give rise to a resting seed, with permeable coverings, which, unless conditions favouring germination quickly follow, becomes at length a shrunken, lifeless seed. (See Note 7 of the Appendix and Chapter V.) From this standpoint impermeability in seeds might be regarded as a decreasing quantity in the plant-world, that is, if minute fungi have become predominant only in the later ages of the earth's life-history. One could conceive how, as a character of seeds, impermeability might thus be banished from our planet, and the permeable seed reign supreme; and quite in harmony with this conception would be the indication that Australia, the land of droughts and the home of the *Acacia*, offers especially favourable conditions for the persistence of impermeability in seeds and for securing their longevity. However, the decision concerning these views lies with the investigator of the future, and so we will let the matter rest.

Mould and
imperme-
ability.

SUMMARY

(1) In order to introduce the subject of the contrast between permeable and impermeable seeds, I have taken the very divergent behaviour, as mainly revealed by the balance, of the seeds of two leguminous plants, that of *Canavalia ensiformis* as a type of the permeable seed, and that of *Guilandina bonducella* as a type of the impermeable seed (p. 69).

(2) Dealing first with the seeds in their coats, the following differences in their behaviour are described:—

- (a) The seed of *Canavalia ensiformis* swells readily in water, and possesses a stable weight subject to the normal hygroscopic variation (p. 70).

- (b) The seed of *Guilandina bonducella* absorbs no water after prolonged immersion, makes no response to the changes in the hygrometric state of the atmosphere, and retains its weight unchanged in the course of years (p. 70).
- (3) Taking at first the seeds bared of their coats, other contrasts in behaviour are brought out :—
- (a) The bared kernel of *Canavalia ensiformis* preserves its average weight, but displays a greater hygroscopic variation than in the case of the kernel protected by the coats (p. 71).
- (b) But with *Guilandina bonducella*, when the seed is deprived of its hard, shell-like covering, the kernel gains 11 or 12 per cent. in weight in a few days by abstracting water from the air. This increase in weight is maintained, but in a diminishing degree, for several months, until stability is reached, when the weight shows a permanent increase of 3 or 4 per cent. The ultimate result is that the kernel behaves like that of a permeable seed (p. 72).
- (4) The ultra-dryness of the kernel of an impermeable seed, which is thus disclosed, is confirmed by the evidence supplied by the oven when the seeds are exposed to a temperature of 100° C. It thus appears that the amount of water regained from the air by the bared seeds of *Guilandina bonducella* represents the deficiency in its water-contents, as compared with the bared seeds of the permeable type belonging to *Canavalia ensiformis* (p. 73).
- (5) The next curious feature in impermeable seeds here brought to light is the fact that the shell-like covering of the seed of *Guilandina bonducella* has the same quality of ultra-dryness, though in a somewhat diminished degree, and the same capacity of supplying this deficiency by absorbing water from the air, the larger water-percentage of the shell being associated with a diminished absorptive capacity of the freshly exposed material. On the other hand, the coats of a seed of *Canavalia ensiformis* behave like the kernel, maintaining the same average weight when removed from the seed, but subject also to ordinary hygroscopic variation (p. 75).
- (6) The same effects are produced by puncturing or filing the impermeable seeds of *Guilandina bonducella*, though the increase in weight is far more gradual and is extended over months. This behaviour is contrasted with that of the permeable seeds of *Canavalia ensiformis*, where the effect of puncturing the coats is merely to increase somewhat the normal hygroscopic variation of the weight (p. 76).
- (7) As first accidentally disclosed and subsequently more fully investigated, it is shown that exposure to a temperature of 100° C. but slightly affects the capacity of the seeds of *Guilandina bonducella* (whether in the case of bared kernels or detached shells) of adding to

their original weight by taking up water from the air. Of two seeds broken up and exposed, the one to the ordinary air of a room, the other at first to a temperature of 100° C., with the resulting loss of 6 or 7 per cent. of its weight, both will ultimately be found after a lapse of a few days to have acquired a weight on the average 11 or 12 per cent. in excess of their original weight in the entire condition. On the other hand, the permeable seed of *Canavalia ensiformis* displays quite a different behaviour after being exposed to the oven test. In a week or two it returns to its original weight, having regained all its lost water from the air (15 per cent.), and then maintains a stable weight subject only to the ordinary hygroscopic variation of 2 or 3 per cent. (p. 78).

(8) It is established from the foregoing results that the capacity of an impermeable seed for absorbing water from the air in the broken state varies inversely with the amount of the water-contents in the entire condition (p. 80).

(9) It is indicated by the preceding observations that the ultra-dryness of the seeds of *Guilandina bonducella* and of the impermeable seeds, of which it forms a type, is maintained by the impermeability of the seed-coats. Though, as compared with permeable seeds, both the coats and the kernel are ultra-dry, the coats contain more water than the kernel (p. 81).

(10) It is suggested on *à priori* grounds that negative germinative results, even those obtained by investigators with the most modern means of research, are not to be relied upon as concerning the longevity of impermeable seeds, provided that the seeds tested are normal in appearance and in weight and display the normal passivity of seeds of the type. It is considered that a much safer test is to be found in the durability of external qualities, all seeds to be regarded as potentially living or "germinable" that are sound, impermeable, non-hygroscopic, and of unchanging weight. It is held that the final proof of a seed's vitality lies almost outside the scope of the direct experimental method (p. 82).

(11) Yet occasionally, through some defect in its coverings, the impermeable seed, that appeared at one time as if it could live for ever, begins to fail. This is shown in the gradual increase of weight extending over months, as a result of which the impermeable seed assumes the rôle of a permeable seed. If this occurred under ordinary soil-conditions the seed would have to choose between germination and death. If it took place in a seed exposed to the air in a room, the seed might retain its germinative power for some years, as was indicated in my experiments (p. 83).

(12) A speculative turn is given to the discussion by the reference made to the "cosmic suggestiveness" of the ultra-dry condition of the

impermeable seed. The suggestion is that if the impermeable seed, as it presents itself in its semi-unconditioned state, cannot withstand for ever the test of the ages, it supplies us with a hint as to the kind of plant-organism that might withstand the strain in this and other planets (p. 84).

(13) The question is put as to which is the original condition, that of the permeable or of the impermeable seed. In this connection it is shown that though the impermeable seed has the appearance of necessity, it has to become permeable in order to germinate, and that with plants possessing both types of seeds the permeable seed may be regarded as a seed where the shrinkage has been checked. It is asked whether impermeability may not be a cosmic character, which, in response to the expanding life-conditions of our particular planet, has largely given place to permeability (p. 85).

CHAPTER V

THE GROUPING OF SEEDS ACCORDING TO THEIR PERMEABILITY OR IMPERMEABILITY

The grouping of seeds according to their permeable or impermeable character.

HAVING introduced the subject of impermeability in the two preceding chapters, I now proceed to discuss the grouping of seeds according to the presence or absence of this quality. We have already seen that impermeable and permeable seeds are often found in the same plant. This is sufficiently frequent to be regarded as quite a normal occurrence, the distinction between the two types being occasionally accentuated by a conspicuous difference in the external characters, thus enabling two kinds of seeds to be recognised in a plant. Impermeability presents itself in a transition stage in so many plants that one feels bound to regard it as an attribute that is either being gradually discarded or being gradually developed ; and indeed the question whether seeds are now in the act of acquiring or of dispensing with this quality was the dividing issue raised at the close of the previous chapter.

It will thus be seen that we cannot divide all seeds between two groups, permeable and impermeable, since there is a large intermediate group where the two kinds of seeds are associated. It is this variable group that will offer some of the best opportunities of observing the stages in the development or in the degradation of impermeability, as the case may be. But seeds belonging to the impermeable group will also be of assistance in this inquiry, since, although normally impermeable, they present at times in their defectively shrunken seeds good materials for study.

As regards the differences in the variable group, it is not often that the distinction between the two types is conspicuously evident to the eye, since similar-looking seeds, as Professor Ewart remarks, may differ greatly in these qualities. Usually the differentiation is made in the course of experiments on the capacity of seeds to withstand immersion in water. However, there are cases, like that of *Entada polystachya*, where the two types of seeds are easily distinguished, one small, dark-coloured, impermeable, and non-hygroscopic, the other large, light-coloured, permeable, and hygroscopic, and both equally capable of reproducing the plant. Then again, Mr Crocker, in the *Botanical Gazette* for October 1906, has shown that *Axyris amaranthoides* has "dimorphic" seeds, the one kind flattened, winged, permeable, and germinating readily, the other rounded, relatively impermeable, and only germinating after considerable delay. Professor Ewart points out that in the course of his experiments on more or less impermeable leguminous seeds, as with the Acacias, these two types of seeds were often differentiated, the seeds that readily swelled being larger than the "hard" seeds that required the employment of artificial means to produce swelling, though both attained the same size when swollen for germination.

In the following tables I have arranged the species of seeds on which experiments were made by me, amounting to about 105, into the three groups:—

- (1) Impermeable group, containing only plants where the seeds are all normally impermeable.
- (2) Variable group, including plants with both permeable and impermeable seeds.
- (3) Permeable group, comprising plants with only permeable seeds.

Since the general question of the frequency and distribution of the quality of impermeability among seeds has been already dealt with in Chapter III on a far more extended basis than my own materials would afford, I will merely confine my remarks on these groups to a few general observa-

tions before proceeding to describe in detail the results of my investigation of these seeds from this particular standpoint.

The pre-
dominance of
leguminous
plants in the
groups
characterised
by imperme-
able seeds.

One of the first noticeable things in these groups is the predominance of leguminous seeds in the two groups of species possessing impermeable seeds exclusively or in part. This has already been established by Dr Gola and others, but principally by Professor Ewart from a more extensive experience ; and one may be content with showing here how this predominance is suggestively emphasised in my own less numerous results. Of the 105 species of seeds named in these groups, 44, or about two-fifths, are leguminous ; and of these three-fourths are claimed by the two groups containing plants with impermeable seeds. If the quality of impermeability was equally distributed amongst the natural orders, we should expect to find leguminous plants and plants of other orders about equally represented in the total of the impermeable and variable groups. As a matter of fact, however, this is far from being the case, since as many as 82 per cent. in the groups just named, and as few as 19 per cent. in the permeable group, are leguminous.

Various points in this classification of seeds will be elucidated as this work proceeds. I will, however, notice that the distinction between the impermeable group, where all the seeds are impermeable, and the variable group, where both kinds of seeds are found, is often rather arbitrary. In truth, it would almost appear from Professor Ewart's tables that very few plants have seeds that are impermeable without exception. But careful consideration has convinced me that the real distinction between the two groups ought to lie not so much in the total absence or in the presence of permeable seeds, but in the degree of constancy of the characters within a species. Without some familiarity with the seeds in question one would be often likely to include amongst impermeable seeds some that have lost their imperviousness through a slight defect developed during the shrinkage process. With typical impermeable seeds there always will be a very high percentage of seeds normal in this respect ; whilst with typically variable seeds there will be, as a rule, con-

siderable variation between different samples, one sample having a low percentage and another a high percentage of permeable seeds. This was well brought out in Dr Gola's observations, already dealt with in Chapter III.

One may add with reference to the short list added to my tables containing seeds also experimented upon by Professor Ewart that the only discrepancy is concerned with those of *Leucaena glauca*, which, according to my observations, are regarded as impermeable instead of permeable, as is indicated in the Australian experiments.

THE GROUPING OF THE SEEDS EMPLOYED IN THIS INQUIRY ACCORDING TO THEIR PERMEABLE OR IMPERMEABLE QUALITIES

I. IMPERMEABLE

Adenanthera pavonina	Leguminosæ	(S)
Colubrina asiatica	Rhamnææ	(F)
Dioclea reflexa	Leguminosæ	(F)
Entada scandens	"	(F)
Guilandina bonduc	"	(S)
" bonducella	"	(F)
" (near) glabra	"	(F)
" melanosperma	"	(S)
Ipomœa dissecta	Convolvulacææ	(S)
" pes-capræ	"	(F)
" tuba	"	(F)
Leucaena glauca	Leguminosæ	(S)
Mucuna urens	"	(F)
Sophora tomentosa	"	(F)
Strongylodon lucidum	"	(F)
Ulex europæus	"	(S)
Vigna luteola	"	(F)

Note.—The capital letters in brackets have the following significations relating to buoyancy in sea-water:—

F=Known to be dispersed by sea-currents, the proportion of buoyant seeds varying from as much as 80 or 90 per cent. in *Guilandina bonducella* to as little as 10 per cent. in *Dioclea reflexa*. However, seeds vary much in this respect in different localities. From my observation of the living plant in Fiji and Ecuador I formed the conclusion that quite half of the seeds of *Entada scandens* have no initial buoyancy; whereas of fresh seeds obtained from the plants growing in the Jamaica woods I found that quite 90 per cent. floated (*vide* the author's *Plant Dispersal*, p. 181).

S=All sink.

II. VARIABLE

(Possessing both permeable and impermeable seeds)

<i>Abrus precatorius</i>	Leguminosæ	95	per cent.	impermeable
<i>Acacia Farnesiana</i>	”	70	”	”
<i>Albizzia Lebbek</i>	”	50	”	”
<i>Aquilegia</i> (species)	Ranunculaceæ	80	”	”
<i>Arenaria peplodes</i>	Caryophyllaceæ	80	”	”
<i>Bauhinia</i> (species)	Leguminosæ	30	”	”
<i>Cæsalpinia Sappan</i>	”	50	”	”
” <i>sepiaria</i>	”	40	”	”
<i>Calliandra Saman</i>	”	30	”	”
<i>Canavalia gladiata</i> (red seeds)	”	35	”	”
” <i>obtusifolia</i>	”	70	”	”
” (species)	”	50	”	”
<i>Canna indica</i>	Cannaceæ	90	”	”
<i>Cassia fistula</i>	Leguminosæ	90	”	”
” <i>grandis</i>	”	90	”	”
” <i>marginata</i>	”	90	”	”
<i>Entada polystachya</i>	”	50	”	”
<i>Enterolobium cyclocarpum</i>	”	90	”	”
<i>Erythrina corallodendron</i>	”	60	”	”
” <i>indica</i>	”	50	”	”
” <i>velutina</i>	”	65	”	”
<i>Ipomœa tuberosa</i>	Convolvulaceæ	35	”	”
<i>Poinciana regia</i>	Leguminosæ	65	”	”
<i>Thespesia populnea</i>	Malvaceæ	80	”	”
<i>Vicia sepium</i>	Leguminosæ	65	”	”

III. PERMEABLE

<i>Achras Sapota</i> (Sapodilla)	Sapotaceæ
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	Hippocastaneæ
<i>Allium ursinum</i>	Liliaceæ
<i>Andira inermis</i>	Leguminosæ
<i>Anona Cherimolia</i> (Cherimoya)	Anonaceæ
” <i>muricata</i> (Sour-sop)	”
” <i>palustris</i> (Monkey-apple)	”
” <i>reticulata</i> (Custard-apple)	”
” <i>squamosa</i> (Sweet-sop)	”
<i>Artocarpus incisa</i> (Bread-fruit)	Artocarpeæ
<i>Arum maculatum</i>	Aroideæ
<i>Barringtonia speciosa</i>	Myrtaceæ

Berberis (species)	Berberideæ
Bignonia (2 species)	Bignoniaceæ
Blighia sapida	Sapindaceæ
Cajanus indicus	Leguminosæ
Canavalia ensiformis	"
Cardiospermum grandiflorum	Sapindaceæ
" Halicacabum	"
Carica Papaya (Papaw)	Papayaceæ
Chrysophyllum Cainito (Star-apple)	Sapotaceæ
Citrus decumana (Shaddock)	Aurantiaceæ
Crinum (species)	Amarylloideæ
Datura Stramonium	Solanaceæ
Dolichos Lablab	Leguminosæ
Faba vulgaris (Broad Bean)	"
Fevillea cordifolia	Cucurbitaceæ
Gossypium hirsutum	Malvaceæ
Grias cauliflora	Myrtaceæ
Hedera Helix (Ivy)	Araliaceæ
Hibiscus elatus	Malvaceæ
" esculentus	"
" Sabdarifa	"
Hura crepitans	Euphorbiaceæ
Iris foetidissima	Irideæ
" Pseudacorus	"
Lonicera Periclymenum (Honeysuckle)	Caprifoliaceæ
Luffa acutangula	Cucurbitaceæ
Mammea americana	Guttiferæ
Momordica Charantia	Cucurbitaceæ
Monstera pertusa	Aroideæ
Montrichardia arborescens	"
Moringa pterygosperma	Capparidæ
Moronobea coccinea	Guttiferæ
Opuntia Tuna	Cactaceæ
Phaseolus multiflorus (Scarlet-runner)	Leguminosæ
" vulgaris (French Bean)	"
Pisum sativum (Pea)	"
Pithecolobium filicifolium	"
Primula veris (Primrose)	Primulaceæ
Pyrus Malus (Apple)	Rosaceæ
Quercus Robur (Oak)	Cupuliferæ
Ravenala madagascariensis	Musaceæ
Ribes grossularia (Gooseberry)	Ribesiacæ
Ricinus communis (Castor-oil)	Euphorbiaceæ
Scilla nutans	Liliaceæ

Stellaria Holostea	Caryophyllaceæ
Swietenia Mahogani (Mahogany)	Meliaceæ
* Tamarindus indica (Tamarind)	Leguminosæ
Tamus communis	Dioscoreæ
Theobroma Cacao (Cocoa)	Buttneriæ
Vicia sativa	Leguminosæ

RESULTS CONCERNING SOME OF THE ABOVE IMPERMEABLE AND VARIABLE SEEDS FROM PROFESSOR EWART'S TABLES (*Proc. Roy. Soc. Vict.* 1908). His results for seeds more than 15 or 16 years old are not given.

Adenantha pavonina, seeds 8 years old, swelled after filing.

Albizzia Lebbek, seeds 11 years old, scratching needed for germination.

Canavalia gladiata, 10 years old, 1 out of 6 seeds required filing for germination.

Canavalia obtusifolia, 16 years old, required sulphuric acid for germination.

Erythrina indica, of 50 seeds, 8 years old, 6 swelled in water.

Guilandina bonducella, seeds 15 years old, required the acid for swelling.

Leucæna glauca, seeds 15 years old, all swelled in water.

Mucuna urens, 10 years old, required filing for swelling.

Poinciana regia, 9 years old, outer skin impermeable until filed.

Impermeability and dispersal by water.

Those who have studied the dispersal of seeds by the ocean-currents have laid stress on the circumstance that many of the seeds capable of transportal over wide tracts of sea belong to leguminous plants; and I need here only allude to the circumstance that the four West Indian and Central American seeds (*Dioclea reflexa*, *Mucuna urens*, *Guilandina bonducella*, *Entada scandens*) that are most frequently stranded intact on the western shores of Europe belong to this order. When Professor Ewart remarked (p. 184) that "macrobiotic" seeds show no special adaptation for dispersal and that "none are wind or water-borne," he apparently had forgotten that there are included in his list the seeds of plants like *Canavalia obtusifolia*, *Erythrina indica*, and *Guilandina*

* Tamarind seeds absorb water very slowly at first, requiring often an immersion of a week or more before there is any marked increase in the weight.

bonducella, that have long been known to be dispersed by ocean-currents. Putting aside the question of adaptation to modes of distribution, a view which I hold ought either to be universally applied or to be discarded altogether, the strand of a coral island would be deprived of several of its most conspicuous and typical plants, such as *Canavalia obtusifolia*, *Colubrina asiatica*, *Erythrina indica*, *Guilandina bonducella*, *Ipomœa pes-capræ*, *Morinda citrifolia*, *Mucuna* (species), *Sophora tomentosa*, etc., if their seeds did not possess impermeable coats, in most if not in all cases associated with the capacity of prolonged vitality.

Our views of the adaptive relations of impermeability, if it is valid to select cases in a world that is one mass of adaptation, might be a good deal coloured by the station of the plants investigated. Thus, it might be considered from a study of the plants of tropical coasts that impermeability was most characteristic of the seeds of beach and estuarine plants dispersed by currents. But it proves to have no exclusive association either with buoyancy or with a littoral station. Thus quite a third of the seeds named in my impermeable group (*Adenanthera pavonina*, *Guilandina bonduc*, *G. melanosperma*, *Ipomœa dissecta*, *Leucœna glauca*, and *Ulex europæus*) have no floating powers; and it may be safely said that the great majority of the 180 "macrobiotic" impermeable species of seeds named in Professor Ewart's list have no buoyancy and no littoral station. In framing any views in support of the adaptive relations of impermeability in seeds, it would be wise to cast one's net widely and to adopt the standpoint taken by Professor Ewart, that there is here a general adaptation to soil-conditions, without committing oneself to any mode of genesis of this quality.

I will now deal with some plants of the variable group possessing the two kinds of seeds, sometimes differing from each other in external characters as well as in the degree of impermeability. They will serve to throw some light on the nature and relations of this quality. Reference has

Impermeability and adaptation.

The lesson of the plants possessing both permeable and impermeable seeds.

already been made in this chapter to Mr Crocker's description of the "dimorphic" seeds of *Axyris amaranthoides*; and I will now contrast the two types of seeds developed by *Entada polystachya*, not only as regards their external characters, but also in other associated qualities.

COMPARISON OF THE TWO TYPES OF SEEDS PRODUCED BY
ENTADA POLYSTACHYA.

GENERAL CHARACTERS.							
	Size in millimetres.	Permeability to water.	Colour.	Weight in grains.	Hygroscopic range stated as a percentage.	Water-percentage.	
A.	Large, 15 × 12 mm.	Permeable	Yellowish brown	6·6	2·0 per cent.	10·0 per cent.	
B.	Small, 13 × 11 mm.	Impermeable	Dark brown	5·0	0·1 „	6·3 „	
Absorption of moisture from the air in the broken condition. (Results stated in percentages.)							
	Not heated.			After exposure for 1½ hours to a temperature of 100° to 105° C.			
	Original weight.	After 4 days.	Absorbing capacity.	Original weight.	After heating.	4 days later.	Absorbing capacity.
A.	100	101·6	Hygroscopic only 9·4 per cent.	100	90	95	less 5·0 per cent.
B.	100	109·4		100	93·7	101	plus 1·0 „

Note.—The full display of the absorptive quality after heating was not elicited in the oven-experiments, since the seeds were merely cut in halves in their coats. A period of at least a week would have been needed for a proper comparison with the absorptive capacity of the unheated seeds, where the coats and kernels, being treated separately, were better able to take up moisture from the air.

We see in the above tabulated results that the two types of seeds exhibited by *Entada polystachya* differ in all the critical points that distinguish permeable and impermeable seeds, viz., in water-contents, hygroscopic behaviour, and absorptive capacity in air; and we see also that they differ

equally in colour, size, and weight. The contrast, though marked, is not quite so great as between typical seeds of the impermeable and permeable groups, because it is not possible to use a test that would completely exclude the other type from a sample without invalidating the experiment, and one has to select merely by the external characters.

The essential characters of the A type as a permeable seed are its hygroscopicity, its relatively large water-contents, and the inability to increase its weight when exposed in a broken condition to the air, ordinary hygroscopic variation being sufficient to explain most of the small increase in weight (1.6 per cent.) noted in the table. On the other hand, B as an impermeable seed is practically non-hygroscopic, has a relatively small water-percentage and a counterbalancing large capacity of absorbing moisture when exposed in the broken condition to the air. The behaviour after being subjected to a temperature of 100° C. is also distinctive, the permeable seeds failing by 5 per cent. to regain their original weight after an exposure of some days to the air; whilst the impermeable seeds ultimately exceed their original weight by about 1 per cent. But, as observed in the note to the table, the full extent of the absorptive capacity after heating was not determined. These results, however, bring the two types of seeds into contrast sufficiently well, when we reflect that each sample of seeds probably contained a small percentage of the other kind, less easily distinguished than usual by their external characters.

When seeking for an explanation of these two sets of seeds in the same plant, one has not far to look, the uncompleted process supplying the clue. This we recognise in a check to the shrinking and drying process that ushers in the rest-period; and Professor Ewart's surmise (p. 197) respecting the differences between *Acacia* seeds of the same species, that the impermeable seeds are smaller "because they are drier," goes towards the root of the matter. With the larger, pale-coloured seeds the shrinking process has been

The clue to the origin of the two kinds of seeds in the same plant lies in a check to the shrinking process.

arrested at an earlier stage than in the case of the smaller, dark-coloured seeds, as is indicated by their size and by their higher percentage of water. But the behaviour of the smaller impermeable seeds themselves when they begin to swell for germination is equally suggestive, since, as soon as they begin to absorb water, they assume the hue, size, and general appearance of the larger impermeable seeds.

The whole question is bound up with the history of the shrinking process of seeds which is discussed in Chapter II, and behind that lies the story of the maturation and drying of the fruit. The immediate cause of this check to the shrinking process of seeds resulting in the production of two types of normal resting seeds must therefore be looked for in the conditions surrounding the final stage of the shrinking process within the drying legume. In the case of *Entada polystachya* the large pods, which are usually 15 or 16 inches long and 3 inches wide, generally dry on the plant, and as the outer skin scales off during this process they begin to break up transversely into separate narrow joints, each containing a seed. It is probable that the check to the shrinking process of the seeds is determined by variations in the behaviour of the drying pod with respect to the shedding of its epidermis and the breaking up into joints. Unfortunately, this explanation of the matter only presented itself to me after the opportunity of further investigation had passed away.

It is generally necessary, in the case of impermeable leguminous seeds, that the last stage of the shrinking process should be completed in the pod. If one gathers a number of full-sized so-called unripe seeds in the swollen, soft condition and allows them to go through the drying and shrinking process detached from the pod, they will usually fail to become impermeable seeds. It is also generally necessary that the seed should remain in the pod whilst it is dehiscing on the plant, since, if we remove the seeds from the unopened fruit, even though it is dry and the seeds are in appearance

The cause of the check is determined by variations in the behaviour of the drying pod.

Association of permeable and impermeable seeds in a plant without differing much in external characters.

normally contracted, they will often prove to have lost their impermeability.

I will take the case of the seeds of *Caesalpinia Sappan*, gathered in the Botanic Gardens of Grenada. The seeds on the ground that had fallen naturally from the tree were rather darker in colour and drier on section than those obtained from the dry but still closed pods on the tree, though the last might have been taken for normal seeds, and indeed were just as capable of reproducing the plant. However, on keeping a number of the seeds of both kinds under observation for ten days, I found that those from the closed pods were slowly losing weight. This led to a detailed comparison of them with the seeds from the ground, the results of which are tabulated below and stated in percentages.

Caesalpinia Sappan.

COMPARISON OF THE SEEDS OF *CÆSALPINIA SAPPAN* ON THE GROUND AND ON THE PLANT.

Conditions.	Character.	Water-percentage.	Absorption of moisture from the air in the broken condition.						
			Not heated.			After exposure for 1½ hours to a temperature of 100–105° C.			
			Original weight.	After 4 days.	Absorbing capacity.	Original weight.	After heating.	3 days later.	Absorbing capacity.
Seeds lying loose on the ground	Most of them impermeable	9·7	100	108·9	8·9 per cent.	100	90·3	104·7	4·7 per cent.
Seeds from the closed dry pod on the tree	All permeable	13·9	100	100·5	0·5 per cent. hygroscopic only	100	86·1	99·9	Less, 0·1 per cent.

Note.—The whole seed (coats and kernel) is used in the absorption experiments.

Thus we get here the same indications as we obtained in the instance of *Entada polystachya*, there being from the gardener's standpoint two sets of seeds, though in nature

probably only one. Those of the closed pod on the tree are characterised by permeability, by a large amount of water, and by their inability to increase their weight when exposed in a broken condition to the air. Those picked up from the ground are mostly impermeable, and have a low percentage of water, a deficiency associated with the capacity of considerably adding to their weight by absorbing moisture when exposed as broken seeds to the air. The behaviour of the seeds of *Cæsalpinia Sappan* is probably typical of many leguminous seeds with impermeable coats, especially in those cases where the difference between the seeds would not be readily detected by the eye. Strong winds and torrential rains would not infrequently affect the somewhat premature detachment of the seed from the parent.

*Ipomœa
tuberosa.*

The seeds of *Ipomœa tuberosa*, a convolvulaceous plant, offer another good instance where divergent behaviour as regards impermeability is not always associated with conspicuous differences in the aspect of the seeds. Whilst some of the seeds swell in water, others have to be filed to induce absorption. As shown in the results given below for the kernels, impermeability is associated with a relatively small water-percentage and a considerable absorptive capacity in air after being heated in the oven. The permeable seeds, on the contrary, contain a large amount of water and fall far short of their original weight when absorbing moisture from the air after the heating process.

COMPARISON OF THE BEHAVIOUR OF KERNELS OF *IPOMŒA TUBEROSA* AFTER EXPOSURE FOR TWO HOURS TO A TEMPERATURE OF 100° TO 105° C. (The materials in each case were rather over 100 grains; the results are given in percentages.)

	Original weight.	After heating.	Water-percentage.	Weight 6 days later.	Absorptive capacity in air.
A. Permeable . . .	100	83	17	93	Minus 7'0
B. Impermeable . . .	100	91	9	103	Plus 3'0

The difficulties a seed may have to contend with before it enters its prolonged rest-period under the protection of its impermeable skin were brought under my notice in the case of *Dioclea reflexa* whilst specially studying the habits of this leguminous climber in its home in the mountain forests of the Grand Etang in the island of Grenada. The rainfall here is heavy even for the tropics, averaging 140 or 150 inches in the year, and very moist conditions prevail in the densely shaded woods. The seeds are freed by the decay of the pod; and if the detachment of the pod from the parent takes place under normal conditions, the typical impermeable seed is produced, such as is at times stranded by the Gulf Stream with coats intact on the shores and islands of Western Europe. This tree-climber often favours a station on the banks of streams and lakes, so that the seed's opportunities of reaching the open sea are numerous.

But if, as frequently happens, the pods are prematurely detached during the prevalence of heavy rains and strong winds, that is to say, before the drying and shrinking stage of the pod and the enclosed seeds is complete, then the seeds usually fail to finish the process, and, being moist and permeable, they either pass on into the germinating condition, a result favoured by the prevailing humidity of the forests, or decay and die. These fallen pods lying on the wet, sloppy ground in the deep shade of the forests readily take up water, and the seeds, as just remarked, soon swell up and either die or germinate. On one occasion I noted that out of 30 seeds obtained from 10 fallen pods lying sodden on the ground in the depths of the forest, 10 were rotting, 10 were germinating, and 10 were in a resting condition; but of these last, 7 or 8 were permeable, with the shrinking process markedly incomplete. Even the two or three impermeable seeds were far from typical in their appearance. It was only occasionally that a typical impermeable seed was found that seemed fit for the Transatlantic passage in the Gulf Stream. Such, then, are some of the difficulties with which a seed may have

Dioclea reflexa, the difficulties attending the development of impermeability in its seeds.

to contend in acquiring impermeability. Though no doubt exceptional in this particular case, they indicate the character of the obstacles under certain climatic conditions.

Contrast between the permeable and impermeable seeds of *Dioclea reflexa*.

The contrast in appearance and in behaviour under different tests between the permeable seed of *Dioclea reflexa* where the shrinking process has been prematurely arrested, and the impermeable seed of the same plant where it has been normally completed, is very striking. The first is brownish black, and its coats bend, but do not crack, in the hand-vice. The second is much lighter in colour, often mottled, and its coats are relatively brittle. The kernel of the impermeable seed is dry and almost friable, whilst that of the permeable seed is moist in appearance and compact in texture. As shown in the tabulated comparison subjoined, the greatest contrast is presented in the water-contents and in the capacity of absorbing moisture from the air after being heated. I may remark here that the behaviour of the bared kernels during the four hours that passed before they were placed in the oven was very significant, that of the impermeable seed gaining nearly 3 per cent. in weight, and that of the permeable seed losing rather over 3 per cent.

COMPARISON OF AN IMPERMEABLE AND A PERMEABLE SEED OF *DIOCLEA REFLEXA* FRESH FROM THE FORESTS OF THE GRAND ETANG IN GRENADA, AND WEIGHING RESPECTIVELY 83·5 AND 83·1 GRAINS. BOTH THE COATS AND THE KERNEL WERE EXPOSED TO A TEMPERATURE OF 100-105° C. FOR 1½ HOURS. (Results are stated as percentages.)

	Original weight.	Weight after heating.	Water-percentage.	Subsequent increase in weight by absorbing moisture during 4 days' exposure to the air.
A. Impermeable . .	100	91·4	8·6	108·8, or a gain of 8·8 per cent. over the original weight.
B. Permeable . .	100	80·0	20·0	94·8, that is to say, failed by 5·2 per cent. to regain the original weight.

Note.—The behaviour of the separate coats and kernel is essentially the same, and differs only in degree.

Whilst showing in the preceding pages that to deficient shrinkage must be attributed the origin of permeable seeds in those plants where impermeability is more or less the rule, but little allusion was made to the changes in the appearance and condition of the outer seed-coverings in this connection. Thus, in the case of deficiently shrunken seeds of *Entada scandens*, the cuticle is traversed by a network of fine cracks; and one of the earliest signs of a normal impermeable seed losing its impermeability is displayed in the development of these fine cracks. But it is in the seeds of *Guilandina bonducella* that we have the best opportunity, though under rather peculiar conditions, of investigating this subject, and of observing how deficient shrinkage deprives the seed-coats of their impervious character.

Changes in the condition of the seed-coats associated with loss of impermeability, illustrated by *Guilandina bonducella*.

Whilst describing the stages in the shrinking process of this seed in a previous chapter (Chapter II), when the connection between deficient shrinkage and loss of impermeability was first pointed out, no reference was made to the singular changes in the condition of the outer coats then displayed. It is very remarkable that the moist, swollen pre-resting seed of the green unopened pod, though destined ultimately to become impervious to water, develops during the earliest stage of the shrinking process a number of parallel transverse fissures or cracks in the outer coat, and that the seed is only impermeable when these fissures become closed and hermetically sealed in the contracted resting seed. In the normal resting seed the cracks formed in the outer coats during the shrinking stage are indicated by faint striæ, now covered by the enamel-like cuticle; but in the deficiently shrunken seed the original cracks are much more evident and are not sealed over by the cuticle, but are more or less open, so that the seed is permeable both to air and water.

If we place in the sun one of these large, soft pre-resting seeds from the green unopened pod, in a few hours its surface will be traversed by regular and widely gaping transverse cracks, and will present the grooved appearance of a boy's top. It is

not uncommon to find seeds in this condition on the plant, when from some cause the pod has opened prematurely or has been injured in the green closed state. It would seem from my experiments that, excepting complete submergence in water, there are no conditions so moist as to prevent the initial shrinking of the soft, full-sized so-called unripe seeds found in the green pods of *Guilandina bonducella*. Two of these seeds placed in water under cover in Jamaica floated heavily, showing only a small portion protruding slightly above the water. Although during three days' immersion they increased their combined weight from 244 to 253 grains, they both developed fine concentric fissures in the small portions of their surfaces that were exposed to the air. On the following day, having reached a weight of 262 grains, they sank. Here immersion in water had completely checked the shrinking process, except in the unsubmerged surfaces exposed to the air.

One could scarcely imagine a method less likely to produce impermeability than that followed by the pre-resting or unripe seeds of *Guilandina bonducella*. As shown by Miss White in the appendix to Professor Ewart's paper, and as also brought out in my own experiments, the seat of impermeability lies principally in the hard prismatic layer of palisade cells beneath the structureless cuticle. Yet the cracks formed normally in the shrinking process are subcuticular, and as the seed contracts their sides become tightly pressed together, and a layer of cuticular enamel ultimately covers all.

It may be here remarked that, as in many leguminous plants, the shrinking of the seed is carried out in its entirety before the dehiscence of the pod. After the pod has opened, the seeds in it lie fully exposed to the sun's rays and become very warm, since the parent plant thrives best on beaches removed from the shade of trees. On one occasion in Jamaica I roughly estimated the temperature of the seeds as they lay in the gaping pod at 150° F. Although this exposure may add somewhat to the seed's durability by hardening the cover-

ings, my observations clearly indicated that the seeds acquire their impervious character in the closed pod.

Any injury of the green pod of *Guilandina bonducella* is likely to produce a defect in the impermeability of the resting seed by interrupting its shrinking process in the pre-resting state. Very premature dehiscence results in excessive shrivelling of the seed ; whilst dehiscence at a later stage, but before the seed has completed its normal shrinking, arrests the process and prevents the development of impermeability, though not depriving it of its power of germination.

Mould or mildew, by attacking the soft coats of the unripe leguminous seed, spoils its prospect of becoming impermeable by partially destroying the cuticle. At times it extends into the kernel, and the result is a rotting embryo ; but at other times the outcome of its attacks is a permeable resting seed, speckled in places where the cuticle is lacking ; and unless conditions favouring germination soon arise, the seed shrinks more and more and finally loses its vitality. These minute fungi take their place amongst the greatest foes of a seed's impermeability in the tropics. As illustrated by *Entada scandens*, this subject is discussed at length in Note 7 of the Appendix, and it has been already referred to at the close of Chapter IV.

I may here remark that Dr Gola in Italy made a prolonged experiment on the action of these small fungi on the impermeability of the seeds of four plants, of which one was *Acacia Farnesiana*. After exposing them to moist conditions for four months, after which they were found to be covered with mould, he ascertained that the percentage of permeable seeds was not much increased. Thus, in the case of *Acacia Farnesiana* the percentage of permeable seeds was only increased from 3 to 5 per cent. These indications are not opposed to my remarks in the preceding paragraph, since Dr Gola experimented on the hard matured resting seed, which would be very likely to resist the attacks of minute fungi. It is in the soft coats of the pre-resting or unripe seed that they find their opportunity.

Mould and impermeability.

Dr Gola's experiments.

Mould and the germinative capacity.

With regard to the effect of these fungi on the germinative capacity of resting seeds in general, all depends on the protection the seed owes to its coats. With both permeable and impermeable seeds it would seem that the coverings would usually offer sufficient protection until the next germinating season commenced ; but whilst the impervious seeds would be able to withstand the attack for a long period, it is likely that the permeable seeds would succumb before a second opportunity of germinating presented itself. We have just seen that, as ascertained by Gola, mould affects but little the impermeability of resting seeds, an inference that may be extended to their germinative capacity. With Rape-seed (Saatraps), which had become covered with these growths after being exposed for forty-three days in moist conditions, Nobbe (p. 107) found that 85 per cent. germinated, the germinative capacity of the sample being 99 per cent. Since these seeds swelled in water, they would illustrate the behaviour of permeable seeds in this respect.

Mould is the enemy of the soft, unripe pre-resting seed.

It would seem, therefore, that the resting seed in its hardened coats is fairly proof against the attacks of mould, and that speculations as to the direct influence of these small fungi on seeds must be restricted to the seed in its unprotected state, as when it is prematurely exposed in the soft condition through the untimely opening of the fruit. Nature usually ensures the safety of the seed by securing that its coverings harden before the exposure to the outer world takes place. As shown in a subsequent chapter, the hardening of the seed-coverings precedes the opening of the fruit, whether moist or dry, whether rupturing through decay or dehiscing in a regular manner. Were it otherwise, propagation by seed would become impossible except in regions where mould and mildew are infrequent. There seems at first glance a special provision here ; but one could read the same into every detail of a plant's life-history. In a world where all is adaptation it seems idle to employ the term at all. Yet in the tropics one would be strongly tempted to use the phrase in this matter of

fruits, seeds, and minute parasitic fungi. In my experiments in those regions, I found it very difficult to dry the bared kernels of seeds, or to dry seeds which had been cut across, since mould used to form in a few days on the unprotected or cut surfaces.

But to return to the principal theme of this chapter, I think enough has been said to connect with deficient shrinkage the origin of permeable seeds in plants where impermeability is more or less the rule. Here, then, permeability is associated with insufficient drying. Various allusions of similar significance occur in different parts of this work, and I have shown that the trend of Professor Ewart's observations on the seeds of the Australian Acacias is in the same direction. But clear as the indications may seem, there has been another view of the origin of impermeability during the seed's maturation which has been advanced by Dr Gola. It is requisite to remember that by an impermeable seed we always imply a seed impervious to water; and this will explain why mention is not made in this connection of the recent researches of Becquerel, which refer principally to imperviousness to air produced by the desiccation of certain normally permeable seeds, such as Peas, Beans, and Lupines (*Annales des Sciences Naturelles Botanique*, 1907).

Dr Gola's view, as stated not only in his original memoir, published in 1905 by the Royal Academy of Science of Turin, but also in the summary he himself contributed to the *Botanisches Centralblatt* in 1906, is that the impermeability of its coats is due to the seed's insufficient maturation under the influence of such climatic and local factors as cold, drought, great humidity, excessive shade, etc. In order to show that impermeability goes with immaturity, he gives in a table the results of experiments on the seeds of seven species of leguminous plants of the genera *Acacia*, *Cytisus*, *Genista*, *Robinia*, and *Trifolium*, in which he connects the greater tendency to absorb water with the greater maturity of the seed. As given in Note 8 of the Appendix, where the table is

The connection between permeability and incomplete shrinkage is established in this chapter.

Dr Gola's view connecting impermeability with immaturity.

reproduced, the results do not appear convincing. With the exception of two of the species experimented on, there is but slight contrast in the behaviour of the more mature and less mature seeds, and even in those two cases the contrast is not striking. Then, again, in the instance of the seeds of the species of *Acacia* (*A. Farnesiana*), it would be difficult to draw any inference from the circumstance that the less matured seeds contained no permeable seeds and the more matured 8 per cent., when the value given in the general table for the ordinary mature seeds is 3 per cent. I must be pardoned for saying that, as presented, the differences are too small to serve as the basis of a theory, whilst the data are hardly sufficient in quantity. Then, again, the expressions "more mature" and "less mature" can only apply to the condition of the coats, since the embryo is as fully mature in the soft full-grown seed of the green pod as it is in the normal resting seed.

Still, the trend of the indications would be in favour of Dr Gola's interpretation in default of a more probable explanation. I made a long study of the shrinking process in seeds, and all my results point to the opposite conclusion, namely, that the occurrence of permeable seeds amongst typically impermeable seeds is due to deficient shrinkage, or, in other words, that immaturity is associated not with impermeability but with permeability. Professor Ewart's extensive researches yielded results supporting the same conclusion; and one may recall his remark (p. 197) concerning leguminous seeds (the same order tested by Dr Gola in this connection), that the seeds which take up water with difficulty are smaller, drier, and in appearance harder than the readily swelling ones of the same species.

It often occurred in my own investigations that shrivelled very immature seeds absorbed water less readily than seeds still immature, though less shrunken. But this was not the test of maturity employed by Dr Gola. Adopting the conclusion that the complete absence of chlorophyll in the integu-

ments is the index of perfect maturation, he proceeded to study the question of permeability from that standpoint. Taking only "germinable" seeds, he finally inferred that the greener seeds are the less mature and the more impermeable. The general trend of my observations is all against such a view, deficient shrinkage and loss of impermeability being uniformly associated. The green colour of imperfectly shrunken seeds, where the normal resting seed was impermeable, often came under my notice; but always connected with loss of impermeability more or less complete.

Taking the seeds of *Acacia Farnesiana*, the shrinking process of which I observed in Grenada and Jamaica, I found that full-sized so-called unripe seeds, when allowed to go through the shrinking stage detached from the pod, remained green, though in other respects resembling the normal brown resting seed. I did not test their permeability, but since 85 per cent. of the brown seeds from the same plants proved to be impermeable, the margin of possible advantage left for the green seeds was small. Dr Gola's results have proved of so much service to me that one feels loth to dissent from him when he associates impermeability with immaturity; but I feel confident that should he ever extend his researches to the shrinking process of seeds, he will arrive at a different conclusion.

This chapter may be concluded with the remark that there are several points in the behaviour of seeds, notably those concerned with the differences in the water-contents of permeable and impermeable seeds, and with their absorptive capacities after the oven test, which will be further elucidated in the succeeding chapters, especially in that dealing with Hygroscopicity.

SUMMARY

(1) According to the existence or absence of impermeable coverings, seeds are here divided into three groups: (a) impermeable, where all the normal seeds are impermeable to water; (b) permeable, where all the seeds are permeable; and (c) variable, an extensive group

where both kinds of seeds occur in the same plant, sometimes, but not usually, distinguished also by external characters. It is the variable group that offers the best materials for study (p. 91).

(2) The author then gives the list of about 105 species of seeds on which he experimented, arranged in these three groups. Two-fifths of them are leguminous, and of these three-fourths are claimed by the two groups with impermeable seeds, a fact indicating the predominance of impermeable seeds amongst the Leguminosæ as compared with other orders, and previously established by the researches of Nobbe, Gola, Ewart, and others (p. 93).

(3) It is shown that impermeable seed-coats, whilst characterising both buoyant and non-buoyant seeds, are indispensable for seeds that are transported by currents, and that the coral island in mid-ocean would be deprived of many of its most conspicuous plants if their seeds were pervious to water. The author proceeds to point out that as regards the adaptive relations of impermeability it would be wise to cast one's net widely and adopt the standpoint of Professor Ewart that in seed-impermeability we have a general adaptation to soil-conditions (p. 97).

(4) The lesson of the plants possessing both permeable and impermeable seeds distinguished by external characters is supplied by *Entada polystachya*. In this connection it is remarked that the clue to the origin of these two kinds of seeds in the same plants lies in the shrinking and drying of the soft pre-resting seed, a process which is completed in the impermeable seed, but arrested at an earlier stage in the permeable seed. The cause of the check in the shrinking and drying of the seed is determined by variation in the behaviour of the drying pod (p. 98).

(5) The same indications are supplied by those numerous plants where permeable and impermeable seeds are associated without differing much in their external characters, as illustrated by *Casalpinia Sappan* and *Ipomœa tuberosa* (p. 101).

(6) The difficulties that may attend the development of impermeability in seeds are then illustrated in detail from a study of *Dioclea reflexa* in the forests of Grenada (p. 103).

(7) The changes in the condition of the seed-coats associated with loss of impermeability are exemplified by *Guilandina bonducella* (p. 105).

(8) Mould or mildew, by attacking the soft coats of the seed in the moist green pod and destroying the cuticle, is regarded as one of the greatest foes to the development of impermeability. That typical hard resting seeds may be largely proof against the attacks of these minute fungi has been shown by the experiments of Nobbe and Gola. But the author observes that it is not there we should look for risks to the seed from this cause, since it is the so-called unripe soft-coated seed

before shrinkage and hardening have begun that offers to these fungi their opportunity (p. 107).

(9) After remarking that the connection between permeability and insufficient shrinkage has been established in this chapter, the author proceeds to discuss Dr Gola's view connecting impermeability with immaturity and shows that his theory cannot be sustained (p. 109).

(10) The reader is reminded that many features in the behaviour of permeable and impermeable seeds, especially those concerned with their capacity of absorbing water from the air after being exposed to a temperature of 100° C., will be elucidated in subsequent chapters, particularly in that on Hygroscopicity (p. 111).

CHAPTER VI

ADDITIONAL EVIDENCE ON THE CONTRAST IN BEHAVIOUR BETWEEN PERMEABLE AND IMPERMEABLE SEEDS

THIS chapter contains the bulk of the data on which are based the distinctions in behaviour between impermeable and permeable seeds as typified by those of *Guilandina bonducella* and *Canavalia ensiformis* in Chapter IV. Some of their differences, such as those concerned with hygroscopticity and permeability, will be found generally treated in the preceding and in following chapters. Here we are at first more especially concerned with the distinctions in their behaviour when bared or punctured or broken up and exposed to the air.

We will take first the additional evidence concerning the effects of puncturing or baring the three types of seeds described in the preceding chapter—the impermeable, the variable, and the permeable—and will commence with some additional results of experiments on punctured impermeable seeds. The effect of increasing the weight through the absorption of water from the air has already been discussed in the case of *Guilandina bonducella* in Chapter IV. The results for the seeds of *Entada scandens* in an experiment covering two years are tabulated below.

Additional
experiments
by punctur-
ing or filing
impermeable
seeds.

[TABLE

RESULTS OF EXPERIMENTS ON SEEDS OF ENTADA SCANDENS BY FILING INTO THE SEED-COATS. (The five seeds employed varied from 323 to 430 grains, but the results are stated in percentages.)

	Original weight.	After 3 weeks.	4½ weeks.	2 months.	4 months.	11 months.	15 months.	18 months.	21 months.	2 years.
A. With coats intact	100	100	100	100	100	100	100	100	100	100
B. Filed into middle layer of the coats	100	100·2	100·3	100·6	101·1	101·6	100·9	101·1	101·3	100·7
C. Do.	100	100·3	100·4	100·8	101·5	101·4	100·5			
D. Filed through the coats, exposing the kernel.	100	100·5	100·7	101·3	102·4	102·8	101·8			
E. Do.	100	100·2	100·3	100·6	101·3	101·4	100·4	100·7	101·1	100·1

Note.—The actual variation of A was only 406·5 to 406·6 during the two years. Seeds C and D failed to germinate when tested; the others were not tried. Probably the failure was due to the method employed, since seeds of *Guilandina bonducella*, subjected to a similar experiment, germinated healthily, after remaining for two years in the condition of B and D. (See Chapter IV.)

The indications given in Chapter IV as regards the relative effects on the subsequent weight of impermeable seeds of puncturing the coats and of removing them altogether may here be supplemented. As before remarked, the increase in weight through the absorption of water from the air is more rapid when the seed is bared than when it is merely punctured or filed, the maximum weight being usually attained in a few days in the one case, whilst the gain in the second case is extended over several weeks and even months. In Chapter IV it has been already shown in the case of a typical experiment on the seeds of *Guilandina bonducella* that whilst the bared kernels reached their maximum weight of 14 or 15 per cent. in excess during five days, the filed seeds occupied four or five months in increasing their weight 10 or 11 per cent. The punctured seeds of *Entada scandens* behave in the same tedious way as indicated in the tabulated results above given, whilst the bared kernels

Impermeable seeds gain weight far more rapidly when bared than when punctured or filed.

attain their maximum weight in a few days. If a number of seeds are bared together in the same experiment, the increase of weight might astonish the observer when unprepared for such a result. A sample of 1000 grains of the seeds of *Guilandina bonducella* would in less than a week weigh from 1100 to 1180 grains; but even the testimony of the bared kernel of a single seed as given below would be sufficiently striking.

The following data represent the result of an experiment on a single bared kernel of *Guilandina bonducella* :—

Original weight	. . .	15·1 grains
After 1 day	. . .	16·8 ”
” 4 days	. . .	17·7 ”
” 7 ”	. . .	17·0 ”
” 15 ”	. . .	17·2 ”
Gain in weight	. . .	17·2 per cent.

The range of the increase of weight of the bared kernels of *Guilandina bonducella*.

Although five or six days are usually sufficient in the case of this and other impermeable seeds for the attainment of the maximum weight, the period may be as short as three or as long as ten days, the time being extended or shortened by the relative dryness or humidity of the air. The varying hygrometric conditions of the air also account for some of the differences between the results of experiments, but only to the extent of 2 or 3 per cent., which represents the ordinary range of hygroscopicity. The results of six experiments on the bared kernels of *Guilandina bonducella*, mostly in the West Indies, the average weight of a kernel being 16 or 17 grains, are given below.

RESULTS OF EXPERIMENTS ON THE BARED KERNELS OF *GUILANDINA BONDUCELLA*, SHOWING THE INCREASE IN WEIGHT BY THE ABSORPTION OF AQUEOUS VAPOUR AFTER AN EXPOSURE OF A FEW DAYS TO THE AIR.

Number of kernels.	Locality of experiment.	Gain of weight in air.
1	Jamaica	10·2 per cent.
1	”	17·6 ”
1	”	17·2 ”
3	Grenada	15·0 ”
3	England	10·2 ”
3	Grenada	16·2 ”

These results indicate a range of from 10 to 17 per cent. in the increase of weight which recently collected seeds of *Guilandina bonducella* experience on being deprived of their coverings. If we allow for the usual hygroscopic reaction, this would probably represent a true range of 12 to 15 per cent.

One other impermeable leguminous seed may here be specially mentioned in connection with the variations in its increase of weight on being exposed to the air after being deprived of its coverings. Four samples of kernels of *Entada scandens* weighing from 100 to 260 grains increased their weight during an exposure to the air of from four to ten days by 4.2, 5.7, 6.8, and 12.2 per cent. The last result was obtained during humid weather in Jamaica; and it is evident from the progress of the experiment which is shown below that if allowance is made for the hygroscopic reaction (that is, by deducting half the variation), the excess weight would not have been much over 10 per cent.

The range
of *Entada*
scandens.

I here append the particulars of this experiment in Jamaica on the bared kernel of *Entada scandens*, which is noteworthy as illustrating the rate of increase and the effect of the ordinary hygroscopic reaction on the materials.

Original weight	.	.	.	100	grains
After 7 hours	.	.	.	102.3	"
" 1 day	.	.	.	106.5	"
" 2 days	.	.	.	109.1	"
" 3 "	.	.	.	110.8	"
" 4 "	.	.	.	112.2	"
" 5 "	.	.	.	112.25	"
" 6 "	.	.	.	110.8	"
" 7 "	.	.	.	110.0	"
" 10 "	.	.	.	111.5	"
" 14 "	.	.	.	108.1	"
" 16 "	.	.	.	111.1	"

The average results of my experiments on the bared kernels of these and other leguminous impermeable seeds are tabulated below, together with those for two species of *Ipomæa*; and it is of importance to note in passing that seeds

General
results for
impermeable
seeds.

of such a different order (Convolvulacæ) display the same quality when impermeable.

TABLE SHOWING THE USUAL INCREASE OF WEIGHT THROUGH THE ABSORPTION OF WATER FROM THE AIR DISPLAYED BY IMPERMEABLE SEEDS, EITHER AFTER BEING BARED OF THEIR COVERINGS OR AFTER BEING CUT ACROSS IN THEIR COATS. (All are leguminous excepting the two last.)

Name of species, with average weight of a single seed.	Gain in weight after exposure to the air for 5 to 7 days.		Locality of experiment.
	Bared kernels.	Cut in halves in their coats.	
<i>Adenanthera pavonina</i> (5 grains)	2.9 per cent.	...	England.
<i>Dioclea reflexa</i> (100 grains) . . .	10.6 "	...	Grenada.
	6.0 "	...	England.
<i>Entada scandens</i> (400 grains) . . .	5.5 "	...	"
	10.0 "	...	Jamaica.
<i>Guilandina bonduc</i> (50 grains) . . .	8.2 "	...	England.
	15.2 "	...	Grenada and
" <i>bonducella</i> (40 grains) . . .			Jamaica.
	10.2 "	...	England.
" <i>glabra</i> (65 grains) . . .	6.0 "	...	"
<i>Leucæna glauca</i> (0.8 grains)	5.0 per cent.	Grenada.
<i>Mucuna urens</i> (90 grains) . . .	6.2 per cent.	...	England.
<i>Strongylodon lucidum</i> (40 grains)	...	5.2 per cent.	"
<i>Ulex europæus</i> (0.1 grain)	5.0 "	"
<i>Ipomœa dissecta</i> (2.5 grains) . . .	6.0 per cent.	...	Jamaica.
" <i>pes-capræ</i> (3 grains)	4.0 per cent.	England.

The seeds in the foregoing list vary greatly in size and weight, from those of *Leucæna glauca*, which average only 0.8 of a grain, to those of *Entada scandens*, which average 400 grains. The samples of kernels used were generally 50 to 100 grains, but greater in the case of the large seeds. The hygroscopic reaction is as far as possible excluded. It will be inferred that it is not possible to strike an average increase of weight for the bared kernels of impermeable seeds when exposed to the air. Each kind of seed has its own régime in this respect, which is influenced not only by the relative dryness of the kernel, but also by the amount of oil it contains. This probably explains the small excess weight of the seeds of *Adenanthera pavonina*.

Speaking very generally, however, we may infer that leguminous impermeable seeds when bared commonly increase their weight from 5 to 10 per cent. by abstracting moisture from the air.

A question of interest here presents itself as to the duration of the ultra-dryness of the kernels of impermeable seeds. My materials for furnishing an answer, though insufficient, tend to show that this condition may be maintained for several years. A seed of *Mucuna urens*, gathered by me from the plant in Hawaii eleven years before, increased its weight when bared of its coats in England 6.5 per cent. in ten days. In the same way, the bared kernels of two seeds of *Guilandina bonducella* obtained by me in Fiji ten years before added 7.2 per cent. to their weight; and a seed of *Strongylodon lucidum*, picked up amongst the drift on a Fijian beach eleven years before, and perhaps a year or two old then, increased its weight by 6 per cent. when bared in England of its coats. In the case of the two last-named species, seeds collected at the same time and place and tested for germination at the time of the above experiment germinated healthily and supplied plants for my greenhouse.

Duration of the ultra-dryness of impermeable seeds.

There is but slight indication here of any marked decrease in the ultra-dryness of impermeable seeds during a period of ten or eleven years. The increase in weight (6.5 per cent.) of the seed of *Mucuna urens* is rather above the average (6.0 per cent.) for three seeds, six to eighteen months old, which were also tested in England. On the other hand, the rate of increase for the Fijian seeds of *Guilandina bonducella* ten years old (7.2 per cent.) is considerably under the average for the tropics (15 per cent.). However, the contrast is not nearly so great as it appears, as the Fijian seeds were experimented on in England, and, as shown in the table below, the rate of increase of the weight of the bared seeds of *Guilandina bonducella* in a temperate climate would average only about 10 per cent.

There are two other points to be referred to in connection with the behaviour of the bared kernels of impermeable seeds, namely, the respective influences of tropical and temperate climates on the gain in weight in air, and the duration of this excess weight. We would expect the bared kernel of a tropical seed to gain more water from the air in the more humid climate of the West Indies than in the drier climate of the south of England. We should also expect the excess in weight to be permanent yet subject to the ordinary hygroscopic reaction, as long as the seed retains its vitality.

RESULTS OF EXPERIMENTS ON THE SEEDS OF THE SAME PLANT IN THE TROPICS (WEST INDIES), AND IN THE SOUTH OF ENGLAND.

	Place of experiment.	Gain of weight in air of bared kernel.
<i>Guilandina bonducella</i>	Jamaica	10'2 per cent.
	"	17'6 "
	"	17'2 "
	Grenada	15'0 "
	"	16'2 "
<i>Entada scandens</i>	England	10'2 "
	"	4'2 "
	"	5'7 "
<i>Dioclea reflexa</i>	"	6'8 "
	Jamaica	10'2 "
	Grenada	10'6 "
	England	6'0 "

The first point is illustrated in the foregoing table. Since the seeds there referred to, as well as those named below, are all tropical, the question, as far as this investigation is concerned, relates to the influence of a temperate climate on the capacity of the bared kernels of impermeable tropical seeds of increasing their weight by absorbing water from the air. The data of the table indicate that the absorptive capacity is diminished in temperate climates.

The next point is concerned with the permanence of the excess weight acquired by the exposure to air of the

The influence of a temperate climate on the absorptive capacity of bared impermeable tropical seeds.

bared kernels of impermeable seeds. This has already been noticed in the case of the seeds of *Guilandina bonducella* in Chapter IV, where it is shown that after the first gain of 13 per cent. the weight began to diminish slowly, though even after two years there was still an excess of 3 per cent., allowing for the hygroscopic variation. This loss of the excess weight in time is not at first sight easily explained. However, since the bared seed in absorbing water from the air assumes the rôle of the kernel of a permeable seed, it is likely that light may be thrown on it when we come to discuss the final fate of permeable seeds in time.

The degree of permanence of the excess weight acquired by bared impermeable seeds.

On the other hand, a different indication is offered where the seed is punctured or filed, when the gain in weight takes place very slowly. Thus it is shown in the table of results given in Chapter IV for punctured seeds of *Guilandina bonducella* that the punctured seeds occupied some months in reaching the maximum excess weight of 10 or 11 per cent., and even after two years were still 7 or 8 per cent. heavier than before they were punctured or filed.

However, experiments of this kind being always conducted under dry conditions are by no means imitations of what occurs in nature, though they indicate latent properties or potentialities of impermeable seeds. In the home of the plant, such a seed, if deprived by some defect or injury of the proper protection of its impervious coverings, would either pass on to the germinating stage or would become mouldy and decay. But it is only with those seeds where there is a great increase in weight, such as occurs with the bared kernels of *Guilandina bonducella*, that one can test the duration of the excess weight by eliminating the ordinary hygroscopic reaction of 2 or 3 per cent. Impermeable seeds, when deprived of their coats, gather weight during the first week or two independently to some degree of the atmospheric conditions. After this they respond normally to the changes in the hygrometric state of

the air ; and if the excess weight, due to the absorption of aqueous vapour by the ultra-dry kernel, is only 3 or 4 per cent., it is difficult to exclude the disturbing influence of the hygroscopic reaction. Such experiments in the tropics are likely to be terminated by attacks of mould, and even in England it is necessary that they should be carried out in a dry room. The appearance of mould is usually preceded by a marked increase in weight. The bared kernels of an inland Jamaican species of *Guilandina* gained about 6 per cent. in weight during the first ten days, and, subject to slight variation, preserved this excess for about two months, when very damp weather followed, and the seeds, after having augmented their weight to 10 per cent., were attacked by mould.

With regard to the "variable" group of seeds, where both permeable and impermeable seeds occur in the same plant, only a few remarks will be needed before giving the tabulated results of my observations. As concerning the bared kernel's capacity for absorbing water from the air, these seeds exhibit the extreme behaviour of the permeable and impermeable seeds, in the first case merely the ordinary hygroscopic variation of 1 or 1.5 per cent. on either side of the mean, in the second case a marked and permanent increase often of 10 per cent. or more. If we had to handle two samples of seeds from the same plant which presented this great contrast in behaviour, we should at once know that one sample consisted only of permeable seeds and the other sample only of impermeable seeds. Almost always, however, the sample would be mixed, and then we should get an intermediate result, for instance, an average increase of weight, after allowing for the hygroscopic reaction, of 4 or 5 per cent. Some seedsman, more practical than the author, might be able to make a scale of comparison which could be used for proving his seeds ; but it would be requisite to have a standard of comparison for each species.

The capacity of the bared kernels of variable seeds of absorbing water from the air.

RESULTS OF OBSERVATIONS ON THE CAPACITY OF VARIABLE SEEDS OF INCREASING THEIR WEIGHT BY ABSORBING WATER FROM THE AIR, EITHER AFTER BEING COMPLETELY DEPRIVED OF THEIR COATS, OR AFTER BEING CUT ACROSS IN THEIR COATS. (The hygroscopic reaction is excluded.)

Note.—The term “variable” is applied when a plant produces both permeable and impermeable seeds. With small seeds it is often more convenient to expose them to the air cut in halves than to bare their kernels. The difference in the results of the two methods is not very great, and will be dealt with in the next chapter. The letters A, B, C, indicate only approximate estimates.

- A. Sample where most seeds are permeable.
- B. ” ” impermeable.
- C. ” they are equally mixed.

	Sample.	Gain in weight after exposure to air for 5 days or more.		Locality of experiment.
		Bared kernels.	Cut in halves in their coats.	
Abrus precatorius . . .	A	1·0 per cent.	...	England.
	B	5·0 ”	...	”
	C	...	2·0 per cent.	Grenada.
Acacia Farnesiana . . .	C	...	2·2 ”	”
Albizzia Lebbek . . .	A	...	Hygroscopic only	England.
Bauhinia (species) . . .	A	Grenada.
Cæsalpinia Sappan . . .	A	1·0 per cent.	...	”
	B	9·0 ”	...	”
” <i>sepiaria</i> . . .	A	Hygroscopic only	...	Jamaica.
Canavalia gladiata . . .	B	7·0 per cent.	...	”
	A	Hygroscopic only	...	England.
” <i>obtusifolia</i> . . .	B	5·0 per cent.	...	”
	B	...	6·0 per cent.	”
Canna indica	Hygroscopic only	”
Cassia fistula . . .	B	...	3·0 per cent.	”
” <i>marginata</i> . . .	B	...	1·9 ”	”
Entada polystachya . . .	A	1·6 per cent.	...	Grenada.
	B	9·4 ”	...	”
	B	...	3·5 per cent.	”
Enterolobium cyclocarpum . . .	B	{ 3·3 per cent. } { (2·5) ” } { 3·0 ” } { (2·6) ” }	...	England.
Erythrina corallodendron . . .	C	”
	C	...	2·4 per cent.	”
” <i>indica</i> . . .	A	...	0·5 ”	Grenada.
	A	...	2·3 ”	”
	B	...	6·2 ”	”
	C	...	4·5 ”	England.
	C	{ 5·0 per cent. } { (4·2) ” }	...	”
” <i>velutina</i> . . .	B	10·0 ”	...	Jamaica.
Ipomœa tuberosa . . .	A	...	Hygroscopic only	England.
	B	...	4·6 per cent.	”
Poinciana regia . . .	A	...	Hygroscopic only	”

Note.—The figures in parenthesis in the “bared kernels” column indicate the result when the coats are included, thus enabling a comparison to be made with the data in the next column.

The effect of depriving a permeable seed of its coverings.

The effect of baring a permeable seed has been already referred to in Chapter IV in the instance of *Canavalia ensiformis*. Since the kernel is placed in hygrometric relations with the atmosphere by its porous coats, one would not look for any marked result with seeds that have completed the drying process. Indeed, the immediate effect on a seed that has reached a stable weight is merely to give a rather freer play to its hygroscopicity. There is, as one would expect, no attempt to permanently increase its weight. The contrary is, in fact, the case with a seed that has yet water to yield to the air, since the drying process is accelerated by the removal of its coverings. The contrast between permeable and impermeable seeds in this respect is well exhibited in those plants producing both types capable of being readily distinguished by the eye, as shown in the results below tabulated.

	Character of seed.	Effect of exposing the bared kernels to the air for 4 or 5 days, stated as a percentage of the original weight.
Entada polystachya .	Permeable	Gained 1·6 per cent.; mainly hygroscopic.
Cæsalpinia Sappan .	Impermeable	Gained 9·4 per cent.
	Permeable	Varied only 0·7 per cent.; entirely hygroscopic.
	Impermeable	Gained 9·0 per cent.

I made a large number of observations on the effect of baring the kernels of permeable completely air-dry seeds, on the results of which are based the above general conclusions. As examples of permeable seeds which merely continue to behave hygroscopically on the removal of their coverings, though often in an increased degree, the following may be cited:—

- Achras Sapota (Sapodilla)
- Anona muricata (Sour-sop)
- „ palustris
- „ reticulata (Custard Apple)
- „ squamosa (Sweet-sop)
- Canavalia ensiformis

Cardiospermum grandiflorum
 Chrysophyllum Cainito (Star Apple)
 Citrus decumana (Shaddock)
 Dolichos Lablab
 Faba vulgaris (Broad Bean)
 Hura crepitans (Sand-box Tree)
 Luffa acutangula (Loofah)
 Phaseolus multiflorus (Scarlet-runner)
 Pisum sativum (Pea)
 Ricinus communis (Castor-oil)

Of the thirteen genera here named five are leguminous and the rest belong to a variety of other families. This list is simply intended to illustrate the subject. A number of additional examples might have been given; whilst others, like the seeds of the Horse-chestnut (*Æsculus Hippocastanum*) and of Acorns (*Quercus*), will be more fittingly dealt with in discussing the drying process of permeable seeds. In this connection it should be observed that this matter has only been handled here in so far as it brings out the contrast in behaviour between permeable and impermeable seeds when deprived of their coverings.

The ultra-dryness of impermeable seeds as compared with permeable seeds which has been disclosed by the various experiments above discussed is confirmed by the evidence supplied when the seeds of the different types are exposed to a temperature of 100° C. In other words, it is associated with a low water-percentage. This was established for the seeds of *Guilandina bonducella* in Chapter IV. Here I will illustrate it by a number of fresh examples and will discuss the subject, therefore, from a more general standpoint. For this purpose all my results for the three types of seeds are given in the table in a later page of this chapter.

There is but little significance in this feature of impermeable seeds until it comes to be contrasted with the behaviour of permeable seeds; and even then the contrast must be made with discretion. For instance, if we were to compare impermeable leguminous seeds indiscriminately with permeable seeds

Additional evidence of the association of the ultra-dryness of impermeable seeds with a low water-percentage.

of other orders, we should find that there is often no sort of relation between them as regards the capacity of absorbing water from the air in the broken condition and the actual water-contents as indicated by the loss of weight in the oven. For example, an average impermeable seed which contained 9 per cent. of water would be able to increase its weight by about 7 per cent. when broken up and exposed to the air. It would be ultra-dry in the entire condition to that extent. On the other hand, this percentage of water in oily seeds like those of *Ricinus* or *Hura* or *Eleis* would be no indication of dryness in the seed, since except for the hygroscopic variation they would remain unchanged in weight on exposure to the air in the broken condition. Here matters are on quite another plane, and for a valid comparison of seeds of different orders we must not look in this direction. It is therefore requisite, if we wish to connect the seed's capacity of increasing its weight by abstracting water from the air with its deficient water-contents, that we should restrict the comparison to seeds of the same order. In this case we take leguminous seeds; but even here disturbing influences may come into play, though they are more easily avoided.

The necessity of confining the inquiry to seeds of the same order.

Leguminous impermeable and permeable seeds contrasted.

So, confining ourselves at present to the Leguminosæ, we will at first refer to the indications afforded by impermeable seeds in the table that a seed's capacity of increasing its weight when bared of its coats or in the broken condition is determined by a low water-percentage.

We can see at once in the results for impermeable leguminous seeds that the seeds which lose least weight when submitted to a temperature of 100° C. are those which add most to their weight when exposed unprotected to the air. Thus, we see that the three kinds of seeds with the lowest water-percentage, *Dioclea reflexa*, *Guilandina bonducella*, and *G. bonduc*, are those which add most to their weight when exposed to the air. On the average these seeds with a water-percentage of 7.5 per cent. add 9.2 per cent. to their weight when exposed in the broken condition to the air. The other impermeable

leguminous seeds (*Adenanthera pavonina*, *Entada scandens*, *Mucuna urens*) give an average gain in air of 5.0 per cent., with an average water-percentage of 11.7. These results may be accepted tentatively as representing the average behaviour of impermeable seeds when broken up and exposed to the air, viz. :

Seeds holding 11.7 per cent. of water gain 5.0 per cent.
 „ 7.5 „ „ 9.2 „

At best this is only a rough indication, as each seed has a régime of its own in this respect. The real significance of these figures becomes more apparent when we contrast them generally with those for permeable seeds of the same order, taking as our examples the seeds of *Canavalia ensiformis*, *Faba vulgaris* (Broad Bean), *Phaseolus multiflorus* (Scarlet-runner), and *Pisum sativum* (Pea), which hold on the average about 15 per cent. of water when the drying process is complete, and make no permanent addition to their weight when broken up or cut open or laid bare and exposed to the air. Contrasted with impermeable seeds we get these general results :—

Impermeable seeds holding 7.5 per cent. of water add 9.2 per cent. to their weight.
 Impermeable seeds holding 11.7 per cent. of water add 5.0 per cent. to their weight.
 Permeable seeds holding 15.0 per cent. of water add 0.0, behaving hygroscopically.

Numerous disturbing influences come into play in making a rough estimate, such as that given above ; but its general indications are confirmed by the results obtained from experiments in which such influences are largely eliminated, namely, by contrasting the seeds of the same plant in those species where both permeable and impermeable seeds are represented, namely, in the variable group. But even here, as indicated in the table, we must be able to distinguish between samples containing very different proportions of these two kinds of seeds. There is a practical difficulty in ascertaining a seed's

The elimination of disturbing influences by contrasting seeds of the same plant where both types occur.

impermeability in water before testing the amount of its water-contents, and this difficulty is very apt to arise in dealing with variable seeds, notably in the seeds of *Poinciana regia*, which behave almost like permeable seeds.

It is to seeds like those of *Cæsalpinia Sappan* and *Entada polystachya*, where we can with some confidence distinguish the two types of seeds by their external characters before the experiment, that we must appeal. In their case it is plainly shown in the table that the seeds which imbibe in the broken condition most water from the air are those which lose least water in the oven, or, in other words, that the ultra-dryness of impermeable leguminous seeds is simply a diminution in the water-contents as compared with permeable seeds. Thus we find for *Cæsalpinia Sappan* that when the seeds held about 14 per cent. of water they did not increase their weight when exposed in a broken state to the air. On the other hand, when their water-contents amounted to less than 10 per cent. they increased their weight about 9 per cent. by abstracting water from the air. Similar results were obtained for *Entada polystachya*. Thus :

<i>Cæsalpinia Sappan</i>	{	Seeds with 14 per cent. of water merely behave hygroscopically when broken.
		Seeds with 9·7 per cent. of water add 9 per cent. to their weight when broken.
<i>Entada polystachya</i>	{	Seeds with 10 per cent. of water add 1·6 per cent. to their weight when broken.
		Seeds with 6 per cent. of water add 9·4 per cent. to their weight when broken.

The data given in the table for permeable seeds of other than leguminous plants are interesting, as they illustrate the fact that many permeable seeds may hold as little water as some of the impermeable leguminous seeds. This is particularly clear when we distinguish between the coats and the kernel, as is done in the table. Here we find that the kernels of permeable seeds like those of *Citrus*, *Hura*, etc., may hold less than 9 per cent. of water. Doubtless the presence of oil goes

to explain this low water-percentage ; but at all events this fact shows how necessary it was to avoid comparing seeds of different families when connecting impermeability with diminished water-contents.

I come now to the additional evidence in support of the principle typified by *Guilandina bonducella* in Chapter IV, that the seed-coverings of impermeable seeds possess the same quality of ultra-dryness as the kernel, though often in a somewhat diminished degree, and the same quality of supplying the deficiency by absorbing water from the air, the larger water-percentage of the coats being usually associated with a diminished absorptive capacity of the freshly exposed material.

Further evidence to show that in impermeable seeds the coverings possess the same quality of ultra-dryness as the kernel.

Most of my results are given in the table a few pages later ; but I will confine the discussion as before to leguminous impermeable seeds. All the kinds of seeds there tested possess this quality of ultra-dryness for the coats as well as the kernel, though the presence of oil in the kernel of *Adenantha pavonina* somewhat alters the régime. Most of the results represent the average of three or four or more experiments, the absorptive capacity in air and the water-percentage being determined independently. In spite of possible disturbing effects, due to variation in the seeds and in the atmospheric conditions, the data thus obtained go fairly well together. But in two cases, those of *Guilandina bonducella* and *Entada scandens*, this disturbing influence was removed by a simple expedient ; and these experiments have been specially added to the others, since they are not only the most critical but the most decisive. With *Guilandina bonducella* the coats and kernel of each seed were divided between two samples, so that the water-percentage and the absorptive capacity in air were simultaneously determined from similar examples. With *Entada scandens* the two samples of the seed-coverings and the two samples of the kernel were obtained from one large seed weighing about 500 grains. They gave the following results for the water-

percentage and for the fresh materials exposed to the air in a broken condition :—

<i>Guilandina bonducella</i>	{	Coats hold 7·6 per cent. of water and gain in weight 12 per cent.
		Kernels hold 4·2 per cent. of water and gain in weight 16 per cent.
<i>Entada scandens</i>	{	Coats hold 13·8 per cent. of water and gain in weight 8 per cent.
		Kernels hold 7·5 per cent. of water and gain in weight 12 per cent.

These two seeds illustrate what is shown by other impermeable seeds in the table, namely, that the smaller absorptive capacity of the seed's coats is associated with a larger water-percentage as compared with the kernel. *Dioclea reflexa* is irregular, however, in this respect. But the behaviour of variable seeds containing a good proportion of impermeable seeds supports the same conclusion. This is shown in the table by samples of seeds of *Cæsalpinia Sappan*, *Entada polystachya*, and two species of *Erythrina*.

Additional evidence to show that the absorptive quality of broken impermeable seeds is not affected by exposure to a temperature of 100° C. whether in the case of the coats or of the kernel.

In Chapter IV I have already referred to the circumstance that the capacity possessed by impermeable leguminous seeds of considerably increasing their weight when exposed in the broken condition to the air is but little affected by first subjecting the materials to a temperature of 100° C. for an hour or two. In that chapter I took the seeds of *Guilandina bonducella* as a type. Here I will discuss the additional evidence for impermeable seeds of the same order.

This double capacity was disclosed in a large number of experiments on impermeable leguminous seeds. In the table I have compared the two results obtained for seeds in the broken condition. In one column we have the gain in weight by abstracting moisture from the air when the materials are not heated. In another column we have the gain after the materials have been exposed to a temperature of 100° C. Many of the experiments on the absorptive capacity of the unheated and heated materials were carried out on different samples and under different climatic conditions, so that disturbing influences were likely to affect

them, and a very close approximation between the two absorptions could not often be looked for. However, in the main, these independent experiments confirm the principle indicated by the seeds of *Guilandina bonducella*, that exposure to a temperature of 100° C. does not seriously affect the absorptive capacity.

But to eliminate such disturbing conditions I made critical experiments on certain impermeable seeds in which the absorptive qualities of the unheated and heated materials were simultaneously tested in similar samples. The seeds in question were those of *Entada scandens*, *Erythrina indica*, and *Guilandina bonducella*. In the case of *Entada scandens*, one large seed weighing nearly 500 grains supplied all the material for the double experiment. In the cases of the two last named, each seed was divided between the two samples, the one for exposure without heat to the air, the other for exposure to the air after being subjected to a temperature of 100° C. The results were as follows :—

A. *Entada scandens*

Gain of coats and kernel : unheated, 10·8 per cent. ; after 100° C., 9·5 per cent.

Gain of coats alone : unheated, 8·2 per cent. ; after 100° C., 8·0 per cent.

Gain of kernels alone : unheated, 12·3 per cent. ; after 100° C., 10·4 per cent.

B. *Guilandina bonducella*

Gain of coats and kernel : unheated, 13·7 per cent. ; after 100° C., 14·2 per cent.

Gain of coats alone : unheated, 12·0 per cent. ; after 100° C., 13·3 per cent.

Gain of kernel alone : unheated, 16·2 per cent. ; after 100° C., 15·5 per cent.

C. *Erythrina indica* (impermeable seeds only selected)

Gain of coats and kernel : unheated, 4·5 per cent. ; after 100° C., 3·4 per cent.

Gain of coats alone : unheated, 2·3 per cent. ; after 100° C., 1·6 per cent.

Gain of kernel alone : unheated, 5·0 per cent. ; after 100° C., 4·1 per cent.

From these similar samples we learn that as a rule exposure to a temperature of 100° C. for from 1½ to 2 hours but little affected the capacities of either the seed-coverings or the kernel for increasing their weight by absorbing moisture from the air in the broken condition. It is scarcely worth while to labour this point. The same indications are supplied in the case of other impermeable seeds mentioned in the table, such as those of *Dioclea reflexa*, *Guilandina bonduc*, *Mucuna urens*, etc., and by the samples of variable seeds where impermeable seeds predominated, such as those of *Cesalpinia Sappan*, *Erythrina corallodendron*, etc.

The be-
haviour of
permeable
seeds.

Coming to permeable seeds of the leguminous type, we notice in the table that during the period of five days following the exposure to a temperature of 100° C., they all regained from the air most of the water lost in the oven. That they failed to return to the original weight is doubtless to be attributed to the limited duration of their exposure to the air, since it is clearly shown in the instances of *Faba vulgaris*, *Phaseolus multiflorus*, and *Pisum sativum* on p. 142 that if the test had covered a period of a week or two instead of only five days, the seeds would have regained their original weight. But they would not have displayed any excess, except such as is included in the ordinary hygroscopic variation of about 3 per cent., and this is the great point of contrast between permeable and impermeable seeds.

As respecting permeable seeds other than those of the Leguminosæ, the data for several kinds given in the table tell much the same story. After exposure to the same temperature of 100° C., they in most cases regained much of their lost weight by taking up water from the air, and, no doubt, if the test had been prolonged, they would have regained all. The behaviour of the seed-coverings of the Shaddock (*Citrus decumana*) is abnormal, but I can throw no light on it here. However, taking all the data for permeable seeds given in the table, it is evident that whether leguminous or otherwise, they as a general rule behave in the same way after being

exposed to a temperature of 100° C. in the broken or divided condition. In five days they regain most of the weight lost, and in a week or two they would regain all, maintaining their original weight subject to ordinary hygroscopic variation.

When comparing the absorptive capacities of permeable and impermeable seeds it is requisite that the drying and shrinking process should be complete. In all these experiments only seeds were employed that had accomplished the drying process and had attained a stable weight. If we place in the oven a seed that has not yet begun to dry, or has not yet completed that process, we meet with a very different behaviour. A bared fresh Horse-chestnut seed (*Æsculus*) cut up in slices, that had had its weight reduced in the oven from 100 to 52 grains, increased its weight by only 7 grains (52 + 7) during eight days. In the same way the seed of a fresh Acorn (*Quercus Robur*), after its weight had been reduced in the oven from 100 to 58 grains, added only 4 grains to its weight during an exposure to the air of eight days. A broken seed of *Dioclea reflexa* which had not completed the drying process lost 20 per cent. of its weight in the oven, and after five days was still 5 per cent. short of its original weight. On the other hand, normal resting seeds of the same plant, which lost 8.6 per cent. of their weight in the oven, behaved like typical impermeable seeds during an exposure of five days to the air, increasing their original weight by 9 per cent.

On the behaviour of seeds exposed to a temperature of 100° C. before they have commenced or before they have completed the drying process, the principle of Berthelot, discussed at length in Chapter VII, throws a flood of light. The water which they subsequently regain from the air is merely the water of hygroscopicity, which they would hold whether living or dead. This amounts on the average to only about 5 per cent. of the weight of the moist fresh seed that has not begun to dry. Most seeds lose quite 50 per cent. of their weight in the normal drying process, so that there would be a large proportion of the water which a fresh

The absorptive capacities of seeds when the drying process has not been completed.

moist seed loses in the oven that it could never regain. Such considerations render necessary a review of the general behaviour of seeds after exposure to the oven test. It will be shown in the following chapters that the whole problem can be stated in quite a different manner if we introduce the principle of Berthelot as a resolving factor.

Explanation
of the follow-
ing table.

The following table is intended to illustrate the contrast between impermeable and permeable seeds in their capacity of increasing their weight by absorbing water from the air when exposed in the broken condition, either with or without a previous exposure to a temperature of 100° to 110° C. It will be noticed that in impermeable seeds both the coats and kernel possess this quality of adding considerably to their weight when exposed unheated to the air; whilst with permeable seeds both coats and kernel retain their weight, merely displaying the normal hygroscopic variation of 2 or 3 per cent., 98·5 to 101·5. Usually the inability to increase the weight, except in the ordinary course of hygroscopic variation, is indicated by 100. A previous exposure in the oven for 1½ or 2 hours does not materially affect the behaviour of the seed or its parts. In the case of impermeable seeds much the same excess weight is attained in about five days after the oven test, whilst in permeable seeds the original weight is more or less regained during the same period after the heating; and in those cases where there is a marked failure to return to the original weight, it can be shown either that the seed had not completed its drying process before the experiment, or that the period of exposure to the air was too short, a week or two being in their case required (see p. 142). The behaviour of variable seeds is of course intermediate in character. . . . "Similar samples" used in certain experiments were samples where each seed tested had been divided between the two samples, so that truly mixed samples were simultaneously experimented on. The same object was effected in the case of large seeds like those of *Entada scandens* (weighing some 500 grains) by employing the same seed for both samples.

TABLE ILLUSTRATING THE CAPACITY OF SEEDS IN THE BROKEN CONDITION OF ABSORBING WATER FROM THE AIR AND THUS INCREASING THEIR WEIGHT. (The explanation of the table is given above. Leguminous seeds are indicated by L.)

	Character of seed.	Water-percentage.				Change of weight of coats and kernel together and of coats and kernel separately, after exposure to the air of about 5 days, the original weight in each case being taken as 100.						General remarks. (For the explanation of "similar samples" see the foregoing explanation of the table.)
		Coats and kernel.		Kernel.		Unheated.			After being first subjected to a temperature of 100° C. for 1½ to 2 hours.			
		Coats	kernel.	Coats.	Kernel.	Coats and kernel.	Coats.	Kernel.	Coats and kernel.	Coats.	Kernel.	
Adenanthera pavonina	L.	12.2	15.1	9.8	102.7	102.5	102.9	102.8	102.7	103.0	...	
Dioecia reflexa	L.	8.6	7.3	9.5	107.1	105.8	109.6	108.8	106.6	110.4	...	
Entada scandens	L.	11.4	15.2	8.9	106.4	105.0	107.2	104.6	103.0	105.0	...	
"	L.	9.9	13.8	7.5	110.8	108.2	112.3	109.5	108.0	110.4	Similar samples.	
Guilandina bonduc.	L.	6.0	7.1	4.9	108.9	109.7	108.2	110.4	110.9	109.8	...	
"	L.	8.0	9.3	5.3	111.5	110.1	112.5	112.0	111.1	113.1	...	
"	L.	6.2	7.6	4.2	113.7	112.0	116.2	114.2	113.3	115.5	Similar samples.	
"	L.	105.2	104.6	105.8	
"	L.	105.0	
Leuceana glauca	L.	106.0	104.5	106.7	104.2	103.0	105.0	...	
Mucuna urens	L.	11.6	12.0	11.5	105.2	105.0	
Strongylodon lucidum	L.	104.0	
Ulex europæus	L.	9.0	106.0	...	106.0	
Ipomœa dissecta	104.0	...	106.1	
" pes-capræ	...	9.8	100.5	100.7	100.1	100.3	101.0	100.1	Hygrosopic only, most seeds permeable.	
Abrus precatorius	L.	14.0	12.0	15.5	100.5	100.7	100.1	100.3	101.0	100.1	...	

TABLE ILLUSTRATING THE CAPACITY OF SEEDS, ETC.—continued.

Character of seed.	Water-percentage.				Unheated.				After being first subjected to a temperature of 100° C. for 1½ to 2 hours.		General remarks. (For the explanation of "similar samples" see the foregoing explanation of the table.)
	Coats and kernel.		Coats, Kernel.		Coats and kernel.		Coats, Kernel.		Coats and kernel.		
	Coats and kernel.	Coats.	Kernel.	Coats, Kernel.	Coats and kernel.	Coats.	Kernel.	Coats, Kernel.	Coats and kernel.		
Abrus precatorius . . . L.	12'0	105'0	106'2	104'3	Mostly impermeable.
Acacia Farnesiana . . . L.	102'0
Albizia Lebbeck . . . L.	102'2
Bauhinia (species of) . . . L.	101'0	Hygroscopic in behaviour.
Cæsalpinia Sappan . . . L.	13'9	15'9	13'2	100'0	100'0	100'0	99'9	102'0	99'0	99'0	Most of sample impermeable.
" . . . L.	9'7	13'1	8'3	108'9	107'5	109'3	104'7	106'4	104'0	104'0	Most of sample impermeable.
" sepiaria . . . L.	16'2	17'4	14'4	100'0	100'0	100'0	Most of sample impermeable.
" . . . L.	106'2	105'4	107'3	105'5	104'6	106'8	106'8	Most of sample impermeable.
Entada polystachya . . . L.	10'0	101'6	101'6	101'7	Most of sample impermeable.
" . . . L.	6'3	109'4	109'3	109'4	Most of sample impermeable.
Enterolobium cyclocarpum L.	102'5	101'8	103'3	Most of sample impermeable.

Variable	10.8	11.6	10.0	102.3	101.8	103.0	102.5	101.5	102.9	Similar samples.
<i>Erythrina corallodendron</i>	L.	11.1	9.3	104.5	102.3	105.0	103.4	101.6	104.1	"
<i>indica</i>	L.	9.2	9.3	100.0	100.0	110.0	103.4	101.6	104.1	"
<i>velutina</i>	L.	100.0	100.0	110.0	99.5	"
<i>Vicia sativa</i> and <i>V. sepium</i>	L.	15.0	...	104.0	100.0	105.0	"
<i>Canavalia gladiata</i>	L.	14.0	...	105.0	100.0	"
<i>obtusifolia</i>	L.	12.0	...	103.0	"
<i>Cassia fistula</i>	L.	101.9	"
<i>marginata</i>	L.	100.0	...	100.0	100.0	"
<i>Poinciana regia</i>	L.	13.0	...	100.0	...	100.0	100.0	"
<i>Canna indica</i>	L.	14.5	...	100.0	...	100.0	93.0	...	93.0	Slightly hygroscopic.
"	L.	17.0	...	104.6	...	102.6	102.6	...	103.0	Mostly permeable.
"	L.	9.9	...	100.0	100.0	100.0	96.4	95.7	97.6	" impermeable.
<i>Thespesia populnea</i>	L.	14.0	15.7	12.0	93.3	Seeds tested before dry-
<i>Canavalia ensiformis</i>	L.	18.0	ing complete.
"	L.	14.5	14.8	14.3	100.0	100.0	99.7	99.5	99.8	Seeds tested when quite
"	L.	16.0	13.4	16.4	100.0	100.0	99.5	air-dry.
<i>Faba vulgaris</i>	L.	15.0	13.8	15.1	100.0	100.0	99.9	"
<i>Phaseolus multiflorus</i>	L.	16.0	14.8	16.5	100.0	100.0	98.0	"
<i>Pisum sativum</i>	L.	13.6	11.7	13.8	Wrinkled variety.
"	L.	14.6	19.0	13.0	100	100	94.6	96.7	93.8	Smooth variety.
<i>Æsculus Hippocastanum</i>	...	12.0	14.2	11.1	100	100	99.8	98.0	100.7	"
<i>anona muricata</i>	...	10.9	13.5	9.5	100	100	98.1	97.4	98.5	"
<i>squamosa</i>	...	13.6	14.6	13.2	100	100	98.0	97.2	98.4	"
<i>Achras Sapota</i>	...	10.0	13.7	7.2	100	100	97.2	95.8	98.2	"
<i>Chrysophyllum Caimito</i>	...	9.5	15.0	7.7	100	100	102.4	107.0	100.7	"
<i>Citrus decumana</i>	...	10.4	14.0	8.7	100	100	98.7	98.6	98.8	"
<i>Hura crepitans</i>	6.0	...	100	99.0	"
<i>Ricinus communis</i>	...	17.0	93.2	Drying of seed not com-
<i>Iris Pseudacorus</i>	pleted before the ex-
"	periment.
<i>Luffa aetangula</i>	...	12.7	9.8	100	100	100	98.3	98.6	98.0	"
<i>Quercus Robur</i>	...	11.3	92.3	"
<i>Cocos nucifera</i>	...	7.0	96.0	"
<i>Sabal umbraculifera</i>	...	11.15	94.9	"
<i>Elaeis guineensis</i>	...	9.0	93.7	"

The resistance offered by impermeable seeds to high temperatures.

We have seen that the ultra-dryness of the kernel of an impermeable seed is maintained through the impervious character of its coats. In further illustration of the great resistance which the seed is able to offer on account of its impermeable coverings to the injurious influence of external conditions, I will discuss the results of some experiments illustrating their behaviour under high temperatures. Although none of the seeds germinated after exposure to a temperature of 100° C., their behaviour under the test was very instructive; and it would seem that in no better way can the contrast between permeable and impermeable seeds be shown than in their modes of responding to different stages of heat.

As exemplified by *Entada scandens* and *Guilandina bonducella*.

It is of course natural that a seed-covering which is neither hygroscopic nor pervious should have this influence. Yet some very curious effects are produced when impermeable seeds, such as those of *Entada scandens* and of *Guilandina bonducella*, are exposed in an oven to a temperature of 100° to 110° C. They are well brought out in the accompanying table, which contains the results of two simultaneous experiments on these seeds; and in order to emphasise the peculiarity in the behaviour of the impermeable seed when heated with its coats intact, I have added the results for the same seed when subjected to a similar high temperature in the broken condition.

It is shown in the columns of this table that in their coats these seeds behaved in a very similar fashion after an exposure for two hours to a temperature of 100° to 110° C. They lost respectively 2.7 and 1.9 per cent. of their weight, the subsequent efforts of both to supply the loss by absorbing water from the air having a very slight result. Both of them then doggedly resumed in their altered condition their previous impermeability, making no hygroscopic response to the variations in atmospheric humidity and gaining back no weight on being immersed in water. If we contrast this with their behaviour when deprived of the protection of their coats (as indicated by the average results of several experiments on other seeds of the same species), we find that in the oven test they lost

RESULTS OF SIMULTANEOUS EXPOSURE FOR TWO HOURS TO A TEMPERATURE OF 100° TO 110° C. OF ENTIRE SEEDS OF ENTADA SCANDENS AND GUILANDINA BONDUCELLA, ILLUSTRATING THE POWERS OF RESISTING HEAT IN THEIR SHELLS OR COVERINGS POSSESSED BY IMPERMEABLE SEEDS, AS COMPARED WITH THE BEHAVIOUR OF THE SEEDS OF THE SAME SPECIES EXPOSED TO THE SAME TEMPERATURE, BUT IN A BROKEN CONDITION, AND THEREFORE NO LONGER PROTECTED BY THEIR SHELLS.

(The results are stated in percentages, the materials tested being 2 entire seeds of *Entada scandens* weighing in all 861·3 grains, and 3 entire seeds of *Guilandina bonducella* weighing 106·8 grains. The data given for the seeds in their broken condition represent the average of a number of experiments made in other connections during the course of this investigation.)

Changes in weight during and after the oven test.

	Condition of seeds.	Original weight.	After 2 hours' exposure to 100° to 110° C.	Weight after the oven test.					After 2 to 7 days' immersion in water.
				1 day.	5 or 6 days.	12 days.	3 months.	4 months.	
Entada scandens	Entire in their coats.	100	97·3	...	97·6	97·6	97·6	97·6	97·6
	In a broken condition.	100	88·6	99·0	104·6	104·5	103·0
Guilandina bonducella	Entire in their coats.	100	98·1	98·4	98·4	98·4	98·4	98·4	98·4
	In a broken condition.	100	92·0	105·0	111·5	111·4	106·0

Entada scandens protected by its coats lost 2·7 per cent. and regained 0·3.
 „ unprotected „ „ 11·4 „ „ 16·0.
 Guilandina bonducella protected „ „ 1·9 „ „ 0·3.
 „ unprotected „ „ 8·0 „ „ 19·5.

11·4 and 8·0 per cent. respectively. This was more than regained after an exposure of some days to the air, there being a final excess over the original weight of 4·6 per cent. in the case of *Entada scandens* and of 11·5 per cent. in the case of *Guilandina bonducella*.

Unfortunately, all the seeds failed to germinate, though

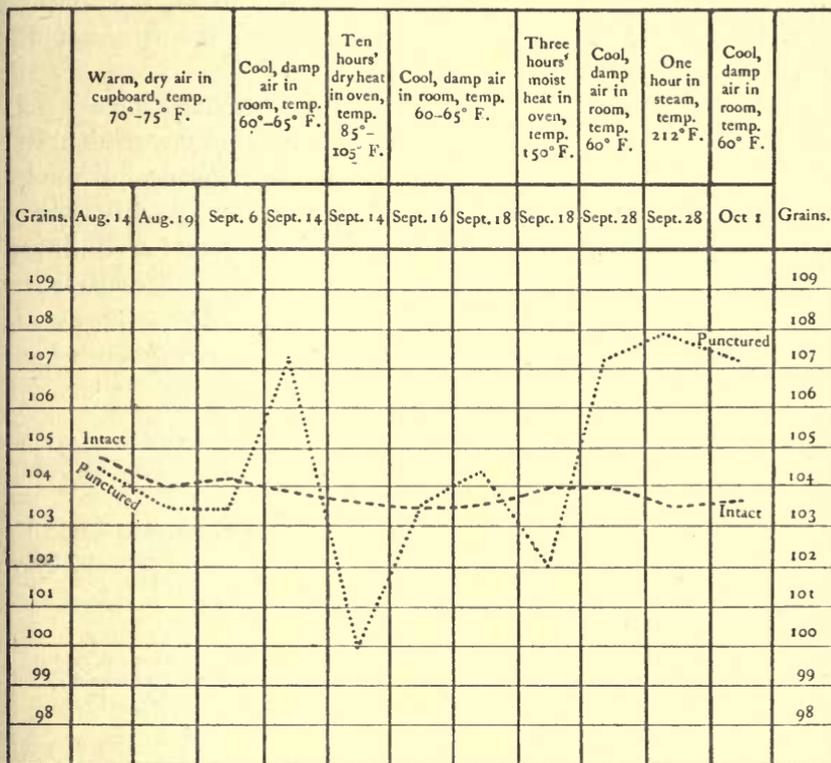
examination proved that their kernels were in appearance sound. A more careful test of their germinative capacity might have produced different results. However, the interest of the experiment lies in its suggestiveness as to the mode in which an impermeable seed might be able to resist a temperature of 100° C. Provided that its water-contents are reduced to a minimum, it could withstand even a greater amount of heat and yet germinate. Becquerel, basing his opinion on the experiments of Dixon, considered 120° C. as the limit for desiccated seeds (*Annales des Sciences Naturelles*, v., 1907). With regard to my own results it may be added that the loss of weight in the oven is not so surprising as the subsequent resumption of impermeability. Behaviour somewhat similar, though under different conditions, is noticed below in the case of the impermeable seeds of another plant.

Another illustration of the method by which impervious coats may enable seeds to resist high temperature was afforded by selected impermeable seeds of *Canavalia obtusifolia* under the strain of a great variety of thermal conditions, both with coats intact and with coats punctured, as shown in the diagram below. Exposed to alternating dry and damp conditions at ordinary temperatures and to extremes of dry and moist heat in the oven, the seed with coats intact varied only about 1·2 per cent. of its weight during a period of seven weeks, whilst the range of the weight of the seed with punctured coats under the same tests and during the same period was 7·5 per cent. But if we disregard the first loss of weight as concerned with influences preceding the experiment, then the variation under these highly contrasted conditions of the seed with coats intact amounted only to 0·7 per cent., which is probably not much greater than the variation that a quartz-pebble would exhibit under the same circumstances. Since the impermeable seeds of *Canavalia obtusifolia* normally increase their weight by 5 or 6 per cent. when exposed to the air bared of their coats, some proportion of the great variation displayed by the punctured seeds must be ascribed to their original

And by
Canavalia
obtusifolia.

DIAGRAM ILLUSTRATING THE DIFFERENT BEHAVIOURS UNDER A GREAT VARIETY OF CONDITIONS OF INTACT AND PUNCTURED SEEDS OF *CANAVALIA OBTUSIFOLIA* OF THE IMPERMEABLE TYPE.

(The experiment extended continuously from August 14 to October 1, and was carried out in England.)



In one case the seed-coats were punctured in several places.

In the other case the coats were left intact.

Nine or ten seeds were employed in each experiment.

The first fall in weight was due to the seeds having been previously kept under less dry conditions, the small loss in the case of the seeds with coats intact being probably connected with tissue adherent to the scar. The loss in weight of the punctured seeds on September 18 after being exposed for three hours to moist air in the oven at a temperature of 150° F. is remarkable. The punctured seeds here displayed a caving-in or collapse of their coverings around each puncture. A vessel of water was placed in the oven during the test, and after cooling down the inside of the oven was covered with moisture.

ultra-dryness. None of the seeds germinated at the close of the experiment, a negative fact which probably depends as

much on the imperfection of the method as on the failure of the seeds, since, as above remarked, experiment has established the ability of certain seeds to withstand for some hours a temperature of 100° to 120° C. However, the original purpose of this experiment has been served in demonstrating the protection an impervious covering affords against extreme thermal and hygrometric conditions.

Very different is the behaviour of the permeable seed under the strain of a high temperature, a difference which its hygroscopicity would lead one to expect. Permeable seeds give up their moisture in the oven almost as readily when protected by their coverings as in the exposed condition. Since we have already seen in the chapter on type seeds that with such seeds the coats merely restrain but do not prevent the hygroscopic reaction of the kernel, the results given below are such as we should have looked for.

The behaviour of permeable seeds under high temperature.

TABLE SHOWING THE INFLUENCE OF THEIR COVERINGS ON THE BEHAVIOUR OF PERMEABLE SEEDS WHEN EXPOSED FOR TWO HOURS TO A TEMPERATURE OF 100° TO 110° C.

(Two samples of each kind of seed were employed, one with the seeds entire, the other with the seeds cut across so as to be deprived of the protection of their coverings. The seeds were eight or nine months old, the samples of the peas weighing 100 grains and of the others 200 grains. The results are given in percentages.)

	Condition.	Original weight.	Weight after the oven test.	Loss in the oven.	Time occupied in regaining original weight.
Faba vulgaris (Broad Bean)	Entire	100	90·0	10·0	6 weeks
	Cut across	100	86·1	13·9	2 ,,
Pisum sativum (Peas)	Entire	100	88·8	11·2	2 ,,
	Cut across	100	85·9	14·1	1 week
Phaseolus multi- florus (Scarlet- runner)	Entire	100	89·2	10·8	6 weeks
	Cut across	100	84·9	15·1	2 ,,

By contrasting the results above tabulated with those given a few pages back for *Entada scandens* and *Guilandina bonducella*, where the seeds were exposed to the same test, we can frame a numerical estimate of the difference in the degree of protection against high temperatures which the coverings offer in the

case of permeable and impermeable seeds. Thus, assuming that the seed gave up approximately all its water when deprived of the protection of its coats, then the permeable seeds entire in their coverings may be regarded as having lost as much as from 70 to 80 per cent. of their water-contents, whilst the impermeable seeds in the same entire condition and exposed to precisely the same test lost barely 25 per cent.

Further contrasts in the behaviour of permeable and impermeable seeds when exposed in their coats to a temperature of 100° to 110° C. for two hours are exhibited when we compare the results of their efforts to regain the lost water from the air. With impermeable seeds we have seen that very little effort is made to gain back their original weight, and that after the oven test they resume their impervious character, doggedly refusing to make any response to the hygrometric changes of the air and adding nothing to their weight when immersed in water. On the other hand, after the oven test permeable seeds slowly regained the water lost, but so very slowly that six weeks in the cases of *Faba vulgaris* and *Phaseolus multiflorus* and two weeks in the case of *Pisum sativum* were occupied in returning to their original weight. The influence of the coats is especially brought out in the case of the two types of seeds, if we regard their behaviour when the seed is broken up and is thus deprived of the protection of its coats. After the oven test the impermeable seed gains back in a few days all the water lost and a considerable percentage (5 to 10 per cent.) more; whilst the permeable seed returns to its original weight in a week or two, and is subject then to only the normal hygroscopic variations.

The differences in the nature of the protection afforded by the coats of permeable and impermeable seeds when exposed for two hours to a temperature of 100° to 110° C. may be thus briefly stated. In the impermeable seed the coats only allow one-fourth of the water-contents to escape, and by subsequently resuming their imperviousness practically frustrate the seed's effort to gain back the loss. In the permeable seed the inhibitive influence of the coats is so slight that three-fourths of

Summing up of the differences in the behaviour of permeable and impermeable seeds when exposed in their coats to high temperatures.

the water-contents are lost in the oven; whilst the seed's attempt to regain from the air the water lost is retarded, but not prevented, the original weight being in time attained. The retardation in the process of re-absorption is, however, very marked, since in the Broad Bean and Scarlet-runner the period is extended from two to six weeks and in the Pea from one to two weeks.

There are several points raised in the foregoing remarks which will be elucidated in the chapter on Hygroscopicity, notably, that concerned with the return of permeable seeds to their original weight after being heated. Only completely air-dry seeds would thus behave, since seeds that are still drying would fall considerably short of the weight they possessed before being placed in the oven.

SUMMARY

(1) This chapter contains the bulk of the data on which are based the distinctions in behaviour between permeable and impermeable seeds, which are described and illustrated by typical examples in Chapter IV.

(2) The capacity of increasing their weight considerably by absorbing moisture from the air, when impermeable seeds are deprived of the protection of their coats, is confirmed by the results of experiments on the seeds of other plants. Other results also go to confirm the conclusion drawn for type seeds in Chapter IV, that the gain in weight is far more rapid when the kernel is completely bared than when the coats are merely punctured. The average results of all experiments on this absorptive capacity of impermeable seeds are tabulated; and it is generally concluded that leguminous seeds of this type when deprived of the protection of their coverings as a rule increase their weight between 5 and 10 per cent. in a few days (p. 115).

(3) The indications, though limited, go to show that impermeable seeds retain their ultra-dryness for a number of years (p. 119).

(4) The data show that the capacity of absorbing water from the air when an impermeable seed is bared of its coats is greater in the tropics than in temperate climates, and that the gain in weight is maintained longer when it is acquired slowly, as in filed seeds, than it is when acquired rapidly, as in bared kernels (p. 120).

(5) The results for variable seeds (permeable and impermeable seeds in the same plant) of baring the kernel, or exposing it by cutting it in halves in its coats, are also tabulated; and it is shown respecting their relations with the moisture of the air (*a*) that the permeable seeds behave hygroscopically, like ordinary seeds of the type; (*b*) that impermeable seeds behave also like seeds of their type and add considerably to their weight; (*c*) that mixed samples of the two types of seeds display intermediate qualities (p. 122).

(6) Additional data are given concerning the behaviour of bared permeable seeds that have completed their drying in air; and it is shown, as in Chapter IV, that the main result is to give a rather freer play to the hygroscopic reaction, the average weight remaining about the same (p. 124).

(7) Further evidence is then supplied of the association of the ultra-dryness of impermeable seeds with a low water-percentage, and in the first place the necessity of restricting the inquiry to seeds of the same order is pointed out.

(8) Thus with leguminous seeds we obtain the following general results for seeds broken up or cut open and exposed to the air:—

Impermeable seeds holding 7.5 per cent. of water add 9.2 per cent. to their weight.

Impermeable seeds holding 11.7 per cent. of water add 5.0 per cent. to their weight.

Permeable seeds holding 15.0 per cent. of water add 0.0, behaving hygroscopically.

(9) The indications of this rough estimate are confirmed by the results of experiments on seeds where both the permeable and impermeable types of seeds are produced by the same plant.

(10) More evidence is adduced to show that in impermeable seeds the seed-coats possess the same quality of ultra-dryness as the kernel.

(11) Additional data are given in support of the conclusion that the capacity possessed by impermeable seeds of considerably adding to their weight when exposed to the air in a broken state is not affected by first exposing the materials to a temperature of 100° C., whether in the case of the coats or of the kernel.

(12) Permeable seeds in this respect present a great contrast to impermeable seeds, since in a week or two they gain back from the air only the water lost in the oven and assume a stable weight subject merely to ordinary hygroscopic variation.

(13) In the case of both permeable and impermeable seeds it is necessary, when comparing their absorptive capacities after heating, to employ only seeds that have completed the drying and shrinking process, since seeds of either type, when incompletely dried, fail to

return to their original weight. On this point the principle of Berthelot, discussed in Chapter VII, throws a flood of light.

(14) The contrast between impermeable and permeable seeds is further illustrated by their different modes of responding to high temperatures under the protection of their coats. Whilst impermeable seeds, when exposed for two hours to a temperature of 100° to 110° C., lose only about 25 per cent. of their water-contents, permeable seeds that have completed their drying in air lose under these conditions in the oven as much as 75 per cent. (p. 138).

(15) But the contrast is extended when we compare the results of their efforts to regain from the air the water lost in the oven. The impermeable seed makes a very slight effort in this direction; and whilst its coats quickly resume their impervious character, the seed doggedly refuses to make any response to the variations in the atmospheric humidity and adds nothing to its weight when placed in water. On the other hand, after the oven test the permeable seed slowly regains from the air the water lost, but so gradually that weeks are taken up in the process, the original weight being ultimately attained subject to the ordinary hygroscopic reaction. The return of the air-dried permeable seed to its original weight after the heat test is a point of importance, since seeds that have not completed their drying in air fail to reach their original weight, a critical distinction discussed in detail in the chapter on Hygroscopicity (p. 139).

(16) The great resistance which a seed protected by impermeable coats is able to offer to extremes of moist and dry heat ranging up to 100° C., and to alternating dry and damp conditions, is shown in the behaviour of impermeable seeds of *Canavalia obtusifolia*. Kept under the strain of a great variety of extreme conditions for seven weeks, seeds with coats intact did not vary 1 per cent. in weight, whilst those with punctured coats varied as much as 7.5 per cent. (p. 140).

CHAPTER VII

HYGROSCOPICITY

HYGROSCOPICITY in a seed may be defined as the variation of its water-contents in response to the changes in the hygrometric state of the atmosphere, such a variation being due to its property of readily imbibing moisture from the air and as readily parting with it. This interesting quality, which is characteristic of all vegetable substances and of much besides, has in recent times been studied by numerous investigators, including amongst others Jodin (1897), Berthelot (1903), Léo Errera (1906), Becquerel (1907), and Demoussy (1907), the years indicating the date of publication of the author's paper consulted.

**Definition of
hygro-
scopicity.**

The most comprehensive treatment of the subject is to be found in the memoir of Léo Errera entitled "Sur l'Hygroscopicité comme cause de l'action physiologique à distance" (*Recueil de l'Institut Botanique Léo Errera, Université de Bruxelles*, tome vi., 1906). Assisted by the previous researches of Warburg and Ihmori, he was able to direct attention to certain principles involved and to show that hygroscopticity in its widest sense has a far more extended significance than is generally imagined, as is sufficiently brought out in his classification of the various forms of this property, both physical and chemical, which I have reproduced in Note 9 of the Appendix. The matter as here dealt with appeals mainly to the physicist and the chemist; but it is essential, before studying hygroscopticity as affecting plants, to bear in mind the broad treatment of the subject which gives so much importance

**Classifica-
tion of its
different
forms by Léo
Errera.**

to this paper. Hygroscopicity is there exhibited in the most comprehensive sense, as displayed (*a*) in the condensation of the water-vapour of the air on the cold surface of a glass ; (*b*) in the capillarity of hair, wool, cotton, wood shavings, etc. ; (*c*) in the imbibition of water from the air by gelatine ; (*d*) in the deliquescence of common salt ; (*e*) in the absorption of water from the air by concentrated sulphuric acid ; and (*f*) in the behaviour of quicklime. Becquerel, in applying this classification to seeds, suggests two kinds of hygroscopicity : (1) physical, where condensation is affected by the cold, smooth sides of the seed or by the walls of very fine capillary pores ; (2) chemical, when induced by the affinity of certain substances for water (*Annales des Sciences Naturelles Botanique*, tome v., 1907).

Coming to the display of this quality by vegetable materials in general, I will, before handling my own observations, take my cue from the researches of Jodin on peas, and will then look to the principle laid down by Berthelot for guidance in the search after the significance of hygroscopicity in plant-tissues. But it is necessary to preface my remarks by pointing out that the hygroscopic reaction understood by these investigators, and always intended in these pages, is the response of the permeable seed (by absorbing or yielding up water-vapour) to the varying hygrometric condition of the air, a never ceasing "give and take" process by which the equilibrium between the seed and the air is maintained.

Jodin approached the subject from the biological and Berthelot from the physical side, and both arrived at the same conclusion, that we are concerned with a quality that is independent of life. Jodin, in his paper published in the *Annales Agronomiques* for October 1897, tells us that living and dead peas (those recently grown and those that had long lost their germinative capacity) exhibited much the same hygrometric variation in the course of a year's exposure to ordinary air-conditions. Stated as a percentage of the average weight of the air-dry resting seed, his results give a variation for the live peas of 8 to 23 per cent., and for the dead peas of 11 to 21

The observa-
tions of
Jodin on
peas.

per cent. It was the work of Jodin that led Becquerel in the paper before quoted to make the critical distinction in a seed's water-contents between the water of hygroscopicity and the water concerned in the latent life of the embryo.

Whilst several years have passed since Jodin directed his attention to the ordinary hygrometric variations experienced by peas, Berthelot in more recent times has opened up the whole subject of the hydration of vegetable matter, and in so doing has thrown an important light on the nature of hygroscopicity in plants ("Recherches sur la desiccation des plantes et des tissus végétaux; conditions d'équilibre et de réversibilité," *Annales de Chimie et de Physique*, April 1903). He shows that the peculiar property possessed by air-dried vegetable matter of regaining from the air the water it has been made to lose by heat and other artificial means is a function of the hygrometric condition of the atmosphere. It is not easy for me to state Berthelot's principle tersely, and accordingly I have above followed Maquenne in his reference to this subject in *Comptes rendus*, October 1905. Nor is it easy to grasp its full significance at first, since, as is natural in such abstruse inquiries, much will seem pointless that does not cross the boundary of one's own researches. To me perhaps it is not so hard, since the principle has cast a flood of light upon the results of my studies of permeable and impermeable seeds.

A plant, says Berthelot, does not dry entirely in air like porcelain or metals (see Note 21 of Appendix). It retains after being thus dried a certain amount of water, which varies in response to the changes in the hygrometricity of the atmosphere. When this water has been driven off by exposure to a temperature of 110° C., it is gained back little by little from the air up to a limit practically the same as that reached when the plant was dried in air. In a word, the water which the air-dried material loses in the oven is regained in the air. This is Berthelot's principle of reversibility, and it is characterised by him as essentially a physico-chemical process independent of life. It applies equally to the plant that has

Berthelot's
principle of
reversibility.

Its applica-
tion to plant-
tissues in
general.

been dried in air, to the plant that has died spontaneously, and to the plant that has been subjected to almost absolute desiccation by heat and other means, all ultimately reaching the same condition of equilibrium with regard to the atmosphere.

We will illustrate Berthelot's principle by combining in one statement the results of his different experiments. Portions of a living grass, a species of *Festuca*, weighing, we will suppose, 100 grammes, are allowed to dry in the air of an ordinary room for some days, until they acquire a stable weight affected only by the usual small hygroscopic fluctuations. Their weight is thus reduced by loss of water to about 66.5 grammes. They are then exposed to a temperature of 110° C. for some hours, with the result that the weight is further reduced to 61 grammes. After being laid aside for some days, the material, by the absorption of moisture from the air, returns to the original air-dried weight of about 66.5 grammes, and there remains, varying slightly with the changing humidity of the atmosphere. It is in the 5½ grammes which the air-dried material lost in the oven and regained when subsequently exposed to the air that the secret of the hygroscopicity of plants lies.

TABLE ILLUSTRATING BERTHELOT'S "PRINCIPLE OF REVERSIBILITY."
(THE RESULTS OF DIFFERENT EXPERIMENTS ARE HERE COMBINED,
THE MATERIALS EMPLOYED BEING PORTIONS OF A SPECIES OF
FESTUCA.)

Weight in grammes under different conditions.				
Fresh weight.	Dried in air of an ordinary room.	Died spontaneously.	After exposure to temperature of 110° C.	After a subsequent exposure of some days in the air of an ordinary room.
100	66.5	...	61	66.5
100	...	66.5	61	66.5
100	61	66.5

Note.—The data representing the effect of exposing fresh and air-dried material to a temperature of 110° C. belong to the same experiment, the rest of the data being supplied from the indications of other experiments.

The feature in this table which will prove to be of the greatest significance to us, in respect to the behaviour of impermeable seeds when exposed to the air, is that which shows that the water regained from the air, after fresh plant-tissues have been exposed to a temperature of 100° to 110° C., is the water of the dead plant and of the plant dried in the air, and is therefore independent of vitality.

In the above table I have pieced together the indications of different experiments in order to emphasise certain points in the behaviour of plants when exposed to natural and artificial desiccation. After reading Berthelot's paper I experimented on some fresh leaves of the Hazel (*Corylus Avellana*), with the results below given. His principle is well illustrated there, and we can see at a glance that the water which the fresh leaves gained back from the air after being exposed to a temperature of 105° C. is the water which they would have contained as ordinary air-dried leaves. For about three years I have been

The testimony of Hazel leaves.

EXPERIMENTS BY THE AUTHOR ON FRESH HAZEL (*CORYLUS AVELLANA*) LEAVES IN ILLUSTRATION OF BERTHELOT'S "PRINCIPLE OF REVERSIBILITY."

Results of the drying and heating tests.					The water of hygroscopicity.		
	Fresh weight.	After drying in air of room.	After exposure to temperature of 105° C. in oven.	Three or four days after the oven test.	Lost in oven after drying in air.	Gain in air after the oven test.	Stated as a percentage of the dry weight.
A	100	31'3	28'0	31'4	3'3	3'4	12'1
B	100	32'8	29'4	33'0	3'4	3'6	12'2
C	100	...	31'0	34'5	...	3'5	11'3
D	100	...	29'6	32'9	...	3'3	11'1

Hundred-grain samples of the fresh material were used. In the case of experiments A and B, the sample was first dried in air for about five days, when it reached a stable weight. It was then subjected to a temperature of 105° C. for 1½ hours, and afterwards left exposed to the air of the room for three or four days, when it ceased to gain weight. In the case of experiments C and D the fresh materials were placed in the oven without previous drying in air.

putting this question to myself as to the significance of the gain in weight of plant-tissues, and more particularly of seeds after being exposed to desiccation in the oven, never dreaming that such a simple experiment would supply the answer. To have been contented with attributing it to hygroscopicity would have explained little. As a disconnected fact it appeared without interest and without meaning. What was required was the establishment of a relation between this property and some other attribute of plant-tissues; and this I ultimately found in the principle of Berthelot.

From this standpoint the water-contents of plants could be divided into two parts, the water of hygroscopicity and the water of vitality. The first, being independent of life, is equally characteristic of the plant living and the plant dead. It is the residuum left in the air-dried material; and it is the water that the same material loses in the oven and regains in the air. The second is the water that distinguishes the plant as a living organism. Its quantity is regulated only by the needs of that organism. Unlike the water of hygroscopicity, it does not directly respond in its variations to the hygrometricity of the air. On the other hand, hygroscopicity being a non-vital process represents the response of the non-vital part of a plant's water-contents to the varying humidity of the atmosphere. We can thus understand how the residuum of water in the air-dried plant is the water that represents a function of the hygrometric state of the air.

This mode of differentiating the water-contents of plant-tissues is of practical importance. There are many ways of stating the proportions, and I have spent much time in trying to harmonise them with the results of my observations. Finally, it became evident that of the numerous methods of describing the "hydratation" of plants there were none so simple and none so true as that implied in the principle of Berthelot. There is the water that the organised tissues contain, whether living or dead, the water of hygroscopicity;

Berthelot's principle distinguishes the water of hygroscopicity from the water of vitality.

The simplest mode of stating the water-contents of plant-tissues.

and there is the water which they hold only as living structures, the water of vitality. The chemist, when producing by synthesis organic vegetable matter, would allow the atmosphere to supply the water of hygroscopticity, whilst he himself in his creative rôle would have to supply the water of vitality. This in a sense is very much what a baker does when he adds water to his flour in making bread. As shown below, bread behaves like fresh plant-tissues when dried in air and when desiccated by heat. The water it regains from the air after heating is the water originally existing in the flour as supplied by the miller, and the water it does not gain back is what the baker put into it.

EXPERIMENTS BY THE AUTHOR ON 100-GRAIN SAMPLES OF BREAD IN ILLUSTRATION OF BERTHELOT'S "PRINCIPLE OF REVERSIBILITY."

Treatment of samples.	Results of the drying and heating tests.				The water of hygroscopticity.		
	Original weight.	After drying in air of room.	After exposure to temperature of 105° C. in oven for 1½ hours.	Three or four days after the oven test.	Lost in oven after drying in air.	Gain in air after oven test.	Stated as a percentage of the dry weight.
Dried in air and then placed in oven	100	70·3	61·2	70·4	9·1	9·2	15·0
Placed at once in oven	100	...	60·5	70·0	...	9·5	15·7

Divided into small squares, the bread occupied about six days in reaching a stable weight in air before being placed in the oven, where it was kept for 1½ hours. Three to four days were passed in acquiring a stable weight after the oven test.

When we come to apply the test of experiment to this principle as it affects seeds, we get the same indications. The simple experiment of drying a fresh seed first under ordinary air-conditions, then in the oven at 100° to 110° C., and afterwards allowing it to remain exposed to the air for a few days until it assumes a stable weight, supplies results that make the

The same principle illustrated in the behaviour of a seed.

statement of a seed's water-contents as easy as it was difficult. All my results on the varying water-percentages of seeds, and on the capacity of regaining from the air the water lost in the oven, arrange themselves in an intelligible system in the light of the principle below typified in the behaviour of the full-grown, moist pre-resting seeds of *Phaseolus multiflorus*. The hydration of these seeds in this condition of active vitality may be thus stated :—

Water of vitality	64·8
Water of hygroscopicity	5·2
Solids	30·0
	100·0

THE PRINCIPLE OF BERTHELOT ILLUSTRATED BY THE BEHAVIOUR OF THE FULL-GROWN UNRIPE OR PRE-RESTING SEEDS OF PHASEOLUS MULTIFLORUS. (Three seeds weighing 140 grains were experimented on by the author ; the results are given as percentages.)

Results of the drying and heating tests.				The water of hygroscopicity.		
Unripe or pre-resting seed from the green pod.	After drying in air of room.	After exposure to a temperature of 105° to 110° C. in oven for 2 hours.	Six or seven days after the oven test.	Lost in the oven after drying in air.	Gain in air after the oven test.	Stated as a percentage of the dry weight.
100	35·3	30·0	35·0	5·3	5·0	17·3

The implications of Berthelot's principle.

Important as the principle of Berthelot is in the differentiation of the water-contents of plant-tissues generally, its application is still more interesting in its results in the case of the hydration of seeds. It not only enables us to recognise in clear outlines the nature of the contrast between permeable and impermeable seeds ; but this implication supplies quite a novel way of viewing the problem of the latent life of seeds. If the implication is valid, its influence on our views should be revolutionary.

In the first place, as regards the contrast between permeable and impermeable seeds, it is evident that an air-dry permeable resting seed, which has assumed a stable weight, subject only to ordinary hygroscopic variations, contains only the water of hygroscopicity, and that the water of vitality disappeared in the drying process. It also becomes apparent that the impermeable seed contains only the water of hygroscopicity, but in a diminished amount, so that when deprived of the protection of its impermeable coverings it at once begins to supply the deficit by abstracting moisture from the air until a stable weight is reached.

The implication of course is that resting seeds completely air-dried, whether permeable or impermeable, possess only the water which is independent of vitality. If Berthelot's principle is true and the implication is valid, there is in the typical resting seed no water that is associated with any vital function. (I am not here speaking of water locked up in chemical combination in the seed's tissues, since that may be a property of both living and dead matter.) Should the seed exposed to a temperature of 100° C. in the oven yield up more water than it subsequently regains from the air, the inference is that it had not completed its drying in air and still contained some of the water of vitality. This residuum of the water of vitality left in the deficiently air-dried seed has nothing to do with the life of a resting seed, but merely represents the remains of the water of the large, soft pre-resting seed of the moist green fruit, a seed that would have proceeded with its growth and with its development into a young plant without any pause, if the resting period had not been imposed on it through external influences. The resting seed needs no water to prolong its life, the presence of water being more likely to curtail its existence than to endow it with longevity. Indeed, there would seem to be more than fancy in the speculation of M. Demoussy that a perfectly dry seed kept protected from

(a) That air-dry resting seeds, both permeable and impermeable, contain only the water of hygroscopicity ;

(b) that in air-dry resting seeds there is no water associated with any vital function.

the air has the potentialities of immortality (*Comptes rendus*, December 1907).

The view of
Becquerel.

Yet it cannot be doubted that the view expressed so clearly by Becquerel (*Ann. des Sciences Nat. Botan.*, v., 1907), that it is absolutely necessary to distinguish in a seed between the hygrometric water that can vary and the water enclosed in the cellules of the embryo and albumen which is invariable, at present holds the field. We must distinguish, he says, between the water of hygrometricity and the water that plays a part in the phenomena of the latent life of the seed. But if Berthelot's principle is correct, the only water that a seed retains after it has completed its drying in air is the water of hygrometricity. According to the implications of this principle, the true resting seed, as already observed, needs no water for the support of its latent life; and the latent life itself becomes almost a figure of speech.

Schröder's
experiments.

Several years ago Schröder ascertained that grains of three cereals (species of *Hordeum* and *Triticum*) retained their germinative capacity, notwithstanding that after undergoing a process of artificial desiccation for nearly three months their water-contents had been reduced respectively to 0.5, 1.0, and 2.0 per cent. (*Untersuch. Botan. Inst. zu Tübingen*, 1886). It would be quite as legitimate to infer from this experiment that resting seeds can dispense with water altogether as to assume that Schröder in his experiment reached the minimum compatible with the preservation of the germinative powers. There is an obsession in the human mind respecting water and active life that makes it difficult to assimilate the notion that a resting seed could possibly do without it. The standpoint adopted in this chapter is that the occurrence of water in a properly air-dried seed is accidental as far as it is concerned with the retention of the germinative capacity. It could have no concern for the student of the latent life of seeds, since its quantity would be the same whether the seed be living or dead.

Later investigations on the desiccation of seeds have been numerous ; but many of them are summed up by Becquerel in his paper on the latent life of seeds (*Ann. Sci. Nat.*, 1907). There are certain seeds, he points out, which are able to resist the most powerful desiccating agencies at our command ; and very significant is his conclusion, after a review of the liquid-air results, that it is the seed where the water and "gaz" have been reduced to the narrowest possible limits by the most active desiccators of the laboratory that best withstands these tests. There seems no necessity to assign a function to the extremely minute amount of water that might survive the desiccating process.

Becquerel on desiccated seeds.

On the contrary, it might be urged that its water is the greatest foe to a seed's longevity. What, we may ask, is the real biological significance of the hygroscopicity of seeds, as far as their longevity is concerned ? It is their hygroscopicity that limits the life of permeable seeds ; or, in other words, the constant reaction between the seed and its atmospheric environment places a term to its existence. Not the least interesting of the conclusions drawn by Jodin from his observations on peas lies in this direction, and we may apply it to permeable seeds in general. The continued hygroscopic reaction, he points out, would in the course of time bring about molecular changes in the seed, terminating in its loss of germinative power and death. Thus we can perceive by implication how the impermeable seed, by not responding to the changes in its atmospheric surroundings, is secured against one great risk to its longevity. Here, again, we perceive that the long life of the seed presents itself as an affair of the coats rather than one concerned with the dormancy of the protoplasm of the embryo. It is the free play of the hygroscopic reaction that curtails the life of a permeable seed. It is the absence of this reaction that gives long life to the impermeable seed.

Water is the greatest foe to a seed's longevity.

The hygroscopic reaction limits the life of seeds, whilst its absence favours their longevity.

After this long digression on the significance of hygroscopicity in seeds, I come to my own studies in this connection.

The author's studies of hygroscopicity in seeds.

Permeable seeds alone are hygroscopic.

The hygroscopic range.

Its characteristics.

Effect of different climates on the weight of the same seed.

My observations on the hygroscopic behaviour of seeds are naturally concerned only with permeable seeds, since the impermeable seed in the usual sense of the word is non-hygroscopic, and when employed in experiments merely serves to give contrast to the results. Hygroscopic seeds weighed daily during a fortnight of changeable weather usually vary $1\frac{1}{2}$ or 2 per cent. of their average weight, an amount, however, which is only about half of what may be regarded as the ordinary extreme of the hygroscopic range, which, as ascertained by a method to be subsequently described, is usually 3 or 4 per cent. This reaction figures as a possible disturbing cause in all experiments on seeds where the balance is employed.

Seeds as a rule continue to lose weight by drying during a period varying from a few weeks to two or three months after being gathered from the plant. If we extend the experiment over a year or more, employing only seeds that have completed the drying process and have acquired a stable weight, we find a response to the varying humidity of the air not only in the minor changes during short intervals, as between day and night, and in the greater changes from week to week, but also between the different seasons. It may here be remarked that the seasonal changes in weight were well exemplified in my experiments on the seed of *Æsculus Hippocastanum* (Horse-chestnut). Seeds that had been kept for three years were usually 1 or $1\frac{1}{2}$ per cent. heavier in the winter than in the summer.

Reference will now be made to the changes of weight which many seeds undergo in transference between regions where different hygrometric régimes prevail, as between tropical and temperate countries. I made some observations in this direction in the case of seeds taken from England to Jamaica in November 1907, seeds which had been gathered fresh in Jamaica in the spring of the same year. Permeable, impermeable, and variable seeds were here represented.

TABLE ILLUSTRATING THE CHANGES IN WEIGHT EXPERIENCED BY TROPICAL SEEDS WHEN TRANSFERRED FROM ENGLAND TO JAMAICA, AND FROM JAMAICA BACK TO ENGLAND. (Seeds obtained fresh in Jamaica in spring of 1907.)

	Character.	Weight in grains.			Change stated as a percentage of the total weight.		
		England, Oct. 1907.	Jamaica, Jan. 1908.	England, April 1908.	Rise.	Fall.	Range.
Canavalia ensiformis (7 seeds; Leguminosæ)	Permeable	167·85	169·60	163·40	1·04	3·66	3·7
Achras Sapota (10 seeds; Sapotacæ; fruit baccate)	Permeable	101·55	102·80	99·80	1·23	2·91	2·9
Chrysophyllum Cainito (4 seeds; Sapotacæ; fruit baccate)	Permeable	51·70	52·15	50·30	0·87	3·55	3·6
Abrus precatorius (69 seeds; Leguminosæ)	Variable	105·40	105·70	105·00	0·28	0·66	0·7
Canavalia obtusifolia (8 seeds; Leguminosæ)	Variable	102·40	102·50	102·55	0·15	...	0·2
Guilandina bonducella (7 seeds; Leguminosæ)	Impermeable	306·60	306·60	306·60	0·00	0·00	0·00
Entada scandens (3 seeds; Leguminosæ)	Impermeable	809·60	809·65	809·45	0·00	0·02	0·00
Adenantha pavonina (22 seeds; Leguminosæ)	Impermeable	104·80	104·80	104·85	0·05	...	0·00

The seeds had been five months in England when weighed in October 1907; two months in Jamaica in January 1908, when weighed in that island; and one month in England when weighed in April 1908. All the seeds retained their germinative powers after the experiment, with the exception of those of *Achras* and *Chrysophyllum*, which were sound, but did not germinate.

It may be concluded from the data in this table that the following were the results of the transportation of these seeds from the temperate zone to the tropics and back. The range of the variation in weight of the permeable seeds was 3 to 4 per cent., and that of the variable seeds considerably under 1 per cent.; whilst the range of the impermeable seeds may be regarded as "nil," or, if present, as probably instrumental and therefore negligible. In the case of both the variable kinds

of seeds the proportion of permeable seeds was probably very small, that is to say, under 10 per cent.; and doubtless the change of weight was experienced by a very few seeds. The rise in weight of the three permeable kinds of seeds in Jamaica and the fall after returning to England are characteristic; but the difference between them is probably due to the varying hygrometric conditions of the air when the two sets of observations in England were made. On the whole, however, it may be considered that the changes in weight experienced by these permeable seeds between warm and cool latitudes are within the limits of the hygroscopic range defined a few pages back.

The first method of determining the hygroscopic range.

In all experiments for determining the limits of hygroscopic variation it is requisite that the seeds should have completed the drying process and that they should be, as far as their water-contents are concerned, in a state of equilibrium with the air. The method at first employed in investigating the hygroscopic behaviour of seeds was, as already indicated, to weigh them daily for ten or fourteen days when the weather was changeable. The variation was then stated as a percentage of the total weight of the seed, and this was termed the "hygroscopic range." In such experiments four or five kinds of seeds, of both the permeable and impermeable types, were experimented on at the same time. The results of one of these experiments in Jamaica are given below in the form of a diagram; and in order to obtain a more graphic effect, they have all been computed for 1000 grains of each kind of seed, whilst the prevailing weather conditions as regards rain have been roughly indicated by black and white squares. The following seeds were employed:—

Experiment in Jamaica.

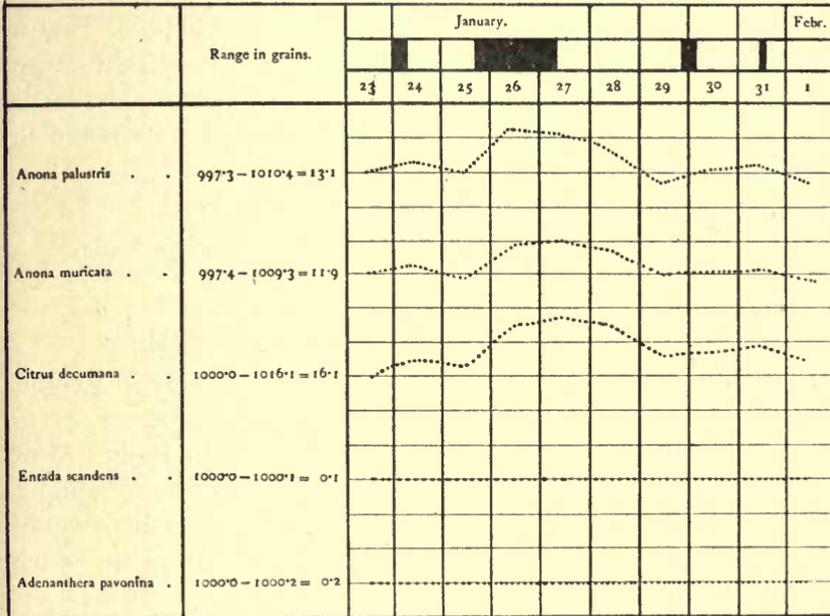
112 seeds of <i>Anona palustris</i> ,	weighing	440·8 grains.
74 " <i>Anona muricata</i> (Sour Sop),	" "	470·8 "
85 " <i>Citrus decumana</i> (Shaddock),	" "	334·7 "
212 " <i>Adenanthera pavonina</i>	" "	1000·0 "
3 " <i>Entada scandens</i>	" "	1087·3 "

The first three are permeable seeds, the ranges for the two species of *Anona* being 1·3 and 1·2 per cent., whilst that for

the Shaddock was 1·6 per cent. But these do not represent the maximum hygroscopic ranges. The Shaddock seeds in another experiment in England gave a range of 2 per cent. ; and probably the swing of the range, including ordinary extremes, would amount to nearly 3 per cent. for all the permeable seeds here experimented on. The last two are typically impermeable, and the small variation exhibited is probably instrumental.

DIAGRAM CONTRASTING THE BEHAVIOUR OF PERMEABLE AND IMPERMEABLE SEEDS AS RESPECTS THEIR VARIATION IN WEIGHT DURING TEN DAYS OF CHANGEABLE WEATHER IN JAMAICA, THE RAIN BEING INDICATED BY BLACK.

(For further explanation see the preceding remarks. The three first-named are permeable and the last two are impermeable.)



In course of time, however, I discovered that although the method described and illustrated in the previous pages exhibited the ordinary hygroscopic response of the permeable seed to the usual weather changes within a limited period, it did not give me the whole range of the variation, such as

The method finally adopted of determining the hygroscopic range.

one would look for if the experiment was continued for a year. A chance observation led me to believe that the whole range was quite twice as much as that indicated in the foregoing experiments; and I soon found, on transferring the seeds from a cool, damp room without artificial heat to a dry cupboard, where the temperature (owing to the vicinity of hot-water pipes) was from 10° to 15° F. warmer, that the range of the hygroscopicity was much increased. In such circumstances the seeds of *Anona*, Shaddock, *Canavalia ensiformis*, etc., which, as first tested, exhibited a variation in weight of 1 to 1½ per cent., now showed an increased range of 2 or 3 per cent. Accordingly, I subjected the seeds to this new proof, and the results are those given in the following pages. The seeds were transferred from the cool room to the warm cupboard for two days and back again to the room, the mean of the two results being taken. Typical impermeable seeds used as checks in many experiments displayed no change in weight, except of a trifling nature.

RESULTS OF THE AUTHOR'S OBSERVATIONS ON THE HYGROSCOPICITY OF SEEDS.

I. IMPERMEABLE SEEDS. (Hygroscopicity "nil.")

A typical impermeable seed exhibits no change in weight, except such as can be attributed to instrumental error, or to a little loose tissue adhering to the scar or to the raphé. For example, a seed of *Guilandina bonducella* 40 grains in weight, and a seed of *Entada scandens* weighing 400 grains, would show the same variation during a month of 0·1 grain, which is so small that it may be safely attributed to other causes than to normal hygroscopicity.

The seeds actually tested by me include the following :—*Adenanthera pavonina*, *Dioclea reflexa*, *Entada scandens*, *Guilandina bonducella*, *Leucæna glauca*, *Mucuna urens*, etc. But of course all the seeds mentioned in the Impermeable Group in Chapter V would, when typical, display no hygroscopic re-

action, excluding seeds like those of *Ipomœa pes-capræ*, where the covering of hairs would give hygroscopicity, though the seed bared of hairs is non-hygroscopic. The influence of hairs is dealt with a few pages further on.

Since impermeable seeds are not infrequent in nature, as is shown in Chapter III, it follows that a large number of seeds fail to make any response to the weather changes, and are therefore non-hygroscopic. Here would belong the seeds of many of the Australian Acacias and a number of the 180 "macrobiotic" or long-lived seeds included in Professor Ewart's list (*Proceedings, Royal Society of Victoria*, 1908), though a large proportion also would belong to the Variable Group, where plants possess both permeable and impermeable seeds.

As illustrating the behaviour of impermeable seeds in the balance, there are appended the actual results obtained in the case of those of four species during periods of from ten to sixty days. It will be noticed, as before remarked, that the same slight variation of from 0.1 to 0.2 grain is displayed by large and small samples, being evidently in great part instrumental. We are here only concerned with the absence of the ordinary hygroscopic reaction in the course of a few weeks. The extent to which this behaviour is persistent will be discussed in Chapter X.

SOME RESULTS ILLUSTRATING THE ABSENCE OF A TRUE HYGROSCOPIC REACTION IN IMPERMEABLE SEEDS, THE SLIGHT VARIATION BEING INSTRUMENTAL. (Daily observations made in the short experiments only.)

	Number of seeds.	Length of experiment.	Variation of weight in grains.	Locality of experiment.
<i>Guilandina bonducella</i> . . .	30	18 days	990.43 - 990.60 or 0.17	England.
" " " "	1	60 "	35.03 - 35.10 or 0.07	England.
Quartz pebble . . .		60 "	38.40 - 38.47 or 0.07	England.
<i>Dioclea reflexa</i> . . .	11	10 "	1042.00 - 1042.2 or 0.20	Grenada.
<i>Entada scandens</i> . . .	3	10 "	1087.4 - 1087.5 or 0.10	Jamaica.
<i>Leucæna glauca</i> . . .	332	10 "	250.0 - 249.9 or 0.10	Grenada.

II. PERMEABLE SEEDS. (Hygroscopicity 2 to 5 per cent.)

(The hygroscopic range of a seed is the amount of variation stated as a percentage of the average weight. Thus, if a seed varied between 98 and 102 grains, the range would be 4 per cent. The methods of obtaining these results are described a page or two back.)

	Hygroscopic range.	Average weight of a seed in grains.
<i>Æsculus Hippocastanum</i> (Horse-chestnut) . . .	4.5 per cent.	130.0 grains.
<i>Allium ursinum</i>	4.0 "	0.12 "
<i>Anona muricata</i> (Sour Sop)	2.8 "	6.0 "
" <i>palustris</i>	2.6 "	4.0 "
" <i>reticulata</i> (Custard Apple)	2.8 "	4.0 "
" <i>squamosa</i> (Sweet Sop)	3.3 "	5.0 "
<i>Bignonia</i> (species of)	3.5 "	5.0 "
<i>Canavalia ensiformis</i>	2.5 "	24.0 "
<i>Chrysophyllum Cainito</i> (Star Apple)	1.8 "	12.0 "
<i>Citrus decumana</i> (Shaddock)	2.4 "	4.5 "
<i>Datura Stramonium</i>	3.0 "	0.13 "
<i>Dolichos Lablab</i>	1.1 "	4.0 "
<i>Faba vulgaris</i> (Broad Bean)	4.0 "	33.0 "
<i>Hura crepitans</i> (Sandbox Tree)	2.2 "	20.0 "
<i>Iris foetidissima</i>	4.0 "	0.8 "
<i>Luffa acutangula</i> (Loofah)	2.2 "	1.0 "
<i>Phaseolus multiflorus</i> (Scarlet-runner)	5.0 "	18.0 "
<i>Pisum sativum</i> (Peas) wrinkled	6.0 "	6.5 "
" " smooth	4.5 "	5.0 "
<i>Primula veris</i> (Primrose)	4.1 "	0.012 "
<i>Ravenala madagascariensis</i> (Travellers' Palm)	2.0 "	5.0 "
<i>Ricinus communis</i> (Castor Oil)	1.5 "	3.5 "
<i>Sapota Achras</i> (Sapodilla)	1.9 "	10.0 "
<i>Scilla nutans</i> (Bluebell)	4.0 "	0.1 "
<i>Swietenia Mahogani</i> (Mahogany)	2.0 "	3.7 "
<i>Tamus communis</i>	4.0 "	0.25 "

III. VARIABLE SEEDS. (Hygroscopicity variable.)

(Variable seeds are those where some are permeable and others impermeable, the proportions being very inconstant, so that the hygroscopic range for different seed-samples would vary much, and could only be characterised as intermediate between that for impermeable seeds (nil) and that for permeable seeds (2 to 4 per cent.).

	Hygroscopic range (variable in different samples).	Average weight of a seed in grains.
<i>Abrus precatorius</i>	0·5 per cent.	1·5 grains.
<i>Acacia Farnesiana</i>	1·5 "	2·0 "
<i>Albizzia Lebbek</i>	2·0 "	2·3 "
<i>Aquilegia</i> (species of)	0·7 "	0·33 "
<i>Bauhinia</i> (species of)	0·5 "	4·0 "
<i>Cæsalpinia Sappan</i> (A), mostly permeable	3·0 "	10·0 "
" (B), mostly impermeable	0·6 "	10·0 "
<i>Cæsalpinia sepiaria</i>	2·0 "	4·5 "
<i>Canavalia obtusifolia</i>	0·3 "	12·0 "
<i>Canna indica</i>	0·3 "	2·7 "
<i>Cassia fistula</i>	0·6 "	4·0 "
" <i>marginata</i>	0·7 "	10·0 "
<i>Entada polystachya</i> (A), mostly permeable	2·0 "	6·6 "
" (B) " impermeable	0·2 "	5·0 "
<i>Enterolobium cyclocarpum</i>	0·6 "	17·0 "
<i>Erythrina corallodendron</i>	0·5 "	3·2 "
" <i>indica</i>	1·0 "	13·0 "
<i>Ipomœa tuberosa</i>	0·5 "	25·0 "
<i>Poinciana regia</i>	1·0 "	10·0 "
<i>Tamarindus indicus</i>	1·0 "	20·0 "
<i>Thespesia populnea</i>	1·5 "	3·0 "

From the results of the observations on the hygroscopicity of a number of seeds which are given above it may be inferred—

(1) That permeable seeds under ordinary weather conditions vary to the extent of 2 or 3 per cent. of their weight in the course of two weeks, though the range may be reduced to 1 per cent. in equable conditions, and increased to 4 or 5 per cent. when the weather is characterised by extreme changes ;

(2) That impermeable seeds have practically no hygroscopic reaction, such small changes as do occur, as of 1 in 1000 or of 1 in 10,000 of the weight, being either instrumental or connected with loose tissue adhering to the scar or to the raphé ;

General conclusions drawn from the author's observations.

- (3) That with variable seeds, where there is a mixture of permeable and impermeable seeds, the range is intermediate in amount, frequently about 1 per cent., but varying of course with the proportion of permeable seeds.

With those "variable" seeds, as with *Entada polystachya* and *Cesalpinia Sappan*, where it is possible to distinguish by inspection between the two types of seeds, the difference in the hygroscopic reaction is well marked. Thus, with the first-named plant, a sample of permeable seeds displayed a range of 2 per cent., whilst a sample of seeds almost all impermeable gave a range of 0.2 per cent. So also with *Cesalpinia Sappan*, I found that seeds which had fallen to the ground in the ordinary way were mostly impermeable and had a range of 0.6 per cent.; whilst those remaining in the dried but closed pod on the tree were nearly all permeable and varied 3 per cent. in their weight. It would be quite possible for the gardener or the agriculturist to devise a rough and ready rule by which the proportions of hygroscopic permeable seeds and of non-hygroscopic impermeable seeds in any sample could be approximately estimated. Thus, assuming that with seeds of a certain kind the complete hygroscopic reaction when all the seeds were permeable was 3 per cent., then a sample of the same seeds that gave a range of 1.5 per cent. might be regarded as probably containing only 50 per cent. of permeable seeds. At all events a marked departure from the normal might give a valuable hint to the gardener in making a selection.

The influence of the coats in restraining the hygroscopic variations of permeable seeds has already been briefly alluded to in Chapter IV. It was there shown that the hygroscopic range of the seed of *Canavalia ensiformis* with its coats intact (2.5 per cent.) was less than in the case of the seed where the coats had been punctured (3.0 per cent.), and that this again was less than with seeds bared of their coverings (4.0 to 4.5 per cent.), thus clearly indicating a progressive increase in the

The hygroscopic reaction as a test for proving seeds.

The influence of the seed-coats on the hygroscopicity of permeable seeds.

hygroscopic variation of the seed in proportion to the degree of loss of the protection it owes to its coats. The same indications are presented below in the tabulated results for five kinds of seeds belonging to the four very different families. It will, however, be noticed that there is a very considerable difference between seeds in respect to the restraining influence of the seed-coverings on the hygroscopic reaction. In watery seeds like those of the Horse-chestnut, Broad Bean, and *Canavalia ensiformis*, it is evidently considerable, whilst with oily seeds like those of *Anona reticulata* it may be so small as to be almost negligible. In such experiments it is requisite that the seed should have completed its drying process, or at all events that it should be drying very slowly.

With reference to the differentiation between the coats and the kernel in this respect, such a contrast would not indicate a factor of much importance in determining the nature of the range, since, although the inner layer of the coats, being often looser in texture than the outer skin, might be expected to be more hygroscopic, it would not be exposed directly to the air, as in the case of the detached seed-coverings in an experiment. However, the results tabulated below show that the seed in its coverings is less hygroscopic than either the coats alone or the bared kernel.

COMPARISON OF THE HYGROSCOPIC RANGE OF PERMEABLE SEEDS
WITH AND WITHOUT THEIR COATS.

(The range is the variation stated as a percentage of the average weight. The seed and its parts were in each case tested together.)

	Seed in its coats.	Bared kernel.	Coats alone.	Age of seeds.
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	1'0	1'9	...	6 months.
<i>Anona reticulata</i> (Custard Apple)	2'8	3'0	3'1	18 months.
<i>Canavalia ensiformis</i>	A 1'5 B 2'5	3'3 4'0	4'1 ...	9 months. 6 months.
<i>Citrus decumana</i> (Shaddock)	2'4	3'1	3'4	4 weeks.
<i>Faba vulgaris</i> (Broad Bean)	2'0	3'2	2'6	8 months.

Note.—These results do not represent the full range in the case of the Horse-chestnut, the experiment being a short one.

The effect of age on a seed's hygrosco-
picity.

A few remarks may be made on the influence of age on the hygrosco-
picity of seeds. If it is a purely physical process and independent of life, we would not expect any marked effect to be shown with age, provided that the seeds, when first experimented on, had completed the drying process. But if the seed is still slowly drying, we should look for a slight increase in the "hygrosco-
picity range" as time goes on, a result that would be due to the seed losing weight, whilst the hygrosco-
picity variation remained unchanged. In such experi-
ments it is absolutely necessary that the seeds of different ages should be subjected at the same time to the same test. Without this condition the results would not be worth com-
paring, and for this reason many of my data are excluded. However, it will be seen from my experiments on the seeds of the Horse-chestnut (*Æsculus Hippocastanum*) and of *Tamus communis*, which fulfilled this condition, that the effect of age is slight.

RESULTS ILLUSTRATING THE EFFECTS OF AGE ON THE HYGROSCOPIC RANGE OF SEEDS, THIS RANGE BEING THE VARIATION IN WEIGHT STATED AS A PERCENTAGE OF THE AVERAGE WEIGHT OF THE SEEDS.

	2 months.	7 months.	13 months.	19 months.	31 months.
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	...	1'95	...	2'08	2'40
<i>Tamus communis</i>	4'03	...	4'00

The samples of the Horse-chestnut consisted of 4 to 7 seeds, weighing in all from 500 to 1000 grains. Those of *Tamus communis* included about 150 seeds, weighing about 37 grains.

The effect of a covering of hairs on a seed's hygrosco-
picity.

At first sight it might appear probable that a seed's hygrosco-
picity would be markedly increased by a hairy covering; but a little reflection will show that this cannot usually be expected. If we take an impermeable seed 100 grains in weight, of which 10 grains belong to the covering of hairs, a proportion, I should imagine, much above the average, and if we assume that the hairs have a hygrosco-
picity variation or range of

10 per cent., which again is much more above than below the average for vegetable materials, then the variation for the entire seed would be only 1 per cent., since, as an impermeable hairless seed, it would be non-hygrosopic. Or let us take a permeable seed corresponding to the above in all its characters, except that when deprived of its hairs it shows a hygrosopic reaction of 5 per cent. It is obvious that this reaction would be but slightly increased by the hairy covering, since the increased hygrosopicity of the hairs would be concerned only with one-tenth of the seed's weight.

But in thus depreciating in advance the effect of hairs on a seed's hygrosopicity we have assumed that the covering of hairs displays a more pronounced hygrosopic reaction than is exhibited by an ordinary hygrosopic hairless seed. My observations and experiments, however, go to show that this is not the case. We will take the impermeable seeds of *Ipomœa pes-capræ*, which have a dense pubescent covering and an average weight of $2\frac{1}{2}$ to 3 grains. As shown in Chapter IX, the weight of the hairs barely amounts to 3 per cent. of the total weight of the seed. To test the influence of the hairs on the hygrosopicity of the seed two samples, containing each about twenty-five seeds, were experimented on, one with the hairs scraped off and the other with the hairs remaining. The first gave a hygrosopic reaction of 0.7 per cent., and the second of 1.0 per cent. The hairs, in fact, made little or no difference, and the slight change that occurred was probably connected with quite a different cause, namely, the occurrence of one or two permeable seeds in each sample, an event which my flotation experiments indicate as not uncommon.

Still more unexpected were the results of my experiments on the hairy seeds of a species of *Gossypium*, probably *G. hirsutum*, which are described in the same chapter. The average weight of the entire seed is about 1.5 grain, and of this nearly one-half, or 44 per cent., is made up by the hairs. A sample of scraped seeds and a sample of hairy seeds displayed a similar but slight hygrosopic reaction of rather

under 1 per cent. Ordinary cotton-wool, it may be added, exhibited under my tests a hygroscopic variation of only 2 per cent., which is merely what one would look for in hairless permeable seeds.

Hygro-
scopicity and
germination.

We may infer from Berthelot's principle that hygroscopicity, being associated with the water which the seed, living or dead, holds in maintaining its equilibrium with the air, has nothing to do with germination. It has, however, often the appearance of bringing about germination. One may gather fresh acorns, separating at a touch from the cupule on the tree, and leave them exposed in a saucer in an ordinary room for two or three weeks, and some of them will germinate. One may stand a dry, open test tube half filled with seeds of *Abrus precatorius* in water in a tall glass vessel which is subsequently covered over, and in the course of a week or two a few of them will be found in a germinating or at least in a swollen condition. But in neither case has this anything to do with the water of hygroscopicity.

In the case of the acorns, as shown in a later chapter, they still contain, on falling out of the cupule, a large excess of water, and it is this excess that is utilised in the early germination. In this freshly detached state the embryo of the future oak as it lies enclosed in the shell is almost in the act of germination, and indeed is apt to germinate in spite of its drying condition. As they lie drying on the table the chances are fairly balanced whether the acorns will germinate before the loss of water renders that impossible, or whether the process of drying will proceed so fast that the germinative capacity is unable to assert itself.

In the case of *Abrus precatorius*, should the vessel be exposed to the usual diurnal changes of temperature, condensation of the water-vapour in the heavily charged air would probably occur and liquid water would be likely to come in contact with the seeds, thus introducing another order of phenomena. Nobbe (pp. 105-108) lays stress on the point that contact with liquid water is essential for inducing

the swelling that precedes germination, and that the increase in the water-contents due to hygroscopicity is quite insufficient for the purpose. The question whether, under ordinary conditions, seeds will take up sufficient water from the air for germination he answers in the negative ; but he considers that germination would be likely to occur when through frequent great changes of temperature, condensation takes place on the surface of the seed. In the extreme conditions reproduced in his experiments, when seeds of Flax and of the Kohl-rabi were exposed for many days to air saturated with moisture, he found that an increase in weight of 22 or 23 per cent. did not lead to germination. In such experiments germination would occur only when, through condensation within the vessel, liquid water comes into contact with the seeds.

Jodin put the distinction between the increase of water due to hygroscopicity and the amount of water required for germination very clearly in the case of peas. He shows that whilst the minimum amount of water required to be absorbed for germination amounts to 67 per cent. of the weight of the resting seed, the greatest increase in weight involved in the hygroscopic range of peas is not more than 23 per cent., a quantity he characterises as insufficient to provoke germination. Although he found that the water of hygroscopicity was quite insufficient to produce germination, the results of one of his experiments described in Note 4 of the Appendix might have been interpreted in this sense by a superficial observer. In order to ascertain the minimum amount of water requisite for germination, he placed the peas on a platinum support suspended in moist air, the metal condensing the aqueous vapour in fine drops and communicating the liquid water to the peas. It is evident from Jodin's experiments that, as far as the water-contents of the seed are concerned, the germination point lies between the maximum of the hygroscopic range and the limit of the seed's capacity for absorbing liquid water, or, in other words, between the hygrometric extreme and the saturation point.

The hygroscopic reaction does not provoke germination.

The germination point lies above the hygroscopic maximum and below the saturation limit.

The maximum of the hygroscopic capacity.

And now we have to inquire into the nature of this extreme limit of a seed's hygroscopicity. This is a difficult matter and one concerning which awkward questions are likely to be raised. In my own experiments the object was to ascertain the hygroscopic range of seeds during a fortnight of changeable weather; and the results procured, as shown in the table, differ but little, whether obtained in the tropical climate of Jamaica or in the temperate climate of England. Permeable seeds, according to my observations, vary usually 3 or 4 per cent. of their weight. Jodin found that in the course of a year's exposure to ordinary air-conditions the water-contents of peas varied according to the temperature and hygrometric condition of the atmosphere from 10 to 30 per cent. of the seed's dry weight, or, as he puts it, between 0·1 and 0·3 gramme for each gramme of water-free material. Stated in terms of the wet weight, that is, of the seed with its water-contents, this represents a variation of from 9 to 23 per cent., and an annual range of 13 or 14 per cent. This hygroscopic range for peas during a year is considerably larger than the range assigned to them in my own observations, namely, 4 to 6 per cent. The difference is probably due as much to the methods employed as it is to the differences in the length of the experiments. Such a range was never indicated in the case of the seeds of *Canavalia ensiformis*, the total variation of which in a two years' experiment amounted to less than 6 per cent. of their weight; nor was it evidenced in the course of my "long-period" weighing experiments, the results of which are discussed in Chapter X.

Nobbe's experiments.

Serious obstacles are apt to arise in testing the maximum capacity of a seed for absorbing water-vapour from the air. They were encountered by Nobbe in his experiments on flax-seeds (pp. 105-108). Such seeds, after being exposed for nine days to air saturated with moisture, increased their weight by $16\frac{1}{2}$ per cent., whilst others kept for the same period in ordinary air added from $\frac{1}{2}$ to $1\frac{1}{2}$ per cent. to their weight. In another experiment on these seeds in saturated air, which covered twenty-six days, it was found that under warm conditions

(mean temperature 18° C., or 64 to 65° F.) there was an increase in weight of 22.5 per cent., and under cool conditions (mean temperature about 5° C., or 41° F.) an increase only of 4.1 per cent., whilst with seeds exposed in turn to both the warm and cool conditions there was an increase of 16.6 per cent.

One is inclined to think that condensation occurred in the experiment under warm conditions. The seeds were placed in a porcelain vessel standing in water and covered with a glass globe, the range of temperature being 13° to 21° C., or 55° to 70° F. With a range of about 15° F., condensation is quite possible; and if it occurred at night it might not be evident in the daytime. We are told that the occurrence of mildew brought the experiment to a close, and that the seeds were still adding to their weight at the end. The same method was adopted with all the flax-seed experiments, and also with the seeds of the Kohl-rabi (*Brassica oleracea caulorapa*), which increased their weight 23.5 per cent. It is to be noted that this investigator was not inclined to accept Hoffmann's much smaller estimates for the hygroscopic increase of weight of the seeds of *Linum* and *Brassica*, namely, 4.7 and 4.6 per cent. respectively.

The trend of my own results is all in the direction of Hoffmann's smaller determinations of a seed's hygroscopicity. I should imagine that flax-seeds (*Linum*), containing as they do so much colloid material capable of combining with water in the form of mucilage, would give results far from typical. But of more importance still is the fact that mould or mildew interfered with both the experiments on flax-seeds made by Nobbe, where the gain in weight reached $16\frac{1}{2}$ and $22\frac{1}{2}$ per cent.; and in neither case had the increase ceased when the experiment ended. The danger in all experiments where seeds are exposed to air saturated with moisture is the development of mould, which, on account of its hygroscopic properties, would go far to vitiate the results. Its onset is insidious; and, as was often indicated in my drying and similar experiments in the tropics, long before the fungus became evident

The danger
of mould in
such experi-
ments.

to the eye there was a marked increase of weight and a slight softening of the affected materials.

The hygroscopic behaviour of pods.

But I may remark that the more moderate view of the range of hygroscopic variation for seeds is supported by the results of my observations on air-dried fruits. Some of them relating to pods or legumes are tabulated below.

A.—RESULTS OF EXPERIMENTS ON THE HYGROSCOPIC RANGE OF ENTIRE AIR-DRIED LEGUMES OR PODS, INDEHISCENT AND CONTAINING THEIR SEEDS. (The hygroscopic range is the variation in weight stated as a percentage of the total weight.)

	Number and weight of pods in grains.	Length of experiment.	Locality of experiment.	Hygroscopic range.	Weather.
Albizzia Lebbek .	One pod 25 grains	11 days	West Indies	4·3 %	Wet and dry.
Cassia fistula . .	„ 1,710 „	2 months	England	3·4 „	Great contrasts.
„ „ . .	„ 1,515 „	2 „	„	3·4 „	Great contrasts.
Poinciana regia .	„ 1,532 „	2 „	„	2·7 „	Great contrasts.
Entada polystachya	„ 164 „	2 „	„	3·8 „	Great contrasts.
„ „ .	The same pod	7 days	West Indies	4·2 „	Wet and dry.
Pisum sativum (Pea)	Two pods, total 120 grains	See note	England	4·7 „	See note.

Note.—In all the experiments except that on Pea-pods, the pods were kept in one room. The experiments, occupying two months, lasted from June to August. The data for the Pea-pods were obtained by transferring them from a cool and moist room (temperature 50° to 55° F.) to a warm and dry cupboard (temperature 65° to 70° F.) and weighing them after four days.

B.—COMPARISON OF THE HYGROSCOPIC RANGES OF THE AIR-DRIED SEEDS AND FRUIT-CASE OF PISUM SATIVUM (POD) AND OF IRIS FETIDISSIMA (CAPSULE) UNDER THE SAME CONDITIONS.

Iris foetidissima .	H. R. of seeds 4·0 per cent.	H. R. of fruit-case 3·6 per cent.
Pisum sativum . .	„ „ 4·5 „	„ „ 4·7 „

It will be seen from these tables that the variation in weight in response to the changes in atmospheric humidity was usually

3 or 4 and never over 5 per cent., whatever the nature or size of the pod. These pods, all of them dry, intact, and containing their seeds, range in length from 3 or 4 inches, as in the case of the Pea, to a couple of feet, as with the pods of the species of *Cassia* and *Poinciana*; and there is a great contrast between the relatively fragile appearance of the first-named and the tough, woody aspect of the two last. However, notwithstanding the great differences in size, weight, and texture of these pods, their changes in weight due to the hygroscopic reaction are not far apart. The long pods of *Cassia fistula* are very sensitive to the hygrometric condition, and vary in weight whilst being handled for the balance. One of them lost 1 per cent. of its weight whilst a wet morning was giving place to a fine evening. This amounts to a great deal in the balance, since the pods when dry range between 1500 and 2000 grains in weight. They are durable, easily weighed, and might prove useful as hygrometers.

It would seem from the foregoing data that permeable leguminous seeds possess much the same degree of hygroscopicity as their pods. Thus under the same conditions peas gave a range of 4.5 per cent., and the pods with seeds removed 4.7 per cent. (The same principle is also indicated in the case of *Iris fœtidissima*, where the ranges for the seeds and the capsular valves were 4.0 and 3.6 per cent.) However, there is no such relation between the impermeable seed and its pod. All the impermeable seeds with which I am acquainted, such as those of *Guilandina bonducella*, *Mucuna urens*, *Dioclea reflexa*, *Entada scandens*, etc., are enclosed in pods that in the dry state readily take up and absorb moisture; whilst in the case of the hygroscopic pods of the species of *Cassia*, *Poinciana*, *Entada*, and *Albizzia*, dealt with in the table, many of the seeds are impermeable, and the hygroscopic range for any sample of seeds chosen at random is consequently low, usually not over 1 or 2 per cent., but varying according to the proportion of permeable seeds. As illustrating the hygroscopic behaviour of pods emptied of their impermeable seeds, I may mention

Pods are hygroscopic whether the seeds are permeable or impermeable.

that the dry open pods of *Guilandina bonducella* and *Cesalpinia Sappan*, as they lay on the table in my room in Grenada, used to vary in their weight as much as 1 or 2 per cent. from day to day, especially between the evening and the following morning.

In concluding this chapter we may observe that the question we put to ourselves a few pages ago as to the extreme limit of a seed's hygroscopicity is very far from being answered, and perhaps it may prove to be not altogether pertinent to the subject we are discussing. With the data at our disposal it seems unnecessary to follow up this special point any further at present; and indeed it will appear from the subsequent chapters that a number of queries claim a reply first.

SUMMARY

(1) Hygroscopicity in a seed is defined as the variation of its water-contents in response to the changes in the hygrometric state of the atmosphere (p. 147).

(2) After referring to the important memoir on the subject of hygroscopicity in general by Léo Errera and to the display of this quality by vegetable materials in particular, special attention is directed to the researches of Jodin and Berthelot. Whilst the first-named investigator approached the subject from the biological and the second from the physical side, both arrived at the same conclusion: that we are here concerned with a quality that is independent of vitality (p. 148).

(3) Jodin, experimenting on living and dead peas, found that they exhibited much the same hygroscopic variation in the course of a year's exposure to ordinary air-conditions (p. 148).

(4) Berthelot, experimenting on different vegetable materials (leaves and stems of grasses, etc.), shows that the peculiar property possessed by air-dried vegetable substances and some other materials of regaining from the air the water which they yield up when exposed to a temperature of 100° to 110° C. is a function of the hygrometric state of the atmosphere and is essentially a physico-chemical process independent of life. We will take as illustrating this principle 100 grammes of fresh plant-substance which is reduced to 50 grammes by air-drying in an ordinary room. Exposing it then to a temperature of 100° to 110° C., its weight is further reduced to 40 grammes; but on being allowed to

remain in the room for a few days, it replaces the water lost in the oven by abstracting it from the air and returns to its original air-dried weight of 50 grammes, subject only to the ordinary hygroscopic variation. Precisely the same air-dried weight is ultimately reached if the fresh material is put at once in the oven. In the same way, the leaf that dries and dies naturally on the plant, if placed in the air after the heat test, regains the water lost in the oven. This is Berthelot's principle of reversibility (p. 149).

(5) The author, after confirming this principle by appealing to his experiments on Hazel leaves, shows that it presents us with the simplest mode of differentiating the water-contents of plant-tissues, namely, into (a) the water of hygroscopicity, which they hold whether living or dead, and (b) the water of vitality, which they lose when they die (p. 151).

(6) He points out that the chemist, when producing by synthesis organic vegetable substances, would allow the atmosphere to supply the water of hygroscopicity, whilst he himself in his creative rôle would have to furnish the water of vitality. To emphasise this point he gives the result of an experiment on bread, and shows that just as moist fresh plants after being exposed to a temperature of 100° C. can only recover from the air the water lost by air-dried plants in the oven, so bread after the same heat test only gains back what was originally in the miller's flour, but cannot recover the water the baker put into it (p. 153).

(7) After giving a further illustration of the principle of Berthelot in the results of an experiment on the seeds of *Phaseolus multiflorus*, the author proceeds to deal with the implications of this principle (p. 154).

(8) The first is that air-dried resting seeds, both permeable and impermeable, contain only the water of hygroscopicity; and the second, which follows from it, is that there is in such seeds no water associated with any vital function (p. 155).

(9) Since some seeds can retain their germinative powers after being desiccated to an extreme degree, the presumption arises that in their resting state they can dispense with water altogether; and it is urged that we are not called upon to assign a function to the minute amount of water that may remain after extreme desiccation. A perfectly dry seed protected from the air alone possesses the potentialities of immortality (p. 156).

(10) Instead of favouring the longevity of a seed, water is regarded here as the source of its greatest danger. Appeal is then made to the biological significance of hygroscopicity in seeds, and it is shown that whilst the constant hygroscopic reaction limits the life of permeable seeds, its absence in impermeable seeds ensures their longevity. The seed that has the best chance of living for

ever is one where a perfectly dry embryo is locked up in a hard impermeable shell or covering (p. 157).

(11) Coming to the details of his own observations on hygroscopicity, the author, after observing that in the nature of things considerations of hygroscopicity are concerned only with permeable seeds, proceeds to discuss the effects of change of climate on the weight of seeds. In this connection he shows that, as a result of transportation from the temperate zone to the tropics and back, permeable seeds varied from 3 to 4 per cent. of their weight, variable seeds (both types in the same plant) less than 1 per cent., and impermeable seeds practically not at all. The changes of weight, he points out, are included within the ordinary hygroscopic range (p. 158).

(12) The methods of determining the range of hygroscopicity in seeds in terms of the variation of their weight are then described, and after giving the results of his observations on more than sixty kinds of seeds, of all sizes and characters, he forms the following general conclusions:—

- (a) That permeable seeds vary usually to the extent of from 2 to 3 per cent. of their weight, though the range may be as little as 1 per cent. in equable atmospheric conditions, and as great as 4 or 5 per cent. when the changes in the relative humidity of the air are extreme;
- (b) That impermeable seeds have practically no hygroscopic reaction, their weight remaining unchanged in spite of great variations in the hygrometric state of the air;
- (c) That with variable seeds, where there is a mixture of permeable and impermeable seeds, the range for any ordinary sample is usually about 1 per cent., differing according to the proportion of permeable seeds (p. 165).

(13) Special stress is laid on the value of the hygroscopic reaction stated in terms of weight as a test for proving seeds (p. 166).

(14) Additional data are given, as supplementing those already given in Chapter IV, on the influence of the coats on the hygroscopicity of permeable seeds, and supporting the previous conclusion that the coats tend to restrain the hygroscopic range (p. 167).

(15) Results of observations are then given on the effects of age on the hygroscopic behaviour of seeds, and they are shown to be slight (p. 168).

(16) Contrary to one's expectation, it is found that a hairy covering, whilst it gives a small hygroscopic range of less than 1 per cent. to impermeable seeds, but slightly if at all increases the hygroscopicity of permeable seeds (p. 169).

(17) Since it follows from the principle of Berthelot that the water of hygroscopicity could have little to do with germination, appeal

is made to the results of experiments made by Nobbe, Jodin, and the author in this connection ; and it is established that the normal hygroscopic reaction cannot provoke germination, the minimum amount of water required for germination being far in excess of that which a seed would take up unaided from the air (p. 171).

(18) The nature of the extreme limit of a seed's hygroscopicity is then discussed ; and the author, after laying stress on the especial risks of mould and condensation to which such experiments are liable, follows the indications of his own experiments in accepting a range in weight of 5 or 6 per cent. of the average weight of the seed as the greatest amplitude of normal hygroscopic variation, the usual range, however, being only 2 or 3 per cent. Hoffmann's results point in the same direction, and precisely the same limits to the hygroscopic range of weight are established by the author's observations on the weight of dry pods (p. 172).

(19) The results of these observations on air-dried legumes are then tabulated, and it is shown that leguminous pods with permeable seeds display much the same degree of hygroscopicity as their seeds, the pod being hygroscopic whether the seeds are permeable or impermeable (p. 174).

(20) Although the ordinary maximum of the normal hygroscopic range has been above stated, the author regards the possible extremes of a seed's hygroscopicity as outside the present inquiry.

CHAPTER VIII

A LAST WORD ON THE HYGROSCOPICITY OF SEEDS

THE seed's capacity of regaining from the air the water driven off by exposure to a temperature of 100° C. has been discussed pretty much in the order in which the investigation has been pursued. We have plodded on without always knowing where the road was leading to, diverging first to one side and then to the other, feeling our way often in the darkness, until at length we have stumbled on a clue that throws much light on the whole inquiry. The principle of Berthelot only came under our notice when the investigation was far advanced, and of course it would be possible to recast much of what has been already written in the light now displayed to us. But it has been found easier to present the work in the stages in which it shaped its course and to introduce this principle much as the romance-writer produces his climax towards the end of the story.

The water of hygroscopicity becomes the central point of the discussion.

In my last word on the subject of permeable and impermeable seeds and the contrasts they present, I therefore view the whole matter from a different standpoint. Up to now the impermeability of seeds has been the most conspicuous feature in the discussion; and most of the results obtained shaped themselves in one way or another in some relation to this quality. Here I propose in a few pages to make the water of hygroscopicity the centre-point of the discussion. The hydration of all living vegetable matter may be thus simply stated. There is the water that is lost when the materials are allowed to dry

under ordinary air-conditions, the water of vitality ; and there is the water that this air-dried material loses in the oven when exposed to a temperature of 100° C. and subsequently regains from the air, the water of hygroscopicity. Air-dried vegetable material, whether living or dead, contains only the water of hygroscopicity, which in these circumstances is one and the same with the water-percentage. There is no room for any more free water in a plant's economy than that which is included in the water of vitality and the water of hygroscopicity. It is the water of hygroscopicity that we are here concerned with, and we have just seen that in air-dried vegetable substances this is the water that such materials lose in the oven. Let us then determine how this principle applies to seeds.

But before we can apply this principle to seeds it is requisite to determine the correlative of the seed in its pre-resting and resting stages with other portions of the plant. Manifestly the correlative of the living leaf and the living stem is the large soft seed of the ripe fruit before the drying and shrinking process begins. Manifestly also the correlative of the dried-up leaf and stem is the same seed after it has completed its shrinking process and has entered upon the resting stage. As far as their water-contents are concerned, there is no difference between the resting seed and the dried-up leaf and stem, all of them holding only the water of hygroscopicity, which is driven off in the oven and subsequently regained from the air. As far as vitality is concerned there is also no difference. We term the leaf dead and say that the vitality of the seed is suspended. What is the difference ? There is room for none.

It is thus clear that the seed's hydration acquires a new significance when we allow the discussion to centre around the water of hygroscopicity and apply the principle of Berthelot. This principle raises the whole question of the necessity of water for the resting seed, and the logical issue is the denial of its necessity altogether. From this point of view

The correlative of the seed with other portions of the plant.

The logical issue of the principle of Berthelot as respects the seed.

there is no use for any free water in the economy of a seed that has gone through the normal shrinking and drying process. With these remarks I would now draw attention to the contents of the following table, which is intended to illustrate the hydration of vegetable substances from this standpoint.

Comparison
of the water-
contents of
leaves, fruits,
and seeds.

One notices at once in the columns on the right side of the next table how constant in amount is the water of hygroscopicity (the water of the air-dried tissue) in the living leaf, fruit, and seed. Stated as a proportion of the living substance, its amount varies usually between 3 and 6 per cent. in different cases; but since its quantity is regulated by the degree of atmospheric humidity, it is evident that if all experiments were conducted under precisely the same conditions, the range of the variation would be much less, probably only 4 to 5 per cent. for these different parts of a plant.

It is, therefore, not in the water of the air-dried tissue (the water of hygroscopicity), but in the water lost by the living tissue when drying under ordinary air-conditions (the water of vitality) that the several parts of the living plant differ from each other. This varies considerably, the range of the results given in the table being 33 to 80 per cent. But notwithstanding this variation, the most important suggestion that this table offers to us is that the leaf, the fruit, and the seed are, as respecting their water-contents, all comparable in the living condition, the living seed being the soft uncontracted seed, such as we see in the ripe capsule and legume before drying begins. So, again, these parts of a plant are all comparable in the air-dried state, the air-dried seed being the typical resting seed. We cannot consider the seed as a thing apart and place it in a category by itself. The resting seed from this point of view is just as dead as the dried leaf. Both are equally inert vegetable substances, and the only free water that they both contain is what they yield up in the oven and gain back from the air. Occasionally in the leaf, and

COMPARISON OF THE WATER-CONTENTS OF LEAVES, FRUITS, AND SEEDS. (All the results are from the author's experiments, except those for the grass (*Festuca*), which is taken from Berthelot's paper. I = impermeable seed; P = permeable seed. *)

The materials tested.	Relative weights.		Water Contents.				Proportion of the water of hygroscopicity.	
	Original weight in the moist condition.	After drying in air at ordinary temperature.	After exposure to a temperature of 100° to 110° C. for 1½ to 2 hours.	Total in the moist condition.	Water lost by the moist material when air-dried (water of vitality).	Water lost by the air-dried material in the oven (water of hygroscopicity).	To the total weight of the moist material.	To the weight of the air-dried material.
Corylus Avellana (Hazel)	100	32.0	28.7	71.3	68.0	3.3	3.3 per cent.	10.3 per cent.
Guilandina bonducella	100	...	38.1	61.9	6.0 "	...
Quercus Robur (Oak)	100	26.2	22.7	77.3	73.8	3.5	3.5 "	13.4 "
Cocos nucifera (Coco-nut)	100	35.6	30.0	70.0	64.4	5.6	5.6 "	15.7 "
Festuca (Grass)	100	22.6	18.3	81.7	77.4	4.3	4.3 "	19.0 "
Pyrus Malus (Apple)	100	66.5	61.0	39.0	33.5	5.5	5.5 "	8.3 "
Citrus Aurantium (Orange)	100	18.3	13.9	86.1	81.7	4.4	4.4 "	24.0 "
Iris fetidissima	100	19.2	15.2	84.8	80.8	4.0	4.0 "	20.8 "
P Phascolus multiflorus (Scarlet-runner)	100	20.0	16.9	83.1	80.0	3.1	3.1 "	18.0 "
P Faba vulgaris (Broad Bean)	100	40.0	34.0	66.0	60.0	6.0	6.0 "	15.0 "
P Canavalia ensiformis	100	40.0	34.4	65.6	60.0	5.6	5.6 "	14.0 "
I Guilandina bonducella	100	43.0	36.6	63.4	57.0	6.4	6.4 "	15.0 "
I Entada scandens	100	33.0	30.4	69.6	67.0	2.6	2.6 "	8.0 "
I Mucuna urens	100	40.0	36.0	64.0	60.0	4.0	4.0 "	10.0 "
I Dioscorea reflexa	100	50.0	45.0	55.0	50.0	5.0	5.0 "	10.0 "
P Æsculus Hippocastanum (Horse-chestnut)	100	50.0	45.7	54.3	50.0	4.3	4.3 "	8.6 "
	100	47.0	40.9	59.1	53.0	6.1	6.1 "	13.0 "

* See Note 21 of the Appendix.

normally in the seed, the life of the air-dried tissues may be re-kindled, but as air-dried substances they have no life in them.

Another subject upon which the data of the table throw light is the contrast in the hydratation of resting seeds of the permeable and impermeable types. There are four typical seeds of each kind there referred to, and we see that in whatever way we state the relation of the water of hygroscopicity this contrast is brought out, its proportion in the impermeable seeds being only about two-thirds of that in the permeable seeds. The difference as re-stated below is not very great, but it serves to illustrate the contrast drawn between these two seed-types from a different point of view in the earlier chapters. We now see that the ultra-dryness of impermeable seeds is due to the diminution of the water of hygroscopicity.

A. In permeable seeds, typified by those of *Faba vulgaris*, *Phaseolus multiflorus*, *Canavalia ensiformis*, and *Æsculus Hippocastanum*, the water of hygroscopicity forms on the average about 6 per cent. of the weight of the moist, living, uncontracted seed, and about 14 per cent. of the weight of the seed in the resting state.

B. In impermeable seeds, illustrated by those of *Guilandina bonducella*, *Entada scandens*, *Mucuna urens*, and *Dioclea reflexa*, its average proportion for the moist, uncontracted seed is about 4 per cent., and for the resting seed about 9 per cent.

And now, in conclusion, let me say that though this treatment of the subject, imperfect as it is in many ways, helps to clear the problem of the resting seed, its lifeless, inert condition remains as mysterious as ever. A seed that only holds the water that it would possess whether or not it retains the power of germination can owe nothing to this constituent. Take, for instance, the permeable resting seed with its water-contents ever varying in response to the hygrometric changes of the air. It holds more water in a moist climate than it does in a dry one, and as the experiments

The hydration of permeable and impermeable resting seeds.

The resting seed has no use for its water-contents.

of several physicists show, it can retain its germinative powers after being long in conditions completely water-free. I would assume that in all experiments where vital processes have been detected in resting seeds the drying process was incomplete. The indications of the balance are that the permeable resting seed, when it has attained a stable weight varying only about a mean in response to the hygrometric changes of the air, has no use for the water it contains; and we may infer the same for the impermeable seed with its diminished water-contents. The water of hygroscopicity which the resting seed alone retains is, as we have seen in the previous chapter, quite insufficient to induce germination. That it is necessary for the preservation of the germinative powers is negatived by the fact that when we have exposed the seed for hours in a broken condition to a temperature of 100° to 110° C. it gains back from the air in the course of a week or two all the water it lost in the oven, and in the case of impermeable seeds considerably more. As a dead seed, therefore, it holds at least as much water as it does when preserving its germinative capacity. The water of hygroscopicity belongs to a plant-tissue, whether living or dead, and this is the only free water that the resting seed contains.

SUMMARY

(1) The water of hygroscopicity becomes the central point of the discussion, and it is shown that there is no room for any more water in a plant's economy than that which is included in the water which the living tissue loses during natural drying, the water of vitality, and the water which such air-dried material loses in the oven and subsequently regains from the air, the water of hygroscopicity. Such are the indications of the balance as interpreted by the principle of Berthelot.

(2) In comparing the water-contents of the leaf, the fruit, and the seed, it is pointed out that just as they are all comparable in the living condition, so they can be compared in the natural air-dried state, the withered leaf with the dried-up fruit-case, and both of them with the normal resting seed. All of them are inert and lifeless, and if we wish

to contrast them we must look for some other point of difference than that presented by their water-contents.

(3) It is shown that the permeable and impermeable seed, when their differences are viewed from this standpoint, may be contrasted as respects their water of hygroscopicity, which is least in the impermeable seed and greatest in the permeable seed.

(4) The lesson of the balance is that the true resting seed has no use for any free water that it holds.

CHAPTER IX

THE RÉGIME OF THE SHRINKING AND SWELLING SEED

ONE mode of comparing the changes which a seed experiences in the shrinking, resting, and swelling stages, or, in other words, in passing from the pre-resting to the resting condition, and thence on to the swollen state that precedes germination, is to compare the relative weights of parts in the several conditions. In Chapter II we discussed this subject at length as respects the seed in its entirety. We will now try to obtain an insight into the details of the régime of the shrinking and swelling seed, with the balance again as our guide. Although the view is limited, it is not without instruction; and perhaps this is one of the first attempts to state in terms of weight the correlated problems concerned with the mysterious resting state, with that strange shrinking process which even immersion in the pulp of a watery fruit cannot inhibit, and with that singular return of the seed by absorption of water to the pre-resting condition whilst preparing for germination. We here endeavour to illustrate numerically the changes which the resting seed has undergone in the shrinking stage and the changes which it has to undergo when swelling for germination.

The relation of parts in the three conditions of the seed.

The relative weights of the coats and the kernel in the resting seed will first be dealt with. Though in themselves of little interest, they acquire importance when we contrast

In the resting-seed.

them with the same data for other seeds, but more especially when we compare them with the proportional weights in the pre-resting seed of the moist fruits, and in the resting seed swollen for germination. I here append in a tabulated form my results stated as percentages for about eighty-two species of plants, arranged in order, the seeds with the smallest proportions of coverings coming first. The data are given in two tables, one for leguminous seeds, and the other for seeds of other orders. For convenience only one value will be referred to in this discussion, that for the seed's coverings, which I will term the "seed-coat ratio." Thus, when *Iris Pseudacorus* is said to have a seed-coat ratio of 20, it is meant that the coverings make up 20 per cent. of the weight of the entire seed.

The great range in the proportional weights of the seed's coverings in the resting state.

We notice in these tables that there is a great range in the proportional weight of the seed's coverings, namely, from 5 to 69 per cent. The maximum of the range is but slightly extended in the case of seeds with abundant hairs. If we were to exclude them altogether we should still have the hairless seeds of *Sapindus Saponaria* representing the maximum limit of 64. But we should be no more justified in disregarding the hairs of a seed than we should in leaving out of our calculation the wing-like appendages of seeds like those of the Mahogany tree (*Swietenia*) or of the Moringa tree. It is noticeable that whether we restrict ourselves to leguminous seeds or to seeds of other orders, the range is much the same. The leguminous seeds belong to 39 species and show a variation from 6 to 61 per cent. The other seeds, which belong to 43 species of 20 different orders, give a range from 5 to 69 per cent. Since, therefore, nearly the whole range is to be found with leguminous seeds, it follows that with seeds of this order there is nothing distinctive in the proportional weight of the seed's coverings; and, generally speaking, except in the case of seeds having a ratio less than 20 per cent., they run fairly well together.

TABLE SHOWING THE RELATIVE WEIGHTS OF THE COATS AND KERNELS OF RESTING LEGUMINOUS SEEDS, TAKING THE ENTIRE SEED AS 100.

	Average weight of a single seed in grains.	Relative weights of coats and kernels, taking the entire seed as 100.		Remarks.
		Coats.	Kernel.	
Phaseolus vulgaris (French Bean)	13'0	6'2	93'8	
Phaseolus (tropical species)	6'5	8'0	92'0	
Pisum sativum (Pea)	6'0	8'5	91'5	Slightly wrinkled seeds.
"	7'0	10'0	90'0	Much wrinkled seeds.
Phaseolus multiflorus (Scarlet-runner)	17'0	12'5	87'5	
Cajanus indicus	3'0	13'0	87'0	
Dolichos Lablab	4'0	14'0	86'0	
Faba vulgaris (Broad Bean)	30'0	14'4	85'6	"Long-pod" variety.
"	38'0	15'0	85'0	Green Windsor variety.
Cassia fistula	4'0	15'0	85'0	
Canavalia ensiformis	25'0	16'0	84'0	Seeds white.
" gladiata	45'0	20'0	80'0	Seeds brownish-red.
" (species)	18'0	21'0	79'0	
Vicia sativa	0'3	21'0	79'0	
Bauhinia (species)	4'0	23'5	76'5	
Cassia grandis	9'0	25'0	75'0	
Vigna luteola	0'7	25'0	75'0	
Mucuna urens	90'0	26'3	73'7	
Canavalia obtusifolia	12'0	27'0	73'0	
Cæsalpinia Sappan	10'0	27'5	72'5	
Tamarindus indica	20'0	28'0	72'0	
Entada polystachya	6'6	28'5	71'5	Seeds permeable.
Cassia marginata	10'0	29'0	71'0	
Abrus precatorius	1'5	30'0	70'0	
Erythrina indica	12'5	30'6	69'4	
" velutina	7'5	31'4	68'6	
Sophora tomentosa	2'4	32'0	68'0	
Entada polystachya	5'0	32'8	67'2	Seeds impermeable.
Erythrina corallodendron	3'2	33'1	66'9	
Dioclea reflexa	100'0	40'0	60'0	
Entada scandens	400'0	39'0	61'0	
Calliandra Saman	4'0	40'6	59'4	
Leucæna glauca	0'8	46'0	54'0	
Guilandina bonduc	50'0	49'0	51'0	
" (glabra?)	60'0	49'0	51'0	An inland Jamaican species with oblong yellow seeds.
Poinciana regia	10'0	49'5	50'5	
Albizzia Lebbek	2'2	50'0	50'0	
Enterolobium cyclocarpum	17'0	52'0	48'0	
Adenanthera pavonina	4'7	53'0	47'0	
Guilandina bonducella	40'0	58'0	42'0	
Acacia Farnesiana	2'0	61'0	39'0	
Cæsalpinia sepiaria	4'0	61'5	38'5	

TABLE SHOWING THE RELATIVE WEIGHTS OF THE COATS AND KERNELS OF RESTING SEEDS BELONGING TO OTHER ORDERS THAN THE LEGUMINOSÆ, THE ENTIRE SEED BEING TAKEN AS 100.

	Order.	Average weight of a single seed in grains.	Relative weights of coats and kernel, taking the entire seed as 100.		Remarks.
			Coats.	Kernel.	
Tamus communis . . .	Dioscoreæ	0'3	5'0	95'0	
Arum maculatum . . .	Araceæ	0'7	12'5	87'5	
Ipomœa tuberosa . . .	Convolvulacæ	25'0	20'0	80'0	
Iris Pseudacorus . . .	Iridææ	0'7	20'0	80'0	
Canna indica . . .	Cannacææ	2'5	21'0	79'0	
Mammea americana . . .	Guttiferæ	550'0	23'5	76'5	
Swietenia Mahogani (Mahogany)	Meliacææ	3'7	25'0	75'0	Without wing 18 and 82.
Citrus decumana (Shaddock)	Aurantiacææ	4'0	26'0	74'0	
Æsculus Hippocastanum (Horse-chestnut)	Hippocastanææ	130'0	27'0	73'0	
Anona reticulata . . .	Anonacææ	4'0	27'0	73'0	
Citrus Aurantium (Orange)	Aurantiacææ	2'5	28'0	72'0	
Ricinus communis (Castor Oil)	Euphorbiacææ	3'0	28'0	72'0	
Bignonia (near æquinoctialis)	Bignoniacææ	5'0	28'0	72'0	
Hura crepitans . . .	Euphorbiacææ	20'0	30'0	70'0	
Anona palustris . . .	Anonacææ	4'0	31'0	69'0	
Moringa pterygosperma . . .	Moringææ	5'0	33'0	67'0	Without wings 30 and 70.
Anona muricata . . .	Anonacææ	6'0	34'0	66'0	
„ squamosa . . .	„	5'0	35'0	65'0	
Momordica Charantia . . .	Cucurbitacææ	3'0	37'5	62'5	
Ipomœa dissecta . . .	Convolvulacææ	2'7	37'5	62'5	
Jatropha Curcas . . .	Euphorbiacææ	12'0	38'0	62'0	
Iris fetidissima . . .	Iridææ	0'8	40'0	60'0	
Bignonia (species) . . .	Bignoniacææ	7'5	40'0	60'0	
Anona Cherimolia . . .	Anonacææ	8'0	42'0	58'0	
Ravenala madagascariensis	Musacææ	6'0	42'5	57'5	
Chrysophyllum Cainito (Star Apple)	Sapotacææ	11'0	43'0	57'0	
Cardiospermum Halicababum	Sapindacææ	1'4	43'0	57'0	
Ipomœa tuba . . .	Convolvulacææ	5'0	44'0	56'0	Without hairs 41'7 and 58'3.
„ pes-capræ . . .	„	3'0	47'0	53'0	Without hairs 45'5 and 54'5.
Hibiscus Sabdarifa . . .	Malvacææ	0'4	47'0	53'0	
Thespesia populnea . . .	„	3'0	48'7	51'3	Without hairs 48 and 52.
Cardiospermum grandiflorum	Sapindacææ	2'5	50'4	49'6	

TABLE SHOWING THE RELATIVE WEIGHTS, ETC.—*continued.*

	Order.	Average weight of a single seed in grains.	Relative weights of coats and kernel, taking the entire seed as 100.		Remarks.
			Coats.	Kernel.	
Hibiscus esculentus . . .	Malvaceæ	0·7	51·0	49·0	
Colubrina asiatica . . .	Rhamnææ	0·6	51·7	48·3	
Achras Sapota (Sapodilla)	Sapotaceæ	9·5	53·5	46·5	
Luffa acutangula . . .	Cucurbitaceæ	1·0	55·0	45·0	
Hibiscus elatus . . .	Malvaceæ	0·6	56·0	44·0	Without hairs 53·4 and 46·6.
Lucuma mammosa . . .	Sapotaceæ	220·0	56·0	44·0	
Gossypium barbadense (Cotton)	Malvaceæ	1·4	57·0	43·0	Without hairs 40 and 60.
Chrysophyllum (species) . .	Sapotaceæ	6·0	59·0	41·0	
Calotropis procera . . .	Asclepiadeæ	0·2	61·0	39·0	Without hairs 50 and 50.
Sapindus Saponaria . . .	Sapindaceæ	13·0	64·0	36·0	
Gossypium hirsutum . . .	Malvaceæ	1·6	68·7	31·3	Without hairs 44·6 and 55·4.

If, then, we group together the results for all these seeds of 82 species, we get the following arrangement:—

GROUPING OF THE SEED-COAT RATIOS FOR THE RESTING SEEDS OF 82 SPECIES OF PLANTS, THE WEIGHT OF THE ENTIRE SEED BEING TAKEN AS 100.

	Below 20 per cent.	20 to 29 per cent.	30 to 39 per cent.	40 to 49 per cent.	50 to 59 per cent.	60 to 70 per cent.	Total.
Leguminous . . .	9	12	8	5	4	2	40
Non-leguminous . .	2	11	8	10	9	3	43
	11	23	16	15	13	5	83

Note.—The total here is not 82 but 83, as *Entada polystachya* with its two types of seeds has been entered twice.

Since just half of the species possess seed-coat ratios between 20 and 40 per cent. (both inclusive), it is probable that the average weight of the seed-coats would be about 30 per cent., rather below for leguminous seeds and rather above for

The general indications supplied by the grouping of the seed-coat ratios.

seeds of other orders. The ratio may have a generic value in some cases, as in *Erythrina*, *Guilandina*, *Phaseolus*, and *Hibiscus*; and in others it may vary considerably within the limits of a genus, as in *Anona* and *Ipomœa*, so that as possible disturbing influences the one may be set against the other. Whilst ranging widely in some orders, as in Leguminosæ, it may be comparatively uniform in others, as in Malvaceæ and Sapotaceæ. Size has little or nothing to do with the ratio, excluding very small seeds less than one-tenth of a grain, which are not here discussed. Looking down the lists, we find large and small seeds frequently associated on account of the similarity in their ratios. Thus the seeds of *Canna indica* and of *Mammea americana* have similar ratios, although about 220 seeds of the first will be required to make the weight of a single seed of the second. So also, if we compare the impermeable seeds of the two species of *Entada*, we find that their ratios are not far apart, notwithstanding that at least 80 seeds of *E. polystachya* are required to weigh down a single seed of *E. scandens*. Then, again, with the two sapotaceous plants, *Lucuma mammosa* and *Achras Sapota*, we notice that the proportional weights of the seed-coats are nearly the same, although the difference between the weights of a single seed are as 220 to 9.5. Size, of course, goes with weight in all these cases.

The constancy of the seed-coat ratio within the limits of a species.

In resting seeds the seed-coat ratio is sufficiently constant to form a character for the species, though, as we have seen above, it may vary considerably within the limits of a genus. Its constancy for a species is illustrated in the results for a few plants given below; but my data do not often lend themselves for such a comparison, since in determining this relation it was my usual practice to employ a number of seeds at the same time.

Guilandina bonducella, number of seeds tested 22, range of seed-coat ratios 53 to 64.

Guilandina bonduc, number of seeds tested 8, range of seed-coat ratios 44 to 52.

Entada scandens, number of seeds tested 5, range of seed-coat ratios 37.7 to 40.5.

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Anona muricata, number of seeds tested 12, range of seed-coat ratios 31 to 38.

Canna indica, number of seeds tested 10, range of seed-coat ratios 18 to 25.

With regard to the influence of variation in size as interpreted by weight on the seed-coat ratio in the same species, I am not able to give many data, as my mode of work rarely admitted such a comparison. The following results for 22 seeds of *Guilandina bonducella* indicate that there is no great difference. The range of the variation in weight was from 33 to 45 grains, the proportion of the seed-coats being slightly greater in seeds above than below 40 grains. Thus :—

The influence of size.

Above 40 grains in weight,	average seed-coat ratio	58·5.
Below	”	57·5.

However, carefully guarded observations on a large number of seeds of the same age and from the same plant are necessary for the elucidation of this point.

As respecting the influence of appendages on the proportional weight of the seed-coverings in resting seeds, we will deal first with hairs and then with wings. In the table subjoined there are given the data for eight kinds of hairy seeds belonging to three families, Asclepiadæ, Malvaceæ, and Convolvulaceæ, of which the two first are especially notable for the hairiness of the seeds in some genera. The results are arranged in order according to the proportional weight of the hairs, commencing with the seeds where the relative weight is smallest. It is evident that ordinary pubescence as illustrated in the case of *Ipomœa pes-capræ* adds but little to the weight of a seed. Nor does it make much difference if a pubescent or puberulous seed, as in the case of *Ipomœa tuba*, is bordered by longer hairs at the angles ; but when these hairs are abundant and woolly, as in the seed of *Ipomœa peltata*, the hairy covering may make up 9 per cent. of the total weight. The proportions for these convolvulaceous seeds are probably typical of a good many seeds of other families. The great development of hairs that we find in some Asclepiads and in some malvaceous genera is not common in the plant-world.

The influence of appendages on the seed-coat ratio.
(A) Hairs.

TABLE ILLUSTRATING THE EFFECT OF HAIRS ON THE PROPORTIONAL WEIGHT OF THE SEED-COATS IN RESTING SEEDS.

	Order.	Average weight of a seed in grains.	Character and extent of the covering of hairs.	Proportion of parts, taking the weight of the entire seed as 100.			Effect of the hairs on the relative weight of the coats.	
				Hairs.	Coats.	Kernel.	Percentage of the seed-weight.	
							With hairs.	Without hairs.
<i>Thespesia populnea</i>	Malvaceæ	3.0	Villous at the base and angles	1.6	47.8	50.6	49.4	48.6
<i>Ipomœa pes-capræ</i>	Convolvulaceæ	3.0	Pubescent over most of surface	2.8	44.4	52.8	47.2	45.7
<i>Ipomœa tuba</i>	do.	5.0	Puberulous, but villous at the angles	4.0	40.0	56.0	44.0	41.7
<i>Hibiscus elatus</i>	Malvaceæ	0.6	Villous down over all surface	6.0	50.0	44.0	56.0	53.3
<i>Ipomœa</i> * <i>peltata</i>	Convolvulaceæ	1.5	Pubescent, but with abundant woolly hair at the angles	9.0
<i>Calotropis procera</i>	Asclepiadææ	0.2	Terminal coma with hairs 1-1½ inches long and spread out like a pappus, the whole easily carried by winds	22.0	39.0	39.0	61.0	50.0
<i>Gossypium</i> † <i>barbadense</i>	Malvaceæ	1.4	Seed invested with abundant woolly hair (cotton)	28.5	28.5	43.0	57.0	40.0
<i>Gossypium</i> † <i>hirsutum</i> (?)	do.	1.6	do.	43.5	25.2	31.3	68.7	44.6

* The proportional weight of the hairs was alone ascertained.

† In *Gossypium (hirsutum?)* the cotton adheres firmly to the black seed, becoming dirty grey and matted next to the seed. Of the relative weight of the hairy covering (43.5 per cent.), white cotton forms 37.1 and the grey matted portion 6.4.

In *G. barbadense* the cotton easily separates from the black seed, there being no adherent covering of matted hairs.

We there have genera, like those of *Calotropis* and *Gossypium*, where the hairs may form a quarter or even nearly half the weight of the seed; and, as in one species of *Gossypium* named in the table, the hairs may be heavier than the kernel.

In illustration of the effect of large wing-like appendages (B) Wings. on the relative weight of the seed-coats, I will take the seeds of three familiar tropical plants, *Swietenia Mahogani*, *Moringa pterygosperma*, and *Tecoma stans*, the data for which are given in the following table.

TABLE ILLUSTRATING THE EFFECT OF WINGS ON THE PROPORTIONAL WEIGHT OF THE SEED-COATS IN RESTING SEEDS.

	Character of the wing or wings.	Weight in grains.					Seed-coat ratio, taking the entire seed as 100.	
		Seed and wing.			Coats and wing.			
		Entire seed.	Wing or wings.	Wing percentage.	Coats without wing or wings.	Coats with wing or wings.	Excluding wing or wings.	Including wing or wings.
Swietenia Mahogani	A terminal oblong wing as in Pinus	3.5	0.35	10%	0.55	0.90	17.5	25.7
Moringa pterygosperma	Seed round with three vertical wings	5.0	0.20	4,,	1.45	1.65	30.2	33.0
Tecoma stans	Thin, flat, oblong seed with marginal wing greatly prolonged at the two extremities	0.15	0.021	14,,
Pinus	Terminal oblong wing, but formed from the scale, and not truly comparable with the above	0.15	0.030	20%

Note.—In *Pinus* the seed is only partially enclosed in the base of the wing, and is exposed on one side.

The indications of the table.

Excluding the Pine seeds, which are not strictly comparable with ordinary winged seeds, we observe that in the three types of seeds here exemplified the weights of these appendages vary in amount between 4 and 14 per cent. of that of the entire resting seed. The wings are here greatly developed, so we may infer that in ordinary "margined" seeds, where the alar appendage is reduced to a narrow border, there is very little addition to the seed's weight. Now wings are functionally useless as we observe them in the resting seed, or we may put it in another way, and say that though actively functioning in the soft living seed within the living fruit, they have no biological significance in the dry seed of the withered fruit. Being dried up and dead they could only serve an accidental function in a resting seed which is practically in the same condition. A more natural comparison of these types of winged seeds would therefore be obtained by contrasting them in the living moist condition within the fruit when the wings are actively functioning organs. In the resting seed the wings are dead and dried up and could only serve accidental ends.

The wings of resting seeds only serve an accidental function.

Withered leaves and dried seeds are in the same category.

As far as the capacity for transportal by wind is concerned the withered leaf and the dry winged seed are in the same category. That the seed possesses the power of reproducing the plant is an accident as regards its fitness for wind-transportal. The puff of wind will carry along both the seeds that are germinable and the seeds that have lost this power; and we cannot distinguish between them as respects either appearance, weight, or size. Yet the dispersal of seeds by winds is real enough. The seeds of *Tecoma stans*, which are about an inch long, weigh just about the same as a piece of newspaper cut to the same size. The wind when strong could carry them great distances, and the like may be said for the seeds of the Pine. The much heavier winged seeds of *Moringa*, as experiment shows, are but little aided in this way by their appendages. In an ordinary breeze a Mahogany seed as it falls out of the dried dehiscing

fruit would be transported, as I find, only a few paces; but during a strong gust I have known it to be carried a hundred feet.

In this connection the remarks of Dr Goebel on the "parachute-apparatus" of fruits are well worth quoting, since they would apply in a sense also to seeds. In his *Organography of Plants* (English edition, ii. 570), he writes as follows:—" . . . Many arrangements which have hitherto been considered merely as a parachute-apparatus on the ripe fruit are in my view to be considered as a transpiration-apparatus for the ripening fruit, and these subsequently can be used for distribution, but are not necessarily for this. . . ." However, the function of the wings of the moist seed in the living fruit would probably be haustorial. In other words, these appendages would greatly increase the seed's capacity for absorbing water. In the instance of the moist white seeds of the Mahogany tree the increase of the area of the receiving or absorbing surface due to the wing is very large, the alar surface-area being more than double that of the seed, as is indicated in the following measurements:—

Goebel's view as concerning fruits.

The author's view as concerning seeds illustrated by Mahogany seeds.

Surface-area of the seed without the wing,	450 square millimetres.
„ wing alone,	1050 „
„ winged seed,	1500 „

In the case of the seed of the Pine it was long ago suggested by Goeppert, as quoted by Nobbe in his *Handbuch der Samenkunde* (p. 49), that the wing exercised the function of a funicle or umbilical cord.

With the Mahogany seed it is probable that in the closed living fruit the wing also serves for storage of water. As shown in the tabulated results of my observations given below, the wing and coverings of the soft white seed in the full-grown fruit hold nearly twice as much water as the kernel, losing about 89 per cent. of their weight in the drying and shrinking process, as against 49 per cent. lost by

the kernel. This excess of water in the wing is probably associated with the watery condition of the fleshy placental column in the living fruit. It will be seen from the discussion of the régime of the drying Mahogany capsule in Note 22 of the Appendix that the placental column loses about 70 per cent. of its weight as the fruit dehisces and dries, the loss of the capsular walls being about 60 per cent. Thus we find a regular gradation in the water-contents of a living Mahogany fruit, viz. about 60 per cent. in the fruit walls, about 70 per cent. in the placental column, and about 90 per cent. in the wings of the seeds. We are here referring to the indications supplied by the loss of weight during the natural drying process.

THE SHRINKING RÉGIME OF THE PRE-RESTING MAHOGANY SEED, THAT IS TO SAY, OF THE SOFT, UNCONTRACTED, MOIST SEED OF THE FULL-GROWN FRUIT.

(The data required for this purpose are the weights of the pre-resting and resting seeds and the proportion of parts in each condition.)

	Condition of the wing.		Absolute and relative weights, the first in grains.		Loss of weight during the natural drying of the fruit.
	Pre-resting.	Resting.	Pre-resting.	Resting.	
Wing and seed-coats	White, heavy, thick, soft, and flabby	Brown, light, thin, and crisp	8·4 (60)	0·95 (25)	88·7%.
Kernel	5·6 (40)	2·85 (75)	49%.
Entire seed	14·0 (100)	3·80 (100)	73%.

The proportional weights of parts in the three conditions of the seed supply data for determining the régime of the shrinking and swelling seed.

We now pass on to the determination of the proportional weight of the seed's coverings in the two other conditions of the seed, the pre-resting state, when the seed attains its full size in the moist ripe fruit, and the state immediately preceding germination, when the resting seed has absorbed much water, and the embryo is on the eve of continuing its growth that was brought to a standstill during the shrinking process. These data being obtained, we shall possess

the seed-coat ratios for the three conditions of the seed, the pre-resting, the resting, and the swollen state preparatory for germination; and in contrasting them we shall be constructing the régime of the shrinking and swelling seed, of the seed as it enters upon the resting period, and of the seed as it subsequently swells for germination.

It has already been established in Chapter II. that the seed takes up when swelling for germination the water that it lost in the shrinking process, the weight lost during the shrinking being approximately regained during the swelling. But it will be brought out in this chapter that in the attainment of this result the parts of the seed take different shares, the coverings of the swelling seed never regaining all the water originally lost, whilst the kernel takes up more water than it held in the pre-resting state. However, the loss of the one tends to counterbalance the gain of the other in the following fashion. The deficiency of the coats is generally larger than the excess of the kernel; but since the coats as a rule are only one-half or one-third of the weight of the kernel, the ultimate result is usually not much affected. Nevertheless, this is sufficient to show that the return of the resting seed when swelling for germination to its original weight as a pre-resting seed is not a simple process, and that such a result of experiments can only be regarded as approximate in value.

In the following table are given the data for constructing the régime of the shrinking and swelling seed in a considerable number of cases. Knowing the weight of the resting seed, the shrinking and swelling ratio, and the proportional weight of the coverings (the seed-coat ratio) in the three conditions of the seed, the determination of the shrinking and swelling régime for any seed named in the table can be readily effected, as shown in the example added.

The return of the swelling seed to its original weight in the pre-resting state is not a simple process.

The elements for determining the shrinking and swelling régime.

TABLE SHOWING THE PROPORTIONAL WEIGHT OF THE SEED'S COVERINGS (SEED-COAT RATIO) IN THE THREE CONDITIONS OF THE SEED, THE LARGE, MOIST, PRE-RESTING SEED OF THE RIPE FRUIT, THE RESTING SEED, AND THE SEED SWOLLEN FOR GERMINATION.

(From the data given in this table the régime of the shrinking and swelling seed can be readily constructed, as explained in the example given. P. = permeable; I. = impermeable; V. = variable.)

	Order.	Average weight of a resting seed in grains.	The shrinking and swelling ratio, the weight of the resting seed being taken as 1.	The seed-coat ratio in the three conditions of the seed, the weight of the entire seed being taken as 100.			Character of seed.
				Pre-resting.	Resting.	Swollen for germination.	
<i>Abrus precatorius</i> . . .	Leguminosæ	1'5	2'25	...	30'0	28'0	V.
<i>Acacia Farnesiana</i> . . .	"	2'0	2'00	59'6	60'8	53'6	V.
<i>Adenanthera pavonina</i> . . .	"	4'7	2'42	...	53'0	50'1	I.
<i>Æsculus Hippocastanum</i>	Hippocastaneæ	130'0	2'20	35'0	27'0	...	P.
<i>Albizia Lebbek</i> . . .	Leguminosæ	2'2	2'27	...	50'0	32'5	V.
<i>Anona muricata</i> . . .	Anonaceæ	6'0	1'43	...	33'0	26'4	P.
<i>Arum maculatum</i> . . .	Araceæ	0'7	1'63	33'0	12'5	...	P.
<i>Bauhinia (species)</i> . . .	Leguminosæ	4'0	2'10	23'0	23'5	24'0	V.
<i>Bignonia (near æquinoctialis)</i>	Bignoniaceæ	5'0	2'30	38'0	28'0	...	P.
<i>Cesalpinia Sappan</i> . . .	Leguminosæ	10'0	2'20	32'5	27'5	26'4	V.
" <i>sepiaria</i> . . .	"	4'0	2'22	61'0	61'4	53'0	V.
<i>Cajanus indicus</i> . . .	"	3'0	2'10	28'0	13'0	16'0	P.
<i>Calliandra Saman</i> . . .	"	4'0	2'50	...	40'6	35'0	V.
<i>Canavalia ensiformis</i> . . .	"	25'0	2'17	...	16'0	21'5	P.
" <i>gladiata</i> . . .	"	45'0	2'11	...	19'8	23'3	V.
" <i>obtusifolia</i> . . .	"	12'0	2'50	45'0	27'0	34'6	V.
" (species of) . . .	"	18'0	1'94	...	21'0	22'3	V.
<i>Cassia fistula</i> . . .	"	4'0	2'50	26'3	15'0	17'2	V.
" <i>marginata</i> . . .	"	10'0	2'10	...	29'0	28'3	V.
" <i>grandis</i> . . .	"	9'0	2'11	...	25'0	26'0	V.
<i>Dioclea reflexa</i> —							
(A) Impermeable . . .	"	90'0	2'07	48'5	40'0	33'5	I.
(B) Permeable seed . . .	"	100'0	1'86	48'5	38'0	36'1	P.
<i>Entada polystachya</i> —							
(A) Impermeable . . .	"	5'0	2'50	27'2	32'8	25'1	I.
(B) Permeable seed . . .	"	6'6	2'25	27'2	28'5	24'0	P.
<i>Entada scandens</i> . . .	"	400'0	2'50	46'0	39'0	31'0	I.
<i>Enterolobium cyclocarpum</i>	"	17'0	2'30	...	51'7	46'0	V.
<i>Erythrina corallodendron</i>	"	3'2	2'16	...	33'1	30'4	V.
" <i>indica</i> . . .	"	12'6	2'49	...	30'6	28'1	V.
" <i>velutina</i> . . .	"	7'5	2'40	...	31'4	34'0	V.
<i>Faba vulgaris</i> (Broad Bean)	"	30'0	2'00	33'0	15'0	13'0	P.
<i>Guilandina bonduc</i> . . .	"	50'0	2'47	...	48'7	48'2	I.

TABLE SHOWING THE PROPORTIONAL WEIGHT, ETC.—*continued*.

	Order.	Average weight of a resting seed in grains.	The shrinking and swelling ratio, the weight of the resting seed being taken as 1.	The seed-coat ratio in the three conditions of the seed, the weight of the entire seed being taken as 100.			Character of seed.
				Pre-resting.	Resting.	Swollen for germination.	
Guilandina bonducella . . .	Leguminosæ	40·0	3·00	60·8	57·8	53·0	I.
„ glabra (?) . . .	„	60·0	2·52	...	49·0	44·4	I.
Hura crepitans . . .	Euphorbiacæ	20·0	2·10	57·0	30·0	44·0	P.
Ipomœa pes-capræ . . .	Convolvulacæ	3·0	2·50	55·0	47·0	40·0	I.
„ tuba . . .	„	5·0	2·63	46·0	44·0	32·0	I.
„ tuberosa . . .	„	25·0	2·50	...	21·0	19·0	V.
Iris foetidissima . . .	Iridææ	0·8	3·10	65·0	40·0	60·0	P.
„ Pseudacorus . . .	„	0·7	2·00	40·0	20·0	25·0	P.
Leucæna glauca . . .	Leguminosæ	0·8	2·60	45·2	46·2	38·5	I.
Luffa acutangula . . .	Cucurbitacæ	1·0	1·77	...	55·0	62·0	P.
Mucuna urens . . .	Leguminosæ	90·0	2·00	47·5	26·3	20·4	I.
Phaseolus multiflorus . . .	„	18·0	2·00	25·0	12·5	9·0	P.
Pisum sativum—							
(A) Smooth seeds . . .	„	6·0	1·90	25·0	8·5	9·0	P.
(B) Wrinkled seeds * . . .	„	7·0	2·40	30·0	10·0	9·4	P.
Poinciana regia . . .	„	10·0	2·30	45·5	49·5	41·0	V.
Ricinus communis . . .	Euphorbiacæ	3·0	1·33	...	28·0	23·0	P.
Swietenia Mahogani . . .	Meliacæ	3·7	3·70	60·0	25·0	...	P.
Tamarindus indica . . .	Leguminosæ	20·0	2·15	...	28·0	33·0	V.
Thespesia populnea . . .	Malvacæ	3·0	1·82	37·0	48·7	45·0	V.

* The collection of water under the coats seriously affects the régime of the wrinkled seed.

I will take the seed of *Entada scandens* to illustrate the employment of the data in the above table for determining the shrinking and swelling régime of a seed. All that is required are the shrinking and swelling ratios of the entire seed and the proportional weight of parts in the three conditions of the seed, the pre-resting, the resting, and the swollen state. The ratios are given in two ways, one where the weight of the resting seed is taken as 1, the other where that of the pre-resting seed is taken as 100, the first method being required for purposes of comparison when, as often happens, the data for the swelling process are alone available.

Illustration of the use of the data in the table.

ENTADA SCANDENS.

(Weight of resting seed 400 grains. Shrinking and swelling ratio 2·5, taking the weight of the entire seed as 1. Pr. = pre-resting seed; R. = resting seed; and Sw. = the seed swollen for germination.)

	Proportional weights stated as a percentage of the weight of the entire seed.			Weights in grains.			Shrinking and swelling ratios.					
	Pr.	R.	Sw.	Pr.	R.	Sw.	Weight of resting seed as 1.			Weight of pre-resting seed as 100.		
Coats . . .	46	39	31	460	156	310	2·95	1	1·99	100	34	67
Kernel . . .	54	61	69	540	244	690	2·21	1	2·83	100	45	128
Entire . . .	100	100	100	1,000	400	1,000	2·50	1	2·50	100	40	100

We will commence with the comparison of the régimes of two types of leguminous seeds, that of *Guilandina bonducella* and that of *Faba vulgaris* (Broad Bean), the first with impermeable, the last with permeable coverings. Employing the data given in the table, we get the following results:—

COMPARISON OF THE SHRINKING AND SWELLING RÉGIMES OF AN IMPERMEABLE AND A PERMEABLE LEGUMINOUS SEED, TAKING THE WEIGHT OF THE PRE-RESTING SEED AS 100.

		Pre-resting seed.	Resting seed.	Seed swollen for germination.
<i>Guilandina bonducella</i> (im- permeable)	Coats	100	32	87
	Kernel	100	36	120
	Entire	100	33	100
<i>Faba vulgaris</i> (permeable)	Coats	100	23	39
	Kernel	100	63	130
	Entire	100	50	100

Note that the pre-resting seed is the soft seed of the full-grown moist fruit.

Illustrations
of the régime
of the shrink-
ing and
swelling
seed.

We here see that whilst in both seeds the coats of the swelling seed fail to regain the water lost in the shrinking process and the kernel ultimately holds more water than it held in the pre-resting state, there is an important dis-

inction in their behaviour, the deficiency in the gain of the coats of the permeable seed being much the largest. But the difference is only one of degree, since both types of seeds illustrate the same general principle. There is much that is extremely suggestive in these figures; and if we compare them with those tabulated below which represent the average results for impermeable, variable, and permeable leguminous seeds, we perceive that the régime illustrated by the two type-seeds just dealt with applies generally to seeds of the family. It is as true of the individual species as it is of the aggregate. Of the seventeen species of leguminous seeds, for which complete data are given in the preceding general table, all but one, that of *Bauhinia*, conform to the principle that during the swelling of the resting seed for germination the coats fail to regain all the water lost in the shrinking process, whilst the kernel not only regains all the lost water but absorbs

TABLE GIVING THE AVERAGE SHRINKING AND SWELLING RATIOS FOR THE COATS, KERNEL, AND ENTIRE SEED OF IMPERMEABLE, VARIABLE, AND PERMEABLE LEGUMINOUS SEEDS.

The impermeable seeds used are those of *Dioclea reflexa*, *Entada scandens*, *Entada polystachya* (impermeable type), *Guilandina bonducella*, *Leucaena glauca*. The variable seeds are those of *Acacia Farnesiana*, *Bauhinia*, *Casalpinia sepiaria*, *Casalpinia Sappan*, *Canavalia obtusifolia*, *Cassia fistula*, *Poinciana regia*. The permeable belong to *Cajanus indicus*, *Pisum sativum*, *Faba vulgaris*, *Phaseolus multiflorus*.

Shrinking and swelling ratios for the pre-resting (Pr.), resting (R.), and swollen (Sw.) seed stated in two ways, the pre-resting seed being taken as 100 in the first way, and the resting seed as 1 in the second way.

	Number of species.	Coats.			Kernel.			Entire Seed.		
		Pr.	R.	Sw.	Pr.	R.	Sw.	Pr.	R.	Sw.
Impermeable . . .	5	100 (2'6	39 1	80 2'1	100 (2'4	42 1	118 2'8	100 (2'5	40 1	100 2'5)
Variable	7	100 (2'5	40 1	85 2'1	100 (2'1	47 1	112 2'4)	100 (2'3	44 1	100 2'3)
Permeable	4	100 (4'5	22 1	42 1'9)	100 (1'7	60 1	122 2'0)	100 (2'0	50 1	100 2'0)

considerably more. It is likely that further investigation may bring the behaviour of the *Bauhinia* seeds into line with that of other seeds. It would appear from the table that as a general rule, although the coats of the permeable seed shrink more than those of the impermeable seed, both double their weight in the swelling process. On the other hand, the kernels of permeable seeds, though shrinking less, only double their weight when swelling for germination, whilst the kernels of impermeable seeds shrink more and increase their weight threefold in the swelling process.

It becomes at once apparent from all the tabulated results that the resting state leaves its impress on the germinating seed, especially with reference to the behaviour of the coats. But the impress is also evident in the contrasts in appearance presented by the coverings in the pre-resting seed and in the seed swollen for germination. In the pre-resting state the coats are usually thick, moist, fleshy, easily marked by the finger-nail or cut with a knife, and elastic or yielding. In the swollen seed on the eve of germination the seed's coverings are thinner, relatively dry, tough, and unyielding. With a seed like that of *Entada scandens* these characteristics are well displayed, and we may take it as a good example of the mechanism of germination in seeds of this type. In the pre-resting or so-called unripe state we have a white, moist, flabby seed with coats 3 to 4 millimetres thick. In the swollen, germinating stage we have a dark brown seed with tougher and drier coverings between 2 and 2½ millimetres thick.

But a more important indication of the impress of the resting state appears when we compare the changes in weight with the changes in size. The seed on the point of germination is usually rather smaller than the so-called unripe or pre-resting seed. This is brought out in the measurements for four leguminous seeds in their several stages below given.

The impress of the resting state on the seed swelling for germination.

MEASUREMENTS IN MILLIMETRES OF LEGUMINOUS SEEDS IN
THE THREE CONDITIONS

	Pre-resting	Resting.	Swollen for germination.
<i>Entada scandens</i> . . .	66·5	47·5	64
<i>Guilandina bonducella</i> . . .	25·0	18·0	24
<i>Cesalpinia sepiaria</i> . . .	14·0	10·0	13
<i>Canavalia obtusifolia</i> . . .	21·0	15·5	20

Taking the case of the disc-shaped seed of *Entada scandens*, we find that the embryo or kernel of the seed swollen for germination is no longer enclosed, as in the pre-resting seed, in soft, yielding coverings, in which it lies easily, filling the space without tension. It is now invested by tough, unyielding, drier coverings; and, whilst the kernel has increased its weight by about 28 per cent. through water-absorption, the coverings are drawn tighter round it than in the pre-resting state. As shown in the régime before illustrated, the kernel that weighed 540 grains in the pre-resting state now weighs 690 grains, and the seed, as we have just seen, is rather smaller. The strain produced by the swelling embryo within its tightened coats must be great, and the coverings yield opposite the hilum, the process being purely physical and not necessarily followed by germination, itself a purely biological process in which the active growth of the hypocotyl is involved. The tension within the seed is well illustrated at times when the rupture of the coats is from some cause delayed and one or both of the thick cotyledons within break right across. The selection of the hilum or scar for the seat of the first rupture of the coats is on physical grounds not easy to explain, since the coverings are here thicker than elsewhere; but this is a point that is discussed in Note 23 of the Appendix.

The conditions of strain within the swelling seed.

The great tension existing within the seed on the eve of germination is also well exemplified in the régimes of the three other leguminous seeds, for which measurements have above been given, viz. *Cesalpinia sepiaria*, *Canavalia obtusifolia*,

and *Guilandina bonducella*. The swollen seed ready for germination is rather smaller than the pre-resting seed of the ripe moist pod. Its coats are tougher and drier, holding in one instance 23, and in two instances 13 per cent. less water than in the pre-resting condition. Yet within these tightened relatively unyielding envelopes lies in each case a kernel that is about 20 per cent. heavier through the absorption of water, and correspondingly larger than in the pre-resting state, a condition of strain necessarily resulting.

As a rule the conditions of strain within the swelling seed are at first rather more pronounced in permeable than in impermeable leguminous seeds. This is well shown in the average results for these two types of seeds already given on a previous page. But in the case of the permeable seed the relatively thin coverings soon give way, whilst with the impermeable seed the tougher and thicker coats resist the strain of the swelling kernel for many days, and the strain, though less at first, becomes very great when the swelling of the kernel is far advanced.

It occasionally happens with impermeable seeds that the conditions of strain are intensified from the beginning, and, as in the case of the seed of *Mucuna urens*, a somewhat abnormal régime is displayed. Whilst its coats behave like those of a permeable seed, its kernel plays the rôle of a seed of its type, but in an exaggerated fashion.

The régime of <i>Mucuna urens</i>	}	Coats : pre-resting 100, resting 28, swollen for germination 43.
		Kernel : pre-resting 100, resting 70, swollen for germination 152.
		Entire : pre-resting 100, resting 50, swollen for germination 100.

Whilst studying this seed in the West Indies, I noticed that the complete soaking of the coats was not requisite for germination, the radicle often protruding through coverings partly dry. This occurs occasionally with seeds like those of *Dioclea reflexa* and *Entada scandens*. In some other leguminous

seeds, usually of the variable type, the tension produced during the swelling of the resting seed is but slight, as with those of *Entada polystachya* and *Poinciana regia*. In other variable seeds again, as with those of *Cassia fistula*, the strain may be great; whilst in rare instances, as with the seeds of *Bauhinia*, there may be none at all. The case of *Cassia fistula* is interesting, as it indicates that albuminous seeds may behave like exalbuminous seeds in this respect.

<i>Cassia fistula</i>	{	Coats: pre-resting 100, resting 23, swollen for germination 65.
		Kernel: pre-resting 100, resting 46, swollen for germination 112.
		Entire: pre-resting 100, resting 40, swollen for germination 100.
<i>Bauhinia</i>	{	Coats: pre-resting 100, resting 49, swollen for germination 105.
		Kernel: pre-resting 100, resting 47, swollen for germination 99.
		Entire: pre-resting 100, resting 48, swollen for germination 100.

This is all that can be said here for the combined shrinking and swelling régime of leguminous seeds, and the data in the general table before given must be allowed to tell their own story in individual cases. The reader can work out for himself the régime of any particular seed. Should he wish to contrast the impermeable and permeable types in the same species, he will find in the cases of *Dioclea* and *Entada* that the permeable seed in its behaviour, strictly speaking, comes between the two.

But the seeds of other orders may behave like leguminous seeds when shrinking before entering upon the rest-period and when swelling previous to germination. What we may term the convolvulaceous régime, as exemplified in the behaviour of the two species of *Ipomœa* illustrated below, does not seem to differ materially from the leguminous régime, although the seeds themselves differ much as respects the albumen, embryo, and other characters. In its conspicuous

The convolvulaceous régime.

features it comes near the average régime of a leguminous impermeable seed as previously given.

THE CONVULVULACEOUS RÉGIME.

	Pre-resting seed.	Resting seed.	Seed swollen for germination.
Ipomœa pes-capræ—			
Coats	100	34	73
Kernel	100	47	133
Entire	100	40	100
Ipomœa tuba—			
Coats	100	37	70
Kernel	100	40	126
Entire	100	38	100

The difficulty of the seeds of *Hura crepitans*.

There are seeds where the shrinking and swelling régime presents special difficulties, as in the case of those of *Hura crepitans*, the well-known Sand-box tree, belonging to the Euphorbiacæ. In this instance when the pre-resting seed is fully matured, the seed-coverings have already lost considerably in weight, whilst the kernel has just attained its maximum development. We encounter here the same difficulty that we meet with when following the development of certain fruits, such as those of *Quercus Robur*, *Barringtonia speciosa*, and *Cocos nucifera* (Coco-nut), in Chapter XIV. The behaviour of the seed of *Hura crepitans* is fully dealt with in Note 24 of the Appendix and requires no further mention here, except the remark that, like other seeds with oily kernels, such as those of *Ricinus* and *Anona*, there is much less water lost in the shrinking process and regained in the swelling process than is required by a typical leguminous seed. Evidently oily seeds have a régime of their own.

Additional data relating to the swelling ratios of the parts of seeds.

We will now utilise the results obtained for the seeds of a considerable number of plants where the swelling phenomena were alone observed, and we shall thus obtain a large accession to our data relating to the swelling ratio of seeds preparing for germination with especial reference to the respective parts

taken by the coats and the kernel in the process. We have, in fact, the "swelling" data for the coats and the kernel in forty-four species, of which all but ten are leguminous, the residue belonging to a variety of orders, such as Convolvulaceæ, Euphorbiaceæ, Iridaceæ, etc.

Many influences come into play in determining the swelling ratios of the coats and of the kernel of the resting seed preparing for germination, influences that are more numerous, however, with the seed's coverings than with its kernel. In the case of the kernel there is the relative dryness of that of the impermeable seed as compared with that of the permeable seed, and there is the peculiar régime of the oily seed, as in *Ricinus*, where the oil seems to take a vicarious part, much less water than usual being required for germination. In the case of the coats there is also the relative dryness of the seed-coverings in typical impermeable seeds; but this influence is at times masked in the swelling process of seeds like those of *Mucuna* and *Dioclea*, where the kernel may begin to germinate whilst its coats are still partly dry. Then we have the diverse influence of the various textures of the coverings themselves, influences that are far more diverse than any that could be offered by the kernel, however much it may vary in consistence, as indicated by such terms as farinaceous, fleshy, horny, oily, etc.

If we begin by comparing the swelling ratios of coats and kernel for all the plants named in the following table, we find that in just about two-thirds the kernel has the largest ratio. But if we except the fact that all the four species of *Canavalia* and both the species of *Iris* are included in the smaller group where the coats have the largest ratio, there is little that is determinate in such an arrangement, species of the same genera being sometimes separated, as in the cases of *Cassia* and *Erythrina*, whilst permeable and variable seeds are more or less divided between the two groups, the larger group being made up of the three types of seeds, impermeable, permeable, and variable. It is not therefore from such an arrangement that we should expect to be able to frame any definite infer-

The disturbing influences.

The swelling ratio of the kernel is usually larger than that of the coats.

ences in this direction, and accordingly I have not burdened my pages with it, though the reader can construct it for himself from the table subjoined, where all the data are grouped in another fashion.

In order to wrest their story from all these data, I will make use of another arrangement as given below. Here the seeds are arranged in two columns. In the first column the seeds are placed in order according to the amount of the swelling ratio of the coats, those with the greatest ratio being placed first. In the second they are placed according to the value of the swelling ratio of the kernel, those with the largest ratio coming first. There is nothing definite to be made out of the arrangement of the seeds in the first column, since permeable, variable, and impermeable seeds, whether or not we restrict ourselves to the Leguminosæ, are fairly well distributed. On the other hand, if we turn to the second column, which contains the data for eleven impermeable, twenty-one variable, and thirteen permeable seeds, we find that all but one of the impermeable seeds occur in the upper half of the column, where the swelling ratio for the kernel is the largest, and all but one of the permeable seeds in the lower half, where the ratio is smallest, the variable seeds being about equally distributed.

We perceive the same contrast between the indications of the two columns when we compare the places occupied by seeds when both permeable and impermeable seeds occur in the same species. Thus with *Entada polystachya* and *Dioclea reflexa*, the permeable and impermeable seeds come close together in the column where the seeds are arranged according to the amount of the swelling ratio of the coats, but lie far apart when the arrangement chosen, as in the second column, is that of the amount of the swelling ratio of the kernel.

Evidently, therefore, although the question of permeability or of impermeability is largely shaping itself in its influence on the swelling ratio of seeds, it is an influence that chiefly affects the kernel. The coats also respond, though in a less degree, to this influence, but their behaviour is often masked by

The most instructive arrangement of the "swelling" data.

The determining influence of permeability.

coverings is well shown, not only in the general lack of correspondence of seeds in this respect, but in extreme cases like that of *Hura crepitans*, where the seeds, on account of the large swelling ratio of the coats, stand nearly at the head of the first column, and on account of the small swelling ratio of the kernel are placed nearly at the bottom in the second column.

The run of the data in the above table would therefore lead us to expect that whilst the coats of permeable, variable, and impermeable seeds would on the average possess swelling ratios not far apart from each other, the kernels of these three seed-types would differ markedly in this feature, the impermeable seed displaying the largest, the permeable seed the smallest, and the variable seed a ratio intermediate in amount. This expectation is fulfilled in the following tabulated results of the table, whether for all the seeds or for the leguminous seeds only, though it is on the indications of the leguminous seed that we must mainly rely, since the disturbing influences of different ordinal characters are then eliminated.

TABULATED SUMMARY OF THE PRECEDING TABLE SHOWING THE AVERAGE SWELLING RATIOS OF THE COATS AND KERNELS OF PERMEABLE, VARIABLE, AND IMPERMEABLE SEEDS WHEN PREPARING FOR GERMINATION.

	Character of the seeds.	Number of species tested.	Swelling ratios, taking the resting seed as 1.	
			Coats.	Kernel.
Leguminous only	Permeable	7	2'06	2'07
	Variable	19	2'20	2'35
	Impermeable	9	2'12	2'69
Leguminous (35 species) and seeds of other orders (10 species)	Permeable	13	2'22	1'89
	Variable	21	2'18	2'34
	Impermeable	11	2'10	2'74

The interesting indications afforded in the tabulated summary just given become more important when we connect them with the water-contents of the resting seed as signified

The indications of the table.

Their connection with the water-percentage.

by the loss of weight of the materials when exposed in the oven to a temperature of about 100° C. We should expect to find with all three types of seeds, where the swelling ratios for the coats are not far apart, that the water-percentages for the seed-coverings would not differ much in amount. We would also expect in the case of the kernels that where the swelling ratio is greatest, as with impermeable seeds, the water-percentage would be lowest; that where the ratio is smallest, as with permeable seeds, the water-percentage would be largest; and that where it is intermediate in value, as with variable seeds, the water-percentage would be also intermediate in amount. These indeed are the actual results that are represented in the tabulated summary to be now given as respecting seeds for which all the requisite data have been obtained. In order to avoid disturbing influences, the summary is restricted entirely to leguminous seeds, not to all leguminous seeds, but to exalbuminous seeds of that order.

TABULATED SUMMARY OF RESULTS SHOWING THE AVERAGE RELATION BETWEEN THE SWELLING RATIOS OF THE COATS AND KERNELS OF PERMEABLE, VARIABLE, AND IMPERMEABLE SEEDS AND THE WATER-PERCENTAGES.

(The swelling ratios are given in the general table in this chapter, and the water-percentages in the table illustrating the absorptive capacities of seeds in Chapter VI.)

Character.	Number.	Coats.		Kernel.	
		Swelling ratio.	Water-percentage.	Swelling ratio.	Water-percentage.
Permeable . . .	4	2'04	13'4	2'04	14'9
Variable . . .	4	2'12	12'3	2'34	11'4
Impermeable . .	6	2'13	11'0	2'61	8'3

The Permeable seeds are *Canavalia ensiformis*, *Pisum sativum*, *Faba vulgaris*, and *Phaseolus multiflorus*.

The Variable seeds are *Abrus precatorius*, *Casalpinia Sappan*, *Erythrina corallodendron*, and *E. indica*.

The Impermeable seeds are *Adenanthera pavonina*, *Dioclea reflexa*, *Entada scandens*, *Guilandina bonducella*, *G. bonduc*, and *Mucuna urens*.

We see here that whilst with the coats the differences in the swelling ratios and water-percentages of all three types of seeds are small, the differences that do exist are in accord with the principles laid down in Chapters IV. and VI. Thus, the coats of permeable seeds have a smaller swelling ratio and a larger water-percentage than the coats of seeds that are more or less impermeable. But the difference is small, and it is to the kernels, where the contrast between the three types of seeds is pronounced, that we chiefly look for evidence in this direction. The determination of the amount of the swelling ratio by the quantity of water held by the seed is fully established by the behaviour of the kernels, the kernel of an impermeable seed holding on the average not much more than half the water held by the kernel of an average permeable seed, and possessing a much larger swelling ratio. In the first we have a water-percentage of 8.3, associated with a swelling ratio of 2.61. In the second the water-percentage amounts to 14.9, and the swelling ratio to 2.04.

The effect of oil on the absorption of water.

The effect of oil on the absorption of water by the kernels of the seeds preparing for germination is another point to be referred to. The effect is shown in the small swelling ratio of such kernels, a fact indicating a relatively small absorption of water. Such seeds have a régime of their own when swelling for germination. Ordinary permeable resting seeds, like those of *Canavalia*, *Faba*, *Pisum*, and *Phaseolus*, dealt with in the tabulated summary given above, display an average swelling ratio for the kernel of 2.04, taking the weight of the kernel of the resting seed as 1. But permeable seeds with more or less oily kernels exhibit a much smaller swelling ratio. Thus, the kernels of the seeds of *Hura crepitans*, *Anona muricata*, and *Luffa acutangula* possess swelling ratios of 1.68, 1.57, and 1.49 respectively; whilst with *Ricinus communis* the swelling ratio for the entire seed is only 1.33, as against 2.04 for typical entire permeable seeds belonging to the four leguminous genera above named. It will thus be seen that whilst an ordinary permeable leguminous seed doubles its weight by

absorbing water when preparing for germination, a *Ricinus* seed adds only one-third to its weight. It is probable that the small swelling ratios of many of the seeds mentioned in the table of the results obtained by Hoffmann and Nobbe in Chapter II. (*Brassica*, *Raphanus*, *Cannabis*, *Camelina*, *Helianthus*, and *Pinus*) result from the oil in the kernels.

That oil takes the place of water in the kernel is shown when we compare the water-percentages of the kernels of permeable resting seeds. In *Hura crepitans* the water-contents of the kernel amount to 8.7 per cent.; in *Ricinus* they form 6 per cent.; whilst with the kernels of the four leguminous plants dealt with in the tabulated summary, the water-percentage ranges between 14 and 16. In the cases of certain Palm seeds oil plays a prominent part in determining the régime. The water-percentage is low when the spontaneous drying is complete. Thus in *Elais guineensis* it is 9 per cent., and in the Coco-nut about 7 per cent., this small percentage of water being connected with the large amount of oil present.

It will be appropriate here to make a few remarks on the decrease in the relative weight of the seed-coats as the seed matures in the ripening fruit. Just as the growth of the pericarp is always in advance of the seed-growth, so the growth of the seed's coverings is always in advance of that of the kernel or seed proper. Thus with *Guilandina bonducella* the weight of the coats of the full-sized soft seed in the mature moist pod is about 61 per cent. of the total weight of the seed. A little earlier in the history of the seed's growth it is about 66 per cent., and earlier still, when the seed is not much over half size and the embryo incompletely formed, it is about 70 per cent. The behaviour of the seeds of the Horse-chestnut (*Æsculus Hippocastanum*) as they ripen in the capsule well illustrate this progressive change. When the seed is only one-fourth grown the coats form 46 per cent. of the weight of the entire seed, when half size 42 per cent., and when full size 35 per cent. In this connection again let us take the data afforded by Peas (*Pisum sativum*) from the same set of plants.

The decrease in the relative weight of the seed-coats as the seed ripens.

In young seeds weighing about 8 grains (when the coats make up one-fourth of the seed's diameter) the weight of the coverings is about 37 per cent. of that of the entire seed. In the mature soft seeds, weighing 12 grains, the proportional weight of the coats is reduced to 27 per cent. In all cases, one may add, there is a further decrease in the relative weight of the coverings in the resting seed. Taking the approximate data for the different stages, we obtain the following results:—

THE RELATIVE WEIGHT OF THE COATS OF THE PRE-RESTING SEED IN DIFFERENT STAGES AND OF THE RESTING SEED, STATED AS A PERCENTAGE OF THE WEIGHT OF THE ENTIRE SEED.

	Pre-resting seed.				Resting seed.
	$\frac{1}{4}$ size.	$\frac{1}{2}$ size.	$\frac{3}{4}$ size.	Full size.	
<i>Guilandina bonducella</i>	70	66	61	58
<i>Æsculus Hippocastanum</i>	46	42	...	35	27
<i>Pisum sativum</i>	37	27	9

The rôle of the embryo in the shrinking and swelling stages of albuminous seeds.

Not the least interesting feature of this discussion relating to the proportion of parts in the three conditions of the seed is that concerning the rôle taken by the embryo in albuminous seeds. I deal here only with types of those dicotyledonous seeds where the embryo has attained the maximum size permitted by the limits of the seed. The general subject of the size and other features of embryos is handled in Chapter XVIII. Here we deal only with those embryos, with large, flat, more or less foliaceous cotyledons, that occupy the length and breadth of the seed and lie usually between two slab-like masses of albumen. A few of the leguminous seeds used in this inquiry, viz. those of species of *Bauhinia*, *Cassia*, and *Poinciana*, have these characters; and for most of them I possess the requisite data for the embryo's weight-relation in the pre-resting, resting, and swollen conditions of the seed. In addition I have also materials for two euphorbiaceous plants possessing albuminous seeds with similar embryos, viz. *Ricinus*

communis and *Hura crepitans*. The seeds of the two plants just named are permeable, whilst those of the leguminous seeds are variable in this respect. If the kernels of the leguminous seeds experimented upon were, as is probable in some cases, ultra-dry, it would only be to a small degree (2 or 3 per cent.), and not sufficient to materially affect their behaviour. For practical purposes we may assume that the kernels of all these seeds attain a more or less stable weight in the resting state.

A singular feature of these dicotyledonous embryos, and we may say the same of other similar embryos, such as those of the sapotaceous genera, *Achras* and *Chrysophyllum*, is that they do not display in the resting seed the dried-up, shrivelled appearance so characteristic of monocotyledonous embryos in the naturally dried seeds of Palms, Cannas, etc. This is probably due in part to the difference in form and situation of the embryos in these two types of seeds. In the dicotyledonous seed the embryo lies flat between two slabs of albumen and contracts with the kernel, leaving no unfilled space. With ordinary seeds of Palms the embryo lies in an elongated cavity, which it completely fills in the moist seed, but in the dry seed it has shrunk away from the walls of the cavity. At all events the water lost by the embryos of the moist seeds of both types when drying spontaneously does not differ much in amount, those of Palm seeds (*Cocos*, *Areca*, etc.) losing about 66 per cent. of their weight, and those of the leguminous embryos (*Bauhinia*, *Cassia*, *Poinciana*) 50 to 62 per cent.

We have already dealt with the behaviour of the kernel in the shrinking and swelling of seeds. Here, then, we are going to differentiate in the case of albuminous seeds between the two components of the kernel, the embryo and the albumen. Allowing for the crudeness of the method, the indications of the table below are clear enough. The embryo and the albumen evidently go fairly well together in the three conditions of the seed, and consequently in the shrinking and swelling stages, each of them taking its proportionate share in the processes. The deviations in opposite directions suffi-

Differentiat-
ing between
the behaviour
of the
embryos and
the albumen.

ciently establish this point, and it would be unwise to place much stress on individual differences. Thus, to take the swelling ratios, although in *Cassia* and *Ricinus* this ratio for the embryo is rather greater than for the albumen, in *Poinciana* it is considerably less, and in *Bauhinia* it is about the same.

TABLE SHOWING THE BEHAVIOUR OF THE EMBRYO IN THE THREE CONDITIONS OF ALBUMINOUS SEEDS, THE PRE-RESTING, THE RESTING, AND THE SWOLLEN STATE PRECEDING GERMINATION. (All are leguminous except the last.)

	The relative weight of the embryo, taking the kernel as 100.			The shrinking and swelling ratios of the embryo and albumen, the first for the embryo, the second in parentheses for the albumen.					
	Pre-resting.	Resting.	Swollen.	The pre-resting state as 100.			The resting state as 1.		
				Pr.	R.	Sw.	Pr.	R.	Sw.
<i>Poinciana regia</i> . . .	47·9	53·5	45·8	100	45	103	2·22	1	2·30
<i>Bauhinia</i> (species) . . .	42·8	45·8	46·1	(100	36	113)	(2·78	1	3·13)
<i>Cassia fistula</i> . . .	27·1	22·4	24·2	100	50·5	106	1·98	1	2·10
„ <i>marginata</i>	18·3	19·1	(100	44·9	93)	(2·23	1	2·07)
„ <i>grandis</i>	14·7	16·2	100	38	100	2·63	1	2·63
<i>Ricinus communis</i>	5·6	6·5	(100	49	117)	(2·03	1	2·38)
				...			1		2·23
							(1		2·10)
							1		2·30
							(1		2·05)
							1		1·67
							(1		1·41)

Method of constructing the shrinking and swelling régime of an albuminous seed.

In order to obtain the data summarised in the foregoing tabular statement a considerable amount of work was done. For the study of the part played by the embryo in the shrinking and swelling régime of an albuminous seed of the type before described it was necessary to make use of a formula containing the elements for the requisite determinations, these elements being :

- (a) The weight of the resting seed ;
- (b) The shrinking and swelling ratios of the entire seed ;
- (c) The relative weights of coats, albumen, and embryo in the three conditions of the seed, that of the uncontracted pre-resting seed, the contracted resting seed, and the swollen seed ready for germination.

THE SHRINKING AND SWELLING SEED 219

The elements for the seeds under discussion are given in the following table. From its columns we can obtain the materials for constructing the complete régime of the shrinking and swelling seed in the case of three of the species of seeds there dealt with, the seeds of *Hura crepitans* being not here included, as they present special difficulties which are treated in Note 24 of the Appendix. In three other cases we have only the elements in part, namely, those for the determination of the swelling régime. As an example of how the formula can be worked, I have appended to the table the complete régime, as thus indicated numerically, for the seeds of *Cassia fistula*. Whilst preparing the tabulated summary given above, I have had before me the régimes of all the seeds dealt with. Guided by the example given, the reader, by using the elements in the following table, can determine the régime for any of the other seeds.

ALBUMINOUS SEEDS.—TABLE SHOWING THE PROPORTIONAL WEIGHTS OF THE COATS, ALBUMEN, AND EMBRYO IN THE THREE CONDITIONS OF THE SEED.

(From these data the complete régime can be constructed for the shrinking and swelling seed.)

	Average weight of a resting seed in grains.	Shrink- ing and swelling ratio, taking the weight of the resting seed as 1.	Relative weights, taking the entire seed as 100.								
			Pre-resting seed.			Resting seed.			Seed swollen for germination.		
			Coats.	Albumen.	Embryo.	Coats.	Albumen.	Embryo.	Coats.	Albumen.	Embryo.
Poinciana regia .	10	2·3	45·5	28·4	26·1	49·5	23·5	27·0	41·0	32·0	27·0
Bauhinia (species)	4	2·1	23·0	44·0	33·0	23·5	41·5	35·0	24·0	41·0	35·0
Cassia fistula .	4	2·5	26·3	53·7	20·0	15·0	66·0	19·0	17·2	62·8	20·0
„ marginata	10	2·1	29·0	58·0	13·0	28·3	58·0	13·7
„ grandis .	9	2·11	25·0	64·0	11·0	26·0	62·0	12·0
Ricinus communis	3	1·33	28·0	68·0	4·0	23·0	72·0	5·0
Hura crepitans .	20	2·1	57·0	38·2	4·8	30·0	61·5	8·5	44·0	48·5	7·5

The seed of *Hura crepitans* presents special difficulties, its régime being discussed in Note 24 of the Appendix.

CASSIA FISTULA.—THE SHRINKING AND SWELLING RÉGIME OF A SEED OF CASSIA FISTULA IN ILLUSTRATION OF THE MODE OF EMPLOYING THE DATA IN THE ABOVE TABLE AS DESCRIBED ON THE PRECEDING PAGE.

	Weights in grains.			Shrinking and swelling ratios, taking the pre-resting state as 100.		
	Pre-resting.	Resting.	Swollen for germination.			
Coats . . .	2'63	0'60	1'72	P. 100	R. 23	S. 66
Albumen . . .	5'37	2'64	6'28	100	49	117
Embryo . . .	2'00	0'76	2'00	100	38	100
Entire. . . .	10'00	4'00	10'00	100	40	100

SUMMARY

(1) In order to illustrate the shrinking and swelling régime of a seed, a comparison is made of the relative weights of the coats and kernel in the three conditions: the pre-resting, the resting, and the swollen state preceding germination (p. 187).

(2) In connection with the requisite data the proportional weights of the coats and kernel of the resting seed are first dealt with, results being given for thirty-nine species of leguminous seeds and for forty-three species belonging to twenty other orders, including Anonaceæ, Convolvulaceæ, Euphorbiaceæ, Malvaceæ, Sapindaceæ, Sapotaceæ, etc. For convenience only one value is generally employed in the discussion, that of the relative weight of the coverings, which is termed the "seed-coat ratio" (p. 188).

(3) Respecting the great range in the proportional weight of the coats of the resting seed, it is shown that although the range is from 5 to 69 per cent. of the seed's weight, nearly the whole of it is presented by the leguminous seeds, and that the maximum of the range is but slightly extended in the case of seeds with abundant hairs (p. 189).

(4) By grouping the results for the eighty-two species, it is found that the average weight of the coats of the resting seed is about 30 per cent. of the total weight, rather below for leguminous seeds and rather above for seeds of other orders. Excluding very small seeds, "size" has little or nothing to do with the ratio (p. 191).

(5) As regards the constancy of the seed-coat ratio within the

limits of a species, it is shown that the relative weight is sufficiently stable, although it may vary considerably within a genus (p. 192).

(6) With reference to the influence of appendages, such as hairs and wings, on the proportional weight of the coverings of a resting seed, that of hairs is first dealt with. Although ordinary pubescence adds but little to the weight of a seed, a copious covering of long hairs may increase it by 10 per cent. ; whilst in the case of the great hair-development occasionally found with seeds, as in certain *Asclepiads* and in some malvaceous genera (*Gossypium*), the weight of the hairs may amount to one-fourth or even to nearly a half of the entire weight (p. 193).

(7) Coming to the influence of wings on the weight of the resting seed, it is shown in the case of *Swietenia*, *Moringa*, and *Tecoma* that the wing or wings may make up between 4 and 14 per cent. of the total weight. With ordinary "margined" seeds there would be but little addition to the seed's weight (p. 195).

(8) Discussing the function of wings in the resting seed, the author points out that they serve only an accidental purpose in aiding dispersal, and that they have no biological significance except in the actively functioning soft seed of the living fruit. Withered leaves and dry resting seeds stand in this respect in the same category. The possession of wings, he shows, does not always materially assist dispersal. In the case of Pine seeds and the light seeds of *Tecoma stans*, wind may carry them a long distance ; but Mahogany seeds are usually only carried a short way ; whilst the seeds of *Moringa pterygosperma* are not much assisted in this respect (p. 196).

(9) With regard to wings in resting seeds, the author adopts the standpoint taken by Dr Goebel respecting the parachute-apparatus of dry fruits, namely, that although at times serviceable for their dispersal, they were not originally developed for this end, but performed quite a different function in the moist pre-resting seed. As regards winged Mahogany seeds, the author contrasts the heavy, moist, flabby seeds of the living, closed capsule with the dry, crisp seeds—only one-fourth of their moist weight—of the dehiscent dead or dying fruit ; and he regards the function of the wing in a seed in the first-named condition as mainly concerned with the absorption and storage of water, the absorbing surface being increased threefold and the quantity of water for the seed's wants greatly augmented (p. 197).

(10) The proportional weight of the coverings in the two other conditions of the seed is then considered, and it is pointed out that, knowing the relative weight of parts (coats and kernel) in all the three conditions of the seed (pre-resting, resting, and swollen for germination), we possess the requisite data for determining the régime of the shrinking and swelling seed (p. 198).

(11) Although, as established in Chapter II., the seed when swelling for germination regains approximately the water lost in the shrinking process, or, in other words, returns to about its original weight in the pre-resting state, it is shown that this result is in a sense accidental, since the coats do not win back all the water they gave up in the shrinking stage, whilst the kernel takes up as a rule considerably more, the two results going to counterbalance each other in determining the ultimate swelling weight (p. 199).

(12) The materials for constructing the shrinking and swelling régime for a considerable number of seeds are then tabulated and explained. Commencing with a typical impermeable and a typical permeable leguminous seed, it is shown that in both cases the coverings of the swelling seed fail to regain all the water lost in the shrinking process, the deficiency being greatest with the permeable seed. On the other hand, the kernel in both cases ultimately holds more water than in the pre-resting state. The same principle, it is pointed out, applies generally to leguminous seeds; but by the employment of the additional materials we are enabled to see a little more into the average details of the processes. As a general rule, although the coats of the permeable seed shrink more than those of the impermeable seed, both double their weight in the swelling process; whilst the kernel of the impermeable seed shrinks more and increases its weight threefold as compared with the kernel of the permeable seed, which shrinks less and only doubles its weight when swelling for germination (p. 200).

(13) It becomes apparent from all the tabulated results that the resting state leaves its impress on the seed swelling for germination, especially with regard to the coats. This is also evident in the contrast in appearance between the drier, tougher, and relatively unyielding coverings of the seed swollen for germination and the moister, softer, and more yielding coats of the pre-resting seed. But it becomes particularly noteworthy when we find that the seed on the point of germinating is a little smaller than the so-called unripe or pre-resting seed (p. 204).

(14) The result is that conditions of strain arise within the swelling seed. Whilst with the pre-resting seed the kernel lies easily within its coverings, with the swollen seed ready for germination the kernel holds considerably more water than in the pre-resting state and lies constrained within its tightened, unyielding coats. Examples of the strain within the seed thus produced are given, and it is shown that within its tightened envelopes lies a kernel on the average more than 20 per cent. heavier through water-absorption than in the pre-resting state. The result is the rupture of the coverings, the process being purely physical and not necessarily succeeded by germination (p. 205).

(15) That the seeds of other orders may possess a régime similar to

that of leguminous seeds is brought out for purposes of illustration in the case of the seeds of the two species of *Ipomæa*, which represent the convolvulaceous régime (p. 207).

(16) The special difficulty presented by the seeds of *Hura crepitans* is next referred to. These seeds follow the fashion of some indehiscent fruits, like those of the Oak (*Quercus*) and of the Coco-nut, the seed-coverings losing considerably in weight before the kernel attains its mature size (p. 208).

(17) The author then utilises a large amount of data obtained for seeds where the swelling phenomena of the coats and kernel were alone observed. The results for forty-four species are thus employed, of which all but ten are leguminous; and it is remarked that although in about two-thirds the kernel has a larger swelling ratio than the coats, there is no very determinate result in this direction, genera behaving sometimes consistently and at other times being divided in this respect (p. 209).

(18) In order to wrest their story, another arrangement of these "swelling" data is adopted, from which it appears that whilst with the coats the swelling ratios, as respects impermeable, variable, and permeable seeds, are not far apart, with the kernels the ratios for all three types of seeds differ markedly from each other, the impermeable seed showing the largest, the permeable seed the smallest, and the variable seed a ratio intermediate in amount (p. 210).

(19) It is then elicited that this behaviour of the coats and the kernel in these three seed-types is to be connected with the water-percentage of the resting seed, but less in the case of the coats, where the differences are small, than with the kernels, where the differences are large, the kernel of an impermeable seed holding on the average not much more than half the water held by the kernel of a permeable seed and possessing a much greater swelling ratio. With the kernels of variable seeds, where the swelling ratio is intermediate in extent, the water-percentage is also intermediate in amount (p. 212).

(20) Two other points are then referred to, the first being that in seeds with oily kernels, where the unusually low water-percentage indicates that the oil supplies the deficiency, the swelling ratio, as in the case of the seeds of *Ricinus*, is also unusually small. The second is the decrease in the relative weight of the coats as the seed ripens; and in this connection it is remarked that just as with fruits the growth of the pericarp is always in advance of the seed-growth, so with seeds the growth of the coats is always in advance of the kernel (p. 214).

(21) Having dealt with the shrinking and swelling processes of the kernel, we now differentiate in the case of dicotyledonous albuminous seeds between the two components of the kernel, the embryo and the albumen. The rôle of the embryo in this connection is now studied. For this purpose only seeds with embryos possessing large, flat cotyledons,

and occupying the length and breadth of the seed, are employed, seeds such as those of *Poinciana*, *Bauhinia*, *Cassia*, *Ricinus*, and *Hura*. It is shown that the embryo and the albumen go fairly well together in the three conditions of the seed, and consequently in the shrinking and swelling stages, each of them taking its appropriate share in the processes (p. 217).

(22) Such a statement implies that the author, with the aid of the balance, has been able to construct a complete régime for the shrinking and swelling stages of a dicotyledonous albuminous seed, not merely for the seed in its entirety, but independently for all its parts: the coats, the albumen, and the embryo. The materials for such determinations are tabulated, and the seed of *Cassia fistula* is taken to illustrate the employment of the data (p. 218).

CHAPTER X

THE FATE OF SEEDS AS INDICATED BY THE BALANCE

WE realise from the results of the recent researches of Becquerel and others that long years are needed for the satisfactory study of the latent life of seeds, a period, to employ the words of this French investigator, far longer than the time during which the seeds preserve their germinative powers. This is as true for the indications of the balance as it is for those of any other method of physical or chemical research. It is necessary that the life of the inquirer should extend beyond that of the seed he is studying ; and too often, as Jodin aptly observes, the savant who commences such an experiment will never know the results. This is the spirit in which we should approach such a difficult subject as the life of the seed, one of the deepest and most mysterious problems that can occupy the wits of man. A study, though unfinished, is not altogether incomplete if we leave it so that others can take it up. Therefore, although the results given in this chapter are derived from experiments two to four and a half years in length, they represent only the beginning of a long series of experiments which, it may be, someone else may continue after my term of life has ended.

Long years
are needed
for the study
of the latent
life of seeds.

Yet we have here a record of the start and sufficient indications to enable us to look a little ahead in the matter. After seeds have entered upon the resting stage and have quite completed the process of drying in air, four possibilities present themselves. As years go on they may either lose or

gain in weight very slowly, or they may remain absolutely unchanged, or they may acquire a stable weight subject only to hygroscopic variation about a mean. A period of a few weeks or of two or three months is usually sufficient for the completion of the process of drying in free air. For most permeable and impermeable seeds this is quite enough, as is shown in Note 12 of the Appendix, though longer periods may be occasionally required, as in the case of *Mammea americana*, specially referred to in Note 6, where the drying was continued for about a year.

The behaviour in time of impermeable, permeable, and variable seeds.

Speaking generally, my data show that impermeable seeds can retain their weight unchanged for at least four years, excluding such small variations, amounting in the case of *Entada scandens* to only about $\frac{1}{2000}$ of the total weight, which are mainly instrumental in their nature. On the other hand, during the same period permeable seeds, assuming what we may call "the hygrometric state," display a variation in weight of 2 or 3 per cent. around a fairly constant mean in response to the varying humidity of the atmosphere. Variable seeds again behave in an intermediate but changeable fashion, the result of their varying proportions of permeable and impermeable seeds, sometimes approaching one type, sometimes the other, but usually holding a half-way position and exhibiting a small hygroscopic range of 1 per cent. or less.

The maintenance of the same weight by impermeable seeds implies the retention of their germinative powers.

Coming first to the impermeable seed, we are justified, I think, in believing that as long as it preserves the same weight and is non-hygroscopic it retains its vitality. It enjoys complete immunity from the dangers of the hygroscopic reaction, which, if continued through years, must, as M. Jodin observes, ultimately induce molecular changes and lead to the loss of germinative capacity in the case of the permeable seed. The impermeable seed, on the contrary, as long as it is true to its original weight, is exposed to no such risk. However, Professor Ewart, in his paper on "The Longevity of Seeds," contends that "even when perfectly inert a macro-

biotic seed (that is to say, a long-living seed with more or less impermeable coats) is subject to slow and gradual molecular changes and rearrangements, such as take place in glass or wood in the progress of centuries, and that these changes cannot take place in the contents of the seed without destroying the molecular arrangements and groupings requisite for the restoration of life."

Admitting for argument's sake the force of this contention, we should be compelled to credit such seeds with the capacity of retaining their germinative powers for many centuries. But this seems to me to be hardly a correct comparison. Glass and wood are at all events exposed to atmospheric influences, and the last named in particular would be continuously subjected to the hygroscopic reaction. The feature of the non-hygroscopic impermeable seed is that as long as its coverings are intact it remains hermetically sealed up and beyond the influence of atmospheric conditions. If we allow that such a seed may be expected to retain its germinative powers as long as it retains its weight, then the question left to determine is concerned with the duration of its capacity of preserving its weight unchanged; and in illustration of this point there are appended the results of some experiments on impermeable seeds extending over a period of from two to four years.

It has already been established in Chapters IV. and VI. that impermeable seeds weighed from day to day give no indication of any response to the varying hygrometric states of the air. The data in the table below given make it plain that these seeds preserve their non-hygroscopic behaviour from year to year. Time alone will show how long they will remain in this irresponsive condition as far as any reaction with their surroundings is concerned. Although, as pointed out in a previous chapter, the experiment truest to nature would consist in burying the seed deep in the soil in a dry climate, still, these tests in free air go to show that impermeable seeds may remain for many years in this inert condition.

THE WEIGHTS OF IMPERMEABLE SEEDS DURING PERIODS OF
FROM TWO TO FOUR YEARS.

	Number of seeds.	Length of experiment in years.	Changes in weight stated in grains.	Proportion of the change stated as a fraction of the total weight of the seed.
Entada scandens	1	4 $\frac{1}{3}$	301·8-302·0	$\frac{1}{1510}$
	1	4 $\frac{2}{3}$	266·7-266·9	$\frac{1}{1335}$
	1	4 $\frac{1}{3}$	241·1-241·3	$\frac{1}{1205}$
	1	3 $\frac{2}{3}$	406·5-406·6	$\frac{1}{4055}$
Guilandina bonducella	7	4 $\frac{2}{3}$	306·6-306·8	$\frac{1}{1535}$
Adenanthera pavonina	22	3 $\frac{2}{3}$	104·8-104·9	...
Ipomœa pes-capræ (with hairs)	20	3	41·15-41·2	...

Note.—The observations were made at irregular intervals every few months. The first three seeds of *Entada scandens* were carried to Jamaica and kept there some months during the first year, which accounts for their rather larger variation of 0·2 grain; but in the last three years in England the weighings only varied 0·1 grain. A pebble of quartz would probably have behaved in the same way; and evidently the cause of the variation is largely instrumental. This is also true of *Guilandina bonducella*. The samples of the seeds of *Adenanthera pavonina* and *Ipomœa pes-capræ* were small in weight; but the results give the same general indications. In connection with the last-named it is shown on page 169 that its pubescent hairs have a very slight disturbing effect.

The aberrant behaviour of an impermeable seed is at once detected by the balance.

However, although this is the rule, cases of failure are not infrequent, and their aberrant behaviour is at once detected by the balance. Some slight defect in the coats, due probably to some imperfection in the shrinking process, gives time its opportunity; and the seed within, brought into relation with its surroundings, responds to the changing atmospheric conditions, first slowly and then more rapidly, until it assumes the rôle and the limited life-duration of a permeable hygroscopic seed. The manner in which this change of state is carried out has been described in Chapters IV. and VI. in connection with the results of puncturing or filing the seed-coverings. The seed gradually gains weight in the course of months, taking up from the air the water which it previously lacked; and, as is shown in the case of filed seeds of *Guilandina bonducella*, it may retain its germinative capacity for two years after it has virtually lost the protection of its coats, an event,

however, only possible when kept in a dry room. A punctured seed in nature would soon fall a victim to the attacks of mould and insects, unless it germinated quickly.

The failures amongst the impermeable seeds are, as one might expect, very instructive. We can trace the slow progress of the loss of impermeability in seeds gathered by ourselves from the plant. In the course of an experiment covering years, a single seed in a sample gradually begins to fail, a change unerringly indicated in the balance by the increase of weight. Two seeds of *Entada scandens*, the shrinking process of which I had watched after collecting them in the immature, uncontracted state, preserved their weight unchanged for a few weeks, and then began slowly to gain weight, until at the end of a year each had added 3 per cent. to its weight. After this they behaved hygroscopically, like ordinary permeable seeds. The explanation was supplied in the development of fine cracks in the cuticle. In another case three seeds, also of *Entada scandens*, which together weighed 1080 grains, gained 1 grain during the first year. By subsequently weighing them separately the culprit was discovered, two of the seeds remaining quite unchanged in weight. The cause of failure in one of the seeds lay in an imperfection of the cuticle. The same thing occurred during an experiment on six seeds of *Guilandina bonducella* weighing in all about 200 grains. A gain in weight of 1 per cent. during the first year led me to weigh them separately, and it was thus discovered that this increase was due entirely to one seed, which on close inspection showed defects in the outer coat.

The above experiences of faulty impermeable seeds show that nature fails at times in endowing a seed with impermeability, but the suggestive implication is that in such failures permeability is presented to us as a quality by default.

Although the indications supplied by my numerous experiments seem clear and unmistakable with reference to the ultimate fate of the impermeable seed, the views held by

The failures in impermeable seeds are instructive in presenting permeability as a quality by default.

Prof. Ewart on the fate of the impermeable seed.

Professor Ewart respecting the matter are opposed to the position adopted in this work. It has been established by my observations that the impermeable seed, more especially the leguminous seed, holds much less water in the entire state than when broken up and exposed to the air. The process of the change is exhibited when the seed develops some defect in its coverings or when we imitate such a defect by puncturing the coats. The seed then slowly gains in weight by abstracting moisture from the air, until in time it assumes the stable hygrometric condition of an ordinary permeable seed.

The *Acacia*
seed.

Now, Professor Ewart takes a very different position. In the case of *Acacia* seeds, which are notable for their impermeability, and often contain less than 5 to 8 per cent. of water, he writes that "such seeds when preserved in a dry atmosphere seem to steadily lose water, until ultimately as dry as if kept in a desiccator" (*Proceedings of the Royal Society of Victoria*, vol. xxi. p. 199, 1908). This is based on the fact that old seeds lost less weight in the oven than fresh seeds. Fresh air-dried *Acacia* seeds, he says, contain 5 to 14 per cent. of moisture; seeds ten to twenty years old contain from 1 to 3 per cent.; whilst fifty-year-old seeds hold less than 1 per cent., losing only 0.7 per cent. of their weight after the prolonged exposure of a day to a temperature of 110° C. Fine capillary glass tubes, he writes, show a greater loss of weight than this, and hence he infers that "old, dry, cuticularised macrobiotic seeds become drier than corresponding inorganic material."

Old seeds
and in-
organic sub-
stances.

Professor Ewart thus observes that in course of time *Acacia* seeds become as dry as if kept in a desiccator, and implies that they behave like inorganic material. This raises the question as to the behaviour of these two types of substances after desiccation. Seeds that have been exposed to such a low temperature that the free water has been completely expelled fall to powder when struck with a hammer and quickly absorb the hygrometric water from the air (P. Becquerel, in *Annales des Sciences Naturelles, Botanique*, tome v., 1907). This is but an extreme form of what occurs in the kernel of an

impermeable seed when its coats are broken. Being normally in a state of partial desiccation, it at once begins to supply the deficiency by absorbing moisture from the air. From inorganic substances like glass, we should look for no such behaviour. They have little or no water to lose under desiccating conditions, and in consequence have little or no water to regain. This matter is discussed in Chapters VII. and VIII. It will be there seen that Berthelot lays stress on the contrast in behaviour between inorganic substances (like porcelain and metals) and plant-tissues, the first drying completely in air, whilst the second do not.

There is nothing to lead us to expect that the kernels of seeds of any type would ever lose their capacity for behaving hygroscopically and become non-hygroscopic, inert substances like porcelain and metals. If this were the case, Berthelot's principle of reversibility would lose much of its significance. It must, however, be admitted that the semi-stony consistence of the kernels of some old permeable seeds would at first sight seem to justify such a belief. At one time I thought that the seeds of *Æsculus Hippocastanum* (Horse-chestnut) and of the Acorn (*Quercus Robur*) would in time assume some of the characters and behaviour of inorganic material, such as chlorite and opal, as regards the diminished water-contents and the small hygroscopic reaction; but this proved to be incorrect. As regards hygroscopicity, reference has already been made to the effect of time on the behaviour of the seeds of the Horse-chestnut in their coats, the results of the experiments being tabulated in Chapter VII. We saw there that, whether six months or thirty months old, the hygroscopic reaction was much about the same, namely, 2.0 to 2.4 per cent. Whilst writing these remarks I have conducted another experiment on the same seeds three or four years old; but in this case the seeds were first bared of their coverings. The three-year-old seeds give a hygroscopic range of 2.4 per cent., and the four-year-old seeds of 3.5 per cent. So also with reference to the bared seeds of the Acorn. I find

The kernels
of old per-
meable seeds.

that two-year-old seeds display a range of 2.0 per cent., and three-year-old seeds 1.6 per cent.

Quercus
Robur.

Respecting the diminution of the water-contents in time in the case of the kernels of permeable seeds, I will first take those of *Quercus Robur*. Here the kernel in the course of time assumes a chocolate-coloured, semi-waxy appearance and almost a stony hardness, changes which begin at the periphery. Of kernels fourteen months old about a third were completely affected. In another third half of the kernel had undergone the change; whilst in the remaining third the transformation was either in its early stage or scarcely noticeable. Here a mixed sample of the kernels proved to contain 11.3 per cent. of water. Every seed in samples two years old and more displayed the change completed, the water-percentage in kernels two years old being 13.2, and in kernels three years old 12.2.

Æsculus
Hippo-
castanum.

So with the old seeds of *Æsculus Hippocastanum*, it was found that at least for the first three or four years there was no diminution in the water-contents. Seeds bared of their coverings exhibited a water-percentage of 13.6 when eleven months old, 14.4 when twenty-six months old, 12.6 when three years old, and 13.8 after being kept for four years. These seeds, it may be added, do not discolour with time like the seeds of *Quercus Robur*. As is well known, the seeds of the Oak only retain their germinative capacity for a few months. With those of the Horse-chestnut the period, as shown in Chapter XVIII., is still less.

Grias
cauliflora.

Now and then one comes upon old seeds that are as hard and seemingly as dry as a stone, seeds that might almost be taken for fossils, yet in the oven they prove to contain 10 or 12 per cent. of water. The old seeds of *Grias cauliflora*, the Anchovy tree of Jamaica, a myrtaceous tree that flourishes in the lower courses of rivers in the West Indies, offer conspicuous examples. A very remarkable alteration in texture takes place in the seeds after their death, when the conditions are dry, as on beaches, where they are stranded in quantities.

The fleshy, though tough living seed, has the singular structure presented by the seeds of some other myrtaceous trees, such as *Barringtonia*, where an enlarged hypocotyl, invested by a thick rind and forming the storehouse of the food-reserve, constitutes the seed. As the seed dries it becomes as hard as a stone, and on section displays the appearance of a fossil fruit, these stone-like seeds being usually 1 to 1½ inches long. Yet on testing the water-contents of one of these old seeds, which must have been at least six or seven years old, and had been almost five years in my possession, I obtained a result of 12 per cent., almost all the water lost in the oven being subsequently regained from the air in the course of a few weeks. I may direct the attention of the botanist engaged in microscopical and chemical research to these remarkable changes in the seeds of this plant. Sometimes a portion of the seed rots, whilst the other portions experience the change; and when such a seed is found in the early stage of transformation, a very puzzling structure is displayed.

Similar questions might be raised with reference to the condition of old seeds of *Barringtonia speciosa*, which possess the structural features above described in the case of the seed of the Anchovy tree. The seeds do not become quite so hard with time, but are sufficiently altered to cause one to look twice in order to be assured that one is not dealing with some non-vegetable substance. Yet old kernels collected three years before lost 10 per cent. of their weight in the oven, and in a few weeks returned almost to their original weight by replacing the lost water with moisture abstracted from the air.

There is, however, an indication in my experiments on impermeable seeds that might seem to point in the direction of the change in seeds as interpreted from Professor Ewart's point of view. In Chapter IV. it is shown in the case of bared kernels of *Guilandina bonducella* that whilst freshly bared kernels added 13·4 per cent. to their weight in five days, this excess was reduced to 7·3 per cent. in three months, and to 3 or 4 per cent. after a year, an excess which was retained

*Barringtonia
speciosa.*

*Guilandina
bonducella.*

during the next twelve months, when the experiment ended. I did not finally test the water-contents, but the fact that in the last year the seeds exhibited a hygroscopic variation of 1.4 per cent. indicates that they must still have held a fair amount of water. But against this indication of Professor Ewart's view must be placed the indications of another experiment on the same seeds, the results of which are also tabulated in Chapter IV. Here I merely filed through the impervious shell, and thus enabled the air to have access to its ultra-dry kernel within. During four months the seed slowly added to its weight as much as 11 per cent.; but at the end of the experiment, which covered two years, the seed was still about 8 per cent. heavier than before its shell was filed through.

Possible
solution of
the difficulty.

However, a solution of the difficulty seems to be offered by Professor Ewart's remark, when discussing the drying in time of *Acacia* seeds, that "it is as though the cuticle allowed traces of water to escape externally, but none to enter" (*ibid.*, p. 199). From this I am inclined to think that his oven-experiments for testing the water-contents were carried out on the seeds whilst protected by their hard, impervious coats. If so, this explains the whole matter. In my experiments on the impermeable seeds of *Entada scandens* and *Guilandina bonducella*, which are described towards the close of Chapter VI., I show that when exposed both in the entire condition and in the broken condition to a temperature of 100° to 110° C. for two hours, the seeds in their hard coverings lost only about a fourth of the water lost by the seeds no longer protected by their coats. It was also elicited that the seeds in their coverings subsequently made little or no attempt to regain the moisture from the air and doggedly maintained their impermeability. Thus Professor Ewart's surmise that the coats of a seed allow the water to escape, but inhibit re-absorption, is certainly applicable to the behaviour of an impermeable seed during and after the oven test. But this does not reproduce the conditions of drying at ordinary temperatures in the course of years.

Nearly all his results relating to the diminution of the water-contents of *Acacia* seeds when kept for years can be explained on the assumption that the oven-experiments were made on seeds in their coverings. The fact that the fresh air-dried seeds sometimes hold as much as 14 per cent. of water sufficiently indicates that the shrinking process was not always complete, and that, as his general table also indicates, they included some permeable seeds, thus accounting for the greater loss of water in the oven. I am inclined to think that the low water-percentages of his old *Acacia* seeds were due to the experiments being carried out on seeds in their impervious coverings.

The protection a seed receives from its coats in the oven was not only exhibited in other experiments on impermeable seeds, as in the case of those on the seeds of *Canavalia obtusifolia* discussed at the close of Chapter VI., but it was well displayed by the differences in behaviour of permeable seeds, when subjected to the oven test in the entire and in the divided condition, as shown in the results tabulated towards the end of the same chapter. After an exposure of two hours to a temperature of 100° to 110° C., the entire seeds of *Pisum sativum*, *Faba vulgaris*, and *Phaseolus multiflorus* lost 10 or 11 per cent. of their weight, whilst seeds of the same set which had been cut across lost 14 or 15 per cent. In the first case the seeds were completely covered by their coats, and in the last case only in part. The seeds were in all cases eight to ten months old.

It is on these grounds that I venture to differ from Professor Ewart. The future inquirer must decide between us.

The hygroscopic variation offers a special difficulty in the examination of the effect of time on the weight of a permeable seed. Notwithstanding that my experiments extend over periods of three to four years, it is only safe to say at present that the seeds are still in the hygrometric state which they assumed when first entering the resting stage, exhibiting a variation about a mean between the several weighings of about

Permeable seeds remain in the same hygrometric state during the first three or four years.

2 or 3 per cent., being lightest in the summer and heaviest in the winter months. Variable seeds, where there is a mixture of permeable with impermeable seeds, display about half this variation, namely, 1 per cent. But, as has been said, the disturbing influence of the hygroscopic reaction is a great obstacle in detecting small differences in such experiments. If there has been a change, it has certainly not involved any increase in the average weight. On the contrary, the indications, such as they are, point slightly in the direction of a diminution; but it will not be possible to obtain definite results until the experiments have been greatly prolonged and one is able to eliminate the effect of the hygroscopic reaction by comparing the averages for groups of years.

In such experiments on hygroscopic seeds it is necessary that they should always be kept in the same room. So sensitive were my seeds to change that a transference from one room to another was sufficient to cause a variation of $\frac{1}{2}$ or even of 1 per cent. Several years ago MM. Van Tieghem and Bonnier published some interesting results in a paper in the *Bulletin de la Société Botanique de France* (tome xxix. 1882), some of which bear directly on the effect of time on the weight of permeable seeds. They found that after two years in free air, peas had gained about $1\frac{1}{2}$ per cent. in weight, haricots about 2 per cent., seeds of a species of *Vicia* about 1 per cent., and *Ricinus* seeds rather more, but the actual increase in the last case is not given. From my own observations it would appear that this rise in weight was within the ordinary hygroscopic range, and that if weighed at another season all the seeds might have displayed a decrease instead of an increase in their weight.

As indicated in Note 25 of the Appendix, the variation in weight of completely air-dried seeds of *Pisum sativum*, *Faba vulgaris*, and *Phaseolus multiflorus* during a period of nearly fifteen months ranged from 2.6 to 3.6 per cent. of the seed's weight. The variation in weight is also there given for the seeds of *Ricinus communis* in the case of experiments

extending over three years and nearly two years, the amount of the change being 1·1 to 1·6 per cent. of the total weight. In all cases the seeds were heavier at the beginning than at the end, a result due to their being kept at first in a damp room. The variation is the normal hygroscopic reaction. There is no sign of any permanent increase in weight. If one was guided only by the run of the figures and disregarded the conditions of the experiment, one might infer that these seeds lose weight as they get older.

The permeable and variable seeds now under observation with the object of testing the influence of time on their weight belong to nearly thirty genera, of which one-third are leguminous, and include *Abrus*, *Achras*, *Anona*, *Cæsalpinia*, *Canavalia*, *Citrus*, *Datura*, *Erythrina*, *Faba*, *Hura*, *Iris*, *Luffa*, *Morinda*, *Phaseolus*, *Pisum*, *Ricinus*, *Thespesia*, etc.

In conducting all experiments of this kind it is, as already remarked, a matter of necessity that the seed should have acquired a stable weight, either as an impermeable seed when, with regard to the hygroscopic reaction, it is absolutely inert, or as a permeable seed when it displays a small variation on either side of a mean. It is not merely requisite to employ resting seeds for the purpose, but they must be resting seeds with a stable weight. The seeds of the berry and of the legume when first liberated by the opening or by the decay of the fruit are, as described in subsequent chapters, in very different stages of drying. In both cases the seed may in colour, hardness, and other features have the appearance of a normal resting seed. Yet if it belongs to a berry it has still to lose 40 or 50 per cent. of its weight by drying in air; whilst if it belongs to a legume it will have already practically completed the drying process. It is true, as shown below, that leguminous seeds usually lose slightly in weight after being gathered from the dehiscing pod; but here we must often be anticipating nature a little. I have not many observations bearing on this point, but they are sufficient for the purpose of illustration.

With regard first to the impermeable seeds of legumes, my

The author's long weighing experiments.

Whilst with legumes and similar fruits the seeds practically complete the drying process before being naturally detached, the seeds of moist, fleshy fruits lose half of their weight after being liberated.

observations indicate in the case of those of *Entada scandens* that resting seeds, weighing about 400 grains when removed from the pod, may lose about 2 grains during the next few weeks whilst exposed to the free air. Most of this small loss is probably connected with surface moisture, since *Entada* pods break up into closed joints from which the seed has to be removed. In the cases of the pod of *Guilandina bonducella*, which dehisces usually in full exposure to the sun, it would be unlikely that seeds after lying in the gaping pod under such conditions would not have completed the drying process. Coming to permeable seeds of dehiscent pods, I will cite the case of those of *Canavalia ensiformis*, which in ten days after collection from the pods lost about 8 per cent. of their weight and then entered the stable hygrometric state. Then, again, the seeds of *Cæsalpinia sepiaria*, which are in some cases permeable and in others impermeable, lost about 10 per cent. of their weight after being gathered from the opening pod. In both these instances of permeable seeds it is highly probable that nature was to some degree anticipated, and that, left alone, they would have completed their drying before detachment from the pod.

Seeds that
"sweat" or
require
"airing"
before being
stored.

However, the loss of weight experienced by resting seeds or seed-like fruits after they have been collected is often far more considerable than in the leguminous seeds above cited. As Nobbe puts it (p. 382), the process here involved is what the agriculturist would term "sweating" in the case of wheat, and what the forester would call "airing" when gathering acorns, chestnuts, and maple fruits for winter storage. My experiments on Acorns (*Quercus Robur*) and on the seeds of the Horse-chestnut (*Æsculus Hippocastanum*) indicate that they have still much moisture to lose when they are first detached in the "browned" condition from the tree. The Horse-chestnut seed, as it lies on the ground freshly liberated from its fruit, has still to surrender one-third of its weight in moisture to the air before its drying process is complete. The Acorn also, when in the early stage of browning it falls

from the cupule, has yet one-fourth of its weight to lose during its drying. Though leguminous seeds as they escape from the withered pod have practically completed the drying process, it is very different with the seeds of watery or fleshy fruits when they are freed, as must often happen, from the moist fruit. As the result of a number of observations I found that after removal from the ripe fruit, and before entering upon the air-dry condition of the normal resting seed, the seeds lost weight as shown below :—

The after-drying of seeds of fleshy or watery fruits.

- (a) The seeds of the Apple (*Pyrus Malus*) lost 45 per cent. of their weight.
- (b) The seeds of the Bread fruit (*Artocarpus incisa*) lost 55 per cent. of their weight.
- (c) The seeds of *Momordica Charantia* lost 30 per cent. of their weight.
- (d) The seeds of *Tamus communis* lost 44 per cent. of their weight.
- (e) The seeds of the Honeysuckle (*Lonicera*) lost 42 per cent. of their weight.
- (f) The seeds of *Arum maculatum* lost 49 per cent. of their weight.
- (g) The seeds of the Shaddock (*Citrus decumana*) lost 40 per cent. of their weight.
- (h) The seeds of *Genipa clusiifolia* lost 43 per cent. of their weight.
- (i) The seeds of *Opuntia Tuna* lost 45 per cent. of their weight.

Before quitting this subject of the drying of seeds after their liberation by nature's means or after their collection by man, I would refer the reader to Note 12 of the Appendix for further details ; but in many ways this stage of the drying process is linked with other processes dealt with in other chapters.

SUMMARY

(1) For the satisfactory study of the latent life of seeds, says Becquerel, the experiment ought to cover a period far exceeding that of the duration of the seed's germinative capacity (p. 225).

(2) The author's investigations into the changes in weight that seeds experience during the first three or four years after their assumption of a stable weight in the drying process give the following indications. The impermeable seed preserves its weight and shows no hygroscopic reaction throughout that period ; whilst the permeable

seed remains always in the same hygrometric state, and retains the same average weight, showing only fluctuations of 1 or 2 per cent. on either side of a constant mean (p. 226).

(3) As regards the impermeable seed, it is urged that as long as it preserves its weight and is non-hygroscopic, we may assume that it retains its germinative powers (p. 226).

(4) The constancy of the weight of impermeable seeds during a period of three or four years is then illustrated in a tabular form (p. 228).

(5) The failures in impermeable seeds are at once detected by the balance. They are instructive in their presentation of permeability as a quality by default, the impermeable seed owing to some defect in its coats gradually gaining weight and slowly assuming the rôle of a permeable seed (p. 229).

(6) Reference is made at some length to the very different view of the ultimate fate of the impermeable seed held by Professor Ewart. In the case of *Acacia* seeds he considers that in the course of years they become as dry as corresponding inorganic material, and may hold less than 1 per cent. of moisture. This view is controverted, and an explanation of its origin is suggested (p. 230).

(7) It is shown that in all experiments on the weight of permeable seeds extending over some time, the disturbing effect of the hygroscopic reaction, involving as it does a variation of 2 or 3 per cent. of the total weight, presents a great obstacle to the detection of small differences. For this reason, therefore, the experiments should cover many years (p. 235).

(8) It is considered that the increase in weight of 1 to 2 per cent. recorded by Van Tieghem and Bonnier, in the case of seeds of peas, haricots, vetches, etc., after a two years' experiment, comes within the ordinary hygroscopic range and does not necessarily imply an increase in the average weight (p. 236).

(9) With the object of testing the influence of time on seed-weight, the author began four years ago a series of experiments on the seeds of nearly thirty genera, the intention being to continue them for many years (p. 237).

(10) The necessity in weighing experiments extending over long periods of first selecting seeds that have completed the drying process is pointed out (p. 237).

(11) In this connection it is shown that whilst some seeds, as those of leguminous pods and of similar dehiscent fruits, are almost completely air-dry when liberated naturally from the fruit, others from fleshy or watery fruits have still 40 or 50 per cent. of their weight to give up to the air. Seed-like fruits, as grains of cereals and acorns, have to submit to a "sweating" or "airing" process before storage (p. 238).

CHAPTER XI

A CLUE TO THE HOMOLOGIES OF FRUITS

SOME casual observations of the berries of a *Berberis* in my garden directed my attention to the fact that the seeds in the ripe fruit were harder, smaller, and lighter in weight than those of the green berry, or, in other words, that seed-contraction had taken place within the moist fruit. This was established by further investigation, as shown by the results tabulated below. The curious circumstance that the seeds of *Berberis* had undergone shrinkage in the ripening berry gave me a clue for attacking the problem concerned with the homologies in the maturation of different kinds of fruits, especially of the berry, capsule, and legume. It led me to study the conditions of seed-shrinkage and of seed-coloration in fruits generally, and as a matter of course this in its turn led to the investigation of the dehiscence and drying of the fruits with which such matters are closely bound up. It kept me clear of the entanglement of the controversy relating to the priority of the

The shrinkage of seeds in the moist berry affords a clue for the comparison of fruits in their ripening stages as illustrated (a) by *Berberis*,

TABLE SHOWING THE CONTRACTION OF THE SEEDS OF BERBERIS
IN THE RIPENING BERRY.

Condition of fruit.	Condition of seeds.	Average weight of a seed.	Average length of a seed.
Full-sized green berry just beginning to colour	Soft and green	0·23 grain	4·5 millimetres.
Ripe berry	Harder and brown	0·19 ,,	3·5-4 ,,

The loss in weight of the seed was about 17 per cent.

capsule and the berry by finally causing me to regard the baccate condition as one that may be imposed on a variety of fruits, not only on the capsule but on the legume, as in the Tamarind, *Acacia Farnesiana*, and some species of *Cassia*, but also on the nucule, as with some Labiatae.

The indications in this table are sufficiently evident. Subsequently, on investigating this point in the cases of *Arum maculatum*, *Tamus communis*, and *Passiflora pectinata*, I found that there also a marked contraction of the seeds occurred whilst the berry was passing from the green unripe stage into the red, juicy, mature condition.

(b) by *Arum maculatum*,

In the instance of *Arum maculatum*, after a comparison of the full-sized green and red berries on the same spike, and containing the same number of seeds for several plants, the following results were obtained.

TABLE SHOWING THE CONTRACTION OF THE SEEDS OF
ARUM MACULATUM IN THE RIPENING BERRY.

Condition of fruit.	Condition of seeds.	Average weight of a seed.	Average size of a seed.
Full-sized green berry	Whitish and unwrinkled.	1·1 grain	6 millimetres.
Red berry	Reddish and wrinkled.	0·9 „	5 „

The loss in weight of the seed was about 18 per cent.

It is thus shown that in spite of their immersion in a moist pulp, the seeds in the reddening berry of *Arum maculatum* underwent a noticeable contraction and loss of weight. To the eye the contrast is greater than appears in the figures of the table, since the change is associated with marked differences in the general appearance and condition of the seeds. On the one hand, the seeds of the green berry are not only larger and heavier, but they are distinguished also by their whitish hue and their unwrinkled surface. On the other hand, the seeds of the red berry, besides differing in size and weight, are reddish, wrinkled, and somewhat harder. The embryo in both

cases is rather less than half of the seed's length, the chief difference being in the albumen, which is rather mealy in the seeds of the red berry and more fleshy in the seeds of the green berry. Another indication of the contraction of the seed in the moist ripening berry is to be found in the decrease in the relative weight of the coats. Since the coats form 33 per cent. of the weight of the entire seed in the green berry, and 25 per cent. in the red berry, we see that these seeds follow the principle laid down for shrinking seeds in Chapter IX.

The fruits of *Tamus communis* give us the same indications, the seeds of the ripe red berries being smaller, less heavy, and rather harder than those of the full-sized unripe green berries. There seemed at first to be an intermediate stage, when the berries assumed a yellowish hue, but this proved to be connected with the premature withering of the parent stem. In making such observations it is necessary to compare berries growing on the same branch. The table subjoined gives the average of a large number of weighings and measurements, almost all yielding similar results.

(c) by *Tamus communis*.

TABLE SHOWING THE CONTRACTION OF THE SEEDS OF
TAMUS COMMUNIS IN THE RIPENING BERRY.

Condition of fruit.	Condition of seeds.	Average weight of a seed.	Average size of a seed.
Full-sized green berry .	Greenish-yellow	0.57 grain	3.9 millimetres.
Red berry	Brown and harder	0.52 ,,	3.6 ,,

The loss in weight of the seed was about 9 per cent.

The loss of weight (about 9 per cent.) of the shrinking seed in the ripening berry is not great, and a much greater loss is sustained when the seed is exposed to the air, as is shown in the results given a page or two later. The individual differences in weight and size in the seeds of *Tamus communis* seem small, but they become considerable when forty or fifty seeds are weighed together or measured in a line. The seeds of

the green berry are greenish yellow, whilst those of the red are brown, the "browning" beginning in the green berry. In both stages the seeds are firm and the albumen solid, but the brown seeds are rather harder.

(d) by *Passiflora pectinata*.

From the berries of *Passiflora pectinata*, a species first described from the Bahamas, the same evidence is obtained. I made a study of these fruits in the island of Grand Turk at the southern end of the group. In the red mature berry the dark purplish crustaceous seeds are enclosed each of them in a moist, pulpy aril, as is characteristic of the genus, the whole interior of the fruit being moist. In the green, full-grown unripe fruit, the seeds are dark green, heavier, larger, and rather softer than in the ripe berry, the interior of the fruit, together with the saccate arils, being relatively dry. The results of my observations may be thus tabulated.

TABLE SHOWING THE CONTRACTION OF THE SEEDS OF
PASSIFLORA PECTINATA IN THE RIPENING BERRY.

Condition of fruit.	Condition of seeds.	Average weight of a seed.		Average length of a seed.		Average breadth of a seed.	
Full-grown, dryish green berry	Dark green and semi-crustaceous in dryish arils	0.35 grain		5.8 millimetres.		3.5 millimetres.	
Red, ripe, moist berry	Dark purplish and crustaceous in moist, pulpy arils	0.31 "		5.3 "		3.3 "	

The loss in weight of the seed was about 11 per cent.

The significance of the shrinking of the seed in the moist berry.

The shrinking of the seed immersed in the moist pulp of a berry is significant in many ways, and particularly because it supplies, as already observed, a clue by which we can trace the homologies in the maturing and drying stages of very different types of fruits. Or perhaps we would better describe it as affording a datum-mark to which we can reduce for purposes of comparison the various conditions presented by such fruits.

It has first to be noticed that the loss of weight which the seeds of these berries undergo in the moist fruit is but a small proportion of the loss which they sustain when subsequently freed by decay of the berry and exposed to the air. If the seed of *Tamus communis* loses 9 per cent. in the reddening berry, its total loss of weight when dried in free air amounts to about 46 per cent., as shown in the results tabulated below. The seeds of *Berberis*, *Passiflora*, and of *Arum maculatum*, which give the same indications, are there compared with it. One can recall familiar instances of the shrinking, hardening, and "browning" of seeds in fleshy fruits such as the Apple, the Sapodilla, and the Star Apple; but here, though the change is evident to the eye, it is not easy to give a numerical value to the difference without a carefully guarded comparison of the average weight of the seeds in a large number of the full-sized unripe and ripe fruits. As the green apple mellow, its soft white seeds become smaller, harder, and brown in colour. The same process is familiar in sapotaceous fruits like the Sapodilla and the Star Apple (*Achras Sapota* and *Chrysophyllum Cainito*), where, as the fruit ripens, the soft white seeds become hard and brown.

In the following table the loss in weight of the seed in the ripening berry is compared with the total loss when the berry dries up.

CHANGES IN THE WEIGHT OF SEEDS OF BERRIES DURING THE RIPENING AND DRYING UP OF THE FRUIT.

	Weight of a seed in grains.			Relative weight of a seed, taking the seed of the green berry as 100.		
	Green berry.	Ripe berry.	Dried-up berry.	Green berry.	Ripe berry.	Dried-up berry.
<i>Berberis</i> (species of) . . .	0·23	0·19	0·12	100	83	52
<i>Arum maculatum</i> . . .	1·10	0·90	0·55	100	82	50
<i>Tamus communis</i> . . .	0·57	0·52	0·31	100	91	54
<i>Passiflora pectinata</i> . . .	0·35	0·31	0·20	100	89	57

This table supplies a means of comparing the behaviour during the maturing and drying stages not only of the seeds of other kinds of fruits, but of the fruits themselves, and particularly of the capsule and the leguminous pod.

We will first take the Horse-chestnut (*Æsculus Hippocastanum*), which almost acquires the baccate habit, though its familiar condition, as it lies open on the ground, is that of a dryish dehiscent fruit. The same preliminary shrinking of the seed, associated with hardening and "browning" of the seed-coverings, takes place in the closed capsule. These changes, however, only occur in the last stage of maturation immediately preceding dehiscence. As the green fruit mellowes with maturity it becomes yellowish, and it is during this mellowing stage that the shrinking, hardening, and browning of the soft white seed take place within.

If the soft white seed is removed and allowed to dry in the air, its coats rapidly harden and assume the characteristic reddish-brown hue, a change which experiment showed to be associated with a loss of 17 per cent. of the original weight. The hardening and coloration of the coverings were completed in twenty-four hours, when the seed was placed in a warm, dry cupboard; whilst in diffuse light in a damp room they occupied two or three days, an indication that these changes are the result of partial drying only and do not require the action of light.

If we wished to designate the particular stage in the maturation of the capsule of the Horse-chestnut corresponding to the ripe berry, we should select the mellowing stage immediately preceding dehiscence, when the green capsule assumes a yellowish tinge. It is then, and we are now indebted to the clue supplied by the seeds of the *Berberis* berry, that the seed undergoes its preliminary shrinking and that the hardening and colouring of its coverings within the closed capsule occur. Like the seeds of the berry also, it has yet much more water to lose. It has been already implied that as soon as the capsule begins to open it displays a well-browned, hard-coated seed (or seeds), which, as indicated by an experi-

Comparison of the behaviour of seeds of the berry with those of other kinds of fruits.

First, Capsules, as in the Horse-chestnut (*Æsculus Hippocastanum*).

ment before described, has already sustained before dehiscence a loss of water to the extent of 17 per cent. of its original weight as a soft white seed. When such seeds after removal from the naturally dehiscing fruit are allowed to dry in the air of a room, the total loss of weight finally amounts to about 53 per cent. Thus, to take an example, a soft white seed freshly removed from a full-sized green capsule and weighing 300 grains would weigh about 250 grains when first exposed as a brown, hardening seed in the fruit commencing to dehisce. In the air it would rapidly dry, until it ultimately assumed a stable weight, subject only to hygroscopic variations, of about 142 grains. Stated as percentages, these changes in weight in the successive stages of drying would be as follows:—

Soft white seed	100
Same seed after some hardening and shrinking in the closed capsule	} 83
Same seed after the drying process has been completed in the open capsule	

Such are the indications supplied by the Horse-chestnut seeds and by comparing them with the data before given for the berries of *Berberis*, *Passiflora*, *Arum maculatum*, and *Tamus communis*, it will be at once perceived that they run well together with the indications of the berry. There is the same preliminary shrinking of the seeds within the closed ripening fruit, and there is the same great loss of weight when the fruit has passed maturity and begins to dry. Whether the seed undergoes the greater part of its drying within a shrivelling berry or exposed in an open capsule, the process belongs to the same stage in the history of the fruit. We can now perceive how the shrinking of the seed in the ripening berry comes to our aid in contrasting other fruits in their several stages of maturation by enabling us to fix on a stage that is common to all.

My next example of a capsular fruit will be that of *Iris Pseudacorus*. Here, as in *Æsculus Hippocastanum*, the Horse-chestnut, the soft white seeds of the green full-sized capsule begin to shrink and harden and commence to “brown,” whilst

*Iris Pseud-
acorus.*

the fruit is mellowing and assuming a yellowish hue before dehiscence. Since the soft white seeds of the green capsule lose 60 per cent. of their weight when allowed to dry, and since the brownish seeds in the capsule on the eve of dehiscence lose about 50 per cent. of their weight when exposed to the air, it follows that about 20 per cent. of their weight is lost by the soft unripe seeds when shrinking in the ripening fruit before dehiscence. We thus get for *Iris Pseudacorus* results very similar to those obtained for the Horse-chestnut. Both display the régime of the berry in the drying of their fruits and seeds, processes quite independent of any distinction that may be drawn between baccate and capsular fruits. Here again the mellowing, greenish-yellow stage immediately preceding dehiscence corresponds to the ripening of the green berry when it reddens in *Arum*, *Tamus*, etc. I have compared the results for these two capsular fruits in the table below with the mean result for a berry as supplied by the data for *Berberis*, *Arum maculatum*, *Tamus communis*, and *Passiflora pectinata*.

COMPARISON OF CAPSULES AND BERRIES WITH REGARD TO THE RELATIVE WEIGHT OF THE SEEDS DURING MATURATION AND DURING THE DRYING PROCESS, THE WEIGHT OF THE SEED IN THE FULL-SIZED GREEN OR UNRIPE FRUIT BEING TAKEN AS 100.

	Soft white seeds in the full-sized green capsule.	Seeds in the ripe capsule on the eve of dehiscence.	Seeds dried in air after being freed from the dehisced capsule.
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	100	83	47
<i>Iris Pseudacorus</i>	100	80	40
	Seeds in the full-sized green berry	Seeds in the ripe berry	Seeds in the shrivelled and dried-up berry
Mean results for a berry (see table before given)	100	86	53

The weights of an average Horse-chestnut seed in the three stages are 300, 250, 142 grains; and for *Iris Pseudacorus*, 2.0, 1.6, and 0.8 grain.

Observations of this kind extend over a year or two and require a little patience, since the same locality has often to be visited several times, and much also has to be done at home.

I will now take a fruit intermediate between a capsule and a berry, the baccate capsule of *Thespesia populnea*, a tropical beach tree of the malvaceous order. The full-sized yellowish-green fruit possesses an abundant, thick yellow juice and white, softish seeds. In the next stage it becomes a darker green, the juice becomes scanty, and the seeds shrink a little, harden, and assume a purplish tinge. Then the fruit begins to "brown" rapidly, and its sides collapse; whilst its seeds also turn brown, and, continuing to dry and harden, ultimately lose about half their original weight when the drying of the fruit is complete. Finally, the fruit breaks down and the seeds are freed by its decay. In the figures 100, 87, and 50, which represent the relative weights of the white softish seed, of the purplish seed before drying of the fruit has actively commenced, and of the brown, hard seed in the fruit when the drying has ended, we have stated numerically the essential stages of the capsule and the berry. The actual weights of an average seed in these three stages would be 5.5, 4.8, and 2.25 grains. An index of the changes in the fruit is afforded by the changes in the condition of the adherent calyx, which remains moist and green long after the seeds within have begun to shrink and harden, and only begins to wither when the capsule commences to "brown" and to lose weight, thus indicating that the first shrinkage of the seed within the still moist fruit, as in the case of the true berry, precedes the active drying of the capsule.

With the ordinary dehiscent leguminous pod there is quite another régime. In illustration I will first take that of *Cæsalpinia sepiaria*, the familiar "Wait-a-bit" of Jamaica. The full-sized green pod with its white, soft seeds represents the green capsules of the Horse-chestnut and *Iris Pseudacorus* and the green berries of *Berberis*, *Arum maculatum*, and *Tamus communis* after they have attained their maximum size. In the next stage, which corresponds to the ripe berry and the mellow-

Second,
Baccate
capsules
illustrated by
*Thespesia
populnea*.

Third,
Leguminous
pods, as in
*Cæsalpinia
sepiaria*.

ing capsule before dehiscence, the pod turns yellowish green and the white seeds experience the preliminary shrinkage and hardening and take on a greenish hue. Then active drying of the pod and seeds commences ; but before dehiscence begins the shrinking and hardening of the seeds have been almost completed, so that in the opening pod we find normal dark, mottled resting seeds that will perhaps lose another 10 per cent. of the original weight in keeping. The respective weights of the seeds in the green pod, in the pod turning yellowish, and in the dried pod on the eve of dehiscing, are 8.3, 6.2, and 3.8 grains, which stand to each other as 100, 75, and 46, and thus indicate the three stages of the berry.

Some of the processes involved in the general shrinking of leguminous pods and seeds will be discussed more in detail in the succeeding chapter. Here I will only refer to cases which seem specially suggestive for determining the stages in maturation and in the drying process that are homologous or are truly comparable with those in the capsule and berry. In this connection the pods of *Ulex europæus* occupied much of my attention. They were the first fruits to which I applied the clue afforded by the *Berberis* berry. Though much of their behaviour is characteristic of the typical leguminous pod, it is not always that we find the stages so well defined.

With *Ulex europæus* practically all the shrinkage, hardening, and coloration of the seeds are carried out in the closed pod ; and when the pod dehisces it exposes to view the normally contracted hard seeds. Three stages in the maturation and drying of the fruit are distinguished by the colour of the seeds. When the green pod has reached its full size they are soft and bright green, a hue that they owe mainly to the dark green embryo which can be seen through the thin coats. Then follows a stage which corresponds seemingly to the first failure of the nutrient supplies from the mother plant. The soft green seeds turn a greenish yellow as the pod begins to dry and darken. But there is no very evident shrinking of the seed, though the cord withers. That is only detected by careful measurement and

*Ulex euro-
pæus* (Gorse).

by the balance, since it is slight in amount. The colour-change again is largely due to the change in colour of the embryo.

The last stage is occupied with the active drying of the darkening pod, the yellow seeds contracting and hardening rapidly and adopting the permanent chocolate-brown colour of the normal resting seed. In this stage, however, the change in seed-colour is mainly an affair of the coverings, whilst in the two earlier stages, marked by green and yellow seeds, it was largely concerned with the embryo. This last stage closes with the completion of the drying of the pod in the sun's rays, and the pod dehisces suddenly, giving rise to those curious little clicks that one hears so frequently when standing near a gorse bush on a sunny day.

Now all these changes in the seeds of *Ulex europæus*, from the soft green state to the hard chocolate-brown condition, are carried on in the closed pod. In fact, all three stages may be observed together in the same pod. The discoloration begins at its distal end, and before the blackening process has extended down one-third of the pod's length all the seeds will have changed their hue from green to yellow. When it has affected four-fifths of the pod, the uppermost seeds will be found actively shrinking, hardening, and colouring chocolate brown; and by the time the whole pod has blackened all the seeds will be in that condition. But although the pod has dried considerably during the blackening process, it is still fairly moist at its completion; and the seeds, though considerably reduced in size and no longer soft, are far from being as hard as in the normal resting seed, and have yet to decrease in size. Up to this point there has been no opening of the pod, and the completion of the drying process and the ultimate dehiscence are soon affected by exposure to the sun.

It has been noted above that the green and yellow seeds have green and yellow embryos, the colouring of the soft seeds depending in these two stages mainly on the colour of the embryos. This change from green to yellow is probably connected with the failing of the nutrient supplies, since it coincides with the commencement of the withering

of the cord or funicle. But the change in the last stage from yellow to chocolate brown is exclusively associated with the drying process. This is indicated by a simple experiment. If a yellow seed is allowed to sink in a glass of water no alteration takes place. But if it is allowed to rest on the surface for a day or two, the lower submerged portion preserves its yellow hue, whilst the upper part exposed to the air turns brown.

TABLE SHOWING THE SHRINKAGE OR CONTRACTION OF THE SEEDS OF *ULEX EUROPEUS* (GORSE) IN THE POD BEFORE DEHISCENCE.

Condition of pod.	Condition of seeds.	Weight of a seed.	Size of a seed.
Green and full-sized . . .	Soft and green.	0·25 grain	4·4·5 millimetres.
Beginning to discolour and to dry	Soft and greenish yellow	0·20 ,,	3·3·5 ,,
Dried and on the eve of dehiscing	Hard and chocolate brown	0·11 ,,	2·5 ,,

The loss in weight in passing from the green to the yellow stage is 20 per cent. ; whilst the total loss experienced is 56 per cent.

If we wished to determine the correspondence in the maturing and drying stages between a leguminous pod like that of *Ulex europæus* and a berry like that of *Berberis*, we would do so in this fashion :—

- The corre-
spondence
between a
legume and
a berry.
1. { Green pod, with soft green seeds of *Ulex*.
 { Green berry, with soft green seeds of *Berberis*.
 2. { Green pod of *Ulex* commencing to darken, with green seeds
 { turning yellow and shrinking slightly.
 { Colouring berry of *Berberis*, with seeds turning brown and
 { becoming smaller and harder.
 3. { Pod of *Ulex* rapidly drying and blackening, with seeds turn-
 { ing brown, shrinking greatly, and hardening.
 { Berry of *Berberis* rapidly shrivelling, with seeds losing much
 { water and hardening.
 4. { Dried pod of *Ulex* liberating its seeds by dehiscence.
 { Shrivelled berry of *Berberis* liberating its seeds through the
 { decay of its coverings.

The correspondence in the fourth stage will perhaps be least expected. But when one reflects that the opening of a pod,

however methodical the process may appear to be, depends on a structural character which was originally developed for a special purpose in the living plant and could have had no concern with the liberation of seeds from a dead pod, we must confess that this appearance of method is purely accidental. It is an accident that I am able to avail myself of the binder's crease in tearing the sheets of a book into regular portions; and to that extent the mode of dehiscence is accidental with the *Ulex* pod. It will subsequently be shown that if this parallelism between the dry, dehiscing pod and the decaying, shrivelled berry is valid, it ought to have a far-reaching influence on our views of adaptation and seed-dispersal.

My readers will in this connection recall those numerous leguminous pods that liberate the seeds only by breaking down through decay, and I shall in a later page point out that the peculiar form of moniliform pods, which is there described, is probably determined by constrictions induced in an earlier stage of the development of the fruit by the abortion of the ovules, and the premature shrinking of the seeds.

COMPARISON OF THE MEAN RESULTS OBTAINED FOR BERRIES, CAPSULES, AND LEGUMES, WITH RESPECT TO THE RELATIVE WEIGHTS OF THE SEEDS DURING THE MATURATION AND DRYING OF THE FRUITS, THE WEIGHT OF THE SEED IN THE GREEN UNRIPE FRUIT BEING TAKEN AS 100.

In the green berry 100	In the ripe berry 86	In the dried-up, shrivelled berry 53
In the green capsule 100	In the ripe capsule on the eve of dehiscence 82	When dried in air after the opening of the capsule 44
In the green legume 100	In the green legume turning yellow or beginning to blacken 78	In the dried-up legume on the point of dehiscing 45

The results here given are for the berries of *Berberis*, *Passiflora*, *Arum maculatum*, and *Tamus communis*; for the capsules of *Esculus Hippocastanum* (Horse-chestnut) and *Iris Pseudacorus*; and for the legumes of *Casalpinia sepiaria* and *Ulex europæus* (Gorse).

The corre-
spondence
between
berries,
capsules, and
legumes.

We see from these results that in the ripe berry only a small shrinkage of the seeds occurs, namely, about 14 per cent., and that the seeds have still much of their water to lose in drying. In the capsule the same small shrinkage takes place before dehiscence, but the principal loss of weight and the greater part of the contraction occur after the seeds have been exposed to the air. In the pod practically all the shrinkage of the seeds is carried out in the closed fruit, and when dehiscence occurs normal resting seeds are exposed. The seeds of a capsule are thus placed at a disadvantage when compared with those of a pod, since in the pod the seeds are protected until sufficiently hardened, whilst in the capsule they are usually exposed in a relatively soft and in a less protected state on account of the dehiscence taking place at a much earlier stage.

The parallelism, or rather the correspondence, between the stages of the maturation and the drying of berries, legumes, and capsules, may be put in the following manner :—

(1) The green berry, the green capsule, and the green legume of maximum size, with their large, soft, white or green seeds, are all in the same stage.

(2) The ripe, juicy berry, the mellowing, still closed capsule, and the legume just beginning to discolour represent the next stage, which is characterised by a slight shrinking of the seeds, and by their coloration when white, or by a change of colour if green. Though evident enough in the berry, this stage is transient and often disguised in the capsule and legume, points which will be further discussed in the succeeding chapter. It is early in this stage that the shrinking of the cord or funicle marks in dehiscent fruits the commencement of the severing of the seed's connection with the parent plant.

(3) The shrivelling berry, the capsule dehiscing and losing much of its water in the air, the drying and blackening but still closed legume, belong to the next stage. Dehiscence occurs at a much earlier stage with the capsule than with the

legume. As shown in Chapter XIII, the legumes lose before dehiscing nearly all the water they can yield to the air ; whilst the capsule before it opens may not even have commenced to dry, or loses only a small proportion of the water that it ultimately gives up in the air-drying process. The greater part of the shrinking and of the hardening of the seeds belongs to this stage.

(4) This stage characterises only the berry and the legume, since the dried capsule has already completed its stages and is lying widely open with its seeds falling out. The shrivelled berry and the dry pod now in their turn liberate their seeds, the one by decay and the other by dehiscence.

Such are some of the principal points brought out in this comparison of the capsule, legume, and berry. Additional evidence will be adduced in support of most of them in the following chapters.

There is much that is significant in this correspondence between these three different kinds of fruits, and much that we should bear in mind when we speak of special adaptation for dispersal of fruits and seeds. Though there is a great deal that may please the eye and captivate the fancy in the mechanisms of a dehiscing pod or capsule, it is doubtful whether they represent anything more in nature than the rotting apple and the shrivelling currant. The exposure of the brightly coloured seed in the opening pod, as in *Abrus*, *Adenanthera*, and *Erythrina*, often adds beauty to the plant ; yet, viewed from this standpoint, it is nothing more than one observes in the seeds exposed in the decaying orange and in the rotting *Anona* fruit as they lie on the ground. If the seeds in the ripe berry, or mature baccate fruit, are in the same stage as those in the mellowing capsule before it opens, or in the closed, full-sized green legume on the eve of drying, then the shrivelled berry represents the dried-up open capsule and the shrunken but still closed legume.

The question
of adapta-
tion.

In all three fruits the shrivelling and drying, whether

accompanied or not by dehiscence, seem to betoken a stage that was not, if I may use the expression, in the original plan laid down for nature. The biological connection being severed with the parent plant, the fruit dies, but the seed lives. There was a time, as I hold, in the age of vivipary, when uniform climatic conditions prevailed, and the embryo was already well advanced in germination and able to start life for itself before the severance from the parent took place. In later ages climatic differentiation has intervened, and the fruit dies, leaving the embryo in all stages of arrested growth, with the chances of its future development by no means assured. The embryo is then dependent for its protection on the hardening of its coverings, a process mainly accomplished after the cord has withered, and in a fruit no longer drawing its nutrient supplies from the parent, but practically dead.

It is hard to detect anything but a baffled design when we see nature suddenly withdrawing the plant's fostering care over its offspring and leaving all to chance. It is difficult to perceive any evidence of adaptation for dispersal in a rotting apple; but if my view is correct, the same should be true of dehiscent fruits, the withering and opening of which, though seemingly displaying more of method, are equally determined by external influences of a haphazard kind.

SUMMARY

(1) The shrinkage of seeds in the moist berry affords a clue for the comparison of fruits in their ripening stages, as illustrated by *Berberis* (p. 241), *Arum maculatum* (p. 242), *Tamus communis* (p. 243), and *Passiflora* (p. 244). Thus guided, we can trace the homologies in the maturing and drying stages of very different types of fruits. This shrinkage within the moist berry, which involves a loss of weight on the average of from 10 to 15 per cent., represents but a small proportion of the total loss which the seed sustains when exposed to the air or dried with the fruit.

(2) It is the shrinking of the seeds in the ripening berry that comes to our aid in contrasting other fruits in their several stages of maturation by enabling us to fix on a stage that is common to all.

Thus in the case of capsular fruits, like those of the Horse-chestnut (*Æsculus Hippocastanum*) and of *Iris Pseudacorus*, we see displayed the régime of the berry in the preliminary shrinking of the seeds within the ripening fruit and in the subsequent great loss of weight when the fruit has passed its maturity and dries in the air. Here, then, it becomes evident that the green berry and the green capsule are in the same stage, the ripe juicy berry and the mellowing still closed capsule in another stage, and the shrivelling berry with the drying, dehiscent capsule in a third stage.

(3) With the ordinary dehiscent leguminous pod, as illustrated by the behaviour of those of *Cæsalpinia sepiaria* and *Ulex europæus*, there is quite another régime, since dehiscence occurs much later than in the capsule; but here also the preliminary shrinking of the seeds and other changes in the fruit enable us to detect the equivalents of the stages of the berry and the capsule in those of the leguminous pod. We thus learn that the berry, the capsule, and the legume, in the full-grown green or so-called unripe condition with large soft seeds, are in the same stage. The ripe, juicy berry, the mellowing, still closed capsule, and the green legume just commencing to discolour represent the next stage in the maturation of the fruit, which is characterised by a slight shrinking and hardening of the seeds. Then the berry shrivels, the capsule dehisces and dries, and the legume darkens and dries rapidly, but still remains unopened, the shrinking and hardening of the seeds being in all cases actively continued. When the last stage arrives the dry capsule has already completed its history and lies gaping widely, with its seeds falling out, whilst the shrivelled berry and the dry legume now liberate their seeds, the first by decay, the second by dehiscence.

(4) If the seeds in the ripe berry are in the same stage as those of the mellowing capsule before dehiscence and of the full-sized moist legume on the eve of drying, then the shrivelled berry represents the dried-up open capsule and the dry legume or pod on the point of dehiscent. From this standpoint, therefore, the mechanism of a dehiscent legume or capsule, however adaptive its appearance, does not count for anything more in nature than the rotting apple or the shrivelling currant. If we are not able to detect any signs of adaptation for dispersal in a decaying berry, the same should be true of dehiscent fruits, the withering and opening of which, though apparently displaying more of method, are equally determined by external influences of a haphazard kind.

CHAPTER XII

THE HOMOLOGIES OF FRUITS AS REVEALED IN THE DRYING PROCESS

THIS chapter is concerned principally with the story of the drying fruit, or rather with the indications that it supplies. Here again it is to the balance that we look for our data, and it will be seen that the results obtained are of some interest and often unexpected in their significance. Without further introductory remarks I will at once plunge into the middle of my subject.

Indications
of the con-
trast between
the berries of
Barringtonia
speciosa and
Ribes
Grossularia
(Goose-
berry).

It is very suggestive that two such different-looking fruits as those of *Barringtonia speciosa* and *Ribes Grossularia* (Gooseberry), both of which are characterised by the systematic botanist as berries, give off when allowed to dry naturally in the air the same amount of water, losing in each case about 85 per cent. of their weight in the ripe condition. The one, a large fruit 8000 to 9000 grains in weight, is described as corticate and fibrous, whilst the other, weighing about 100 grains, is described as succulent and pulpy. Even if the air-dried fruits of both plants were subsequently exposed in the oven to a temperature of 100° C., the relative weight of the water-free residues would not differ greatly in amount, that of the Gooseberry being probably about 10 per cent., and that of *Barringtonia speciosa* about 13 or 14 per cent. of the moist fruit. For details of the experiments on the Gooseberry see Note 10 of the Appendix.

When comparing two such different-looking kinds of

berries we are likely to begin with a misconception. The dry, husky, symmetrical fruit of *Barringtonia speciosa*, such as the currents disperse over the coral islands of the Pacific, is a dried berry, and as such is only to be compared with the shrivelled fruit of the Gooseberry. This lack of adjustment is frequently met with in comparing the stages of fruits. Take, for instance, the distinction which the systematist usually draws between a berry, as fleshy and indehiscent, and a capsule, as dry and dehiscent. Here we are contrasting the air-dried capsule with the moist berry, two quite different stages in the history of these fruits. Naturally, the true correlative of the dry dehiscent capsule would be the shrivelled berry, whilst the ripe berry would find its homologue in the full-grown moist capsule as we find it living on the plant. This relation between the berry and the capsule has been already dealt with in Chapter XI. The necessities of the systematist are partly responsible for the incongruities in the comparison of fruits, since he gives a place to the dry fruit that retains its shape, but refuses to recognise as on the same footing the dried-up berry or the shrivelled drupe. But part of the blame must lie with one's natural repugnance to the shrivelling process, seemingly so significant of inutility and death. Let but the form be preserved, even though the life of the fruit has gone, and we become apt to attach importance to a distinction which is purely accidental and in no sense ordinal in character.

These remarks do not at all exaggerate the lack of true adjustment which prevails in the general classifications of fruits. It is far from easy to see how this can be avoided in practical systematic botany, but the inconsistency remains. There lies beside me *The Handbook of the British Flora*, by Bentham and Hooker (5th edit., 1887), and there I read (p. 36) that fruits are generally divided into "succulent" and "dry," the first being usually indehiscent, whilst the second are often dehiscent and open at maturity. The succulent fruits are there typified by the berry and the drupe, and the dry fruits by the capsule, legume, achene, etc. Of

Misconception arising from the comparison of fruits that are not in the same stage.

The distinction drawn by the systematist between succulent and dry fruits.

the dehiscent capsule and legume it is stated that when ripe the pericarp usually splits into valves. One may note in passing that this can only be said of the capsule. However, each of these statements taken independently has the sanction of experience; but it is an error to connect them together in a classification of fruits, since they are essentially incongruous.

In the first place, as regards the two main divisions into succulent and dry fruits, it is apparent that we are here contrasting moist fruits that have yet to dry with those that have more or less completed the drying process. As already indicated in Chapter XI, the moist fruit is a living fruit, whilst the dry fruit is a dead one. Strictly speaking, there is no such marked distinction in nature between moist and dry fruits, except such as is connected with the difference between a living and a dying or dead fruit. To be convinced on this point we have only to look at the columns of the following tables, though this view has already been established in the previous chapter. Where, for instance, are we to find amongst other types of fruits the stage that is representative of the air-dried capsule of *Datura*? If we followed the method of the systematist we should find it in the moist drupe of the Sloe (*Prunus communis*). A glance at the tables will show that in so doing we should be comparing a dead and dry fruit with a moist and living one. Both the living capsule and the living drupe in these two plants lose about the same amount of water when they die and dry up (70 to 73 per cent. of their weight); and if we contrast them we should either compare them when they have attained their maximum size on the plant as moist living fruits, or when they have lost their vitality and have dried up. This is the only valid mode of comparing fruits, and the failure to adopt it leads to erroneous conceptions of the biological significance of the process of dehiscence. The dried dehiscing capsule and the shrivelled drupe go together.

Nature does not recognise such a distinction.

The same rule applies when we look for the representative of the *Datura* capsule amongst the legumes or the berries. A *Canavalia* pod, an *Arum* berry, and a *Datura* capsule contain about the same amount of water in the full-grown living state, and can only be compared in the same condition either as moist living fruits or as dry dead ones. We thus come to perceive that all fruits, when they reach maturity on the plant, whether drupes, legumes, berries, capsules, etc., are moist fruits and cannot be distinguished from each other by their water-contents. Nature does not recognise the distinction between moist drupes and berries on the one hand and dry legumes and capsules on the other. Group for group, the contrast between capsules, legumes, berries, drupes, etc., as regards their water-contents in the full-grown living condition, is relatively small; and in each group we find much the same variation in the amount of water lost in drying, namely, between 50 and 80 or 85 per cent.

The differences are mainly developed when we allow the drying to take place in all cases, the berry and the drupe to shrivel up, and the capsule and the legume to dry and dehisce, the ultimate contrast between the asymmetry of the one kind and the retention of the regular form in the other being dependent on the nature of the tissues composing the pericarp. Nature makes no deliberate effort to assist the systematist, and inconsistencies of the kind above noted are inseparable from our necessarily arbitrary endeavours to systematise her processes. The error involved above is of course the comparison of fruits that are not in the same stage. But other inconsistencies are apt to follow. Thus, as already noticed, it is implied in the above statements from *The Handbook of the British Flora*, that dry dehiscent fruits like those of the capsule and the pod open when they are "ripe." This might indicate that dehiscence occurs in these fruits in the moist, mature condition. But, as we will see in Chapter XIII, this is only true of the capsule, the legume opening when the fruit

All mature living fruits are moist fruits.

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dry and dead. The typical capsule which opens before drying begins, or in the early stage of drying, is just as much entitled to the designation of "moist" as a berry. I venture, therefore, to think that these remarks indicate the necessity of renovating our prime conceptions of the differences between fruits.

THE LOSS OF WEIGHT OF MATURE FRUITS, INCLUDING THEIR SEEDS,
WHEN DRIED IN AIR UNDER ORDINARY CONDITIONS OF TEMPERA-
TURE. (The full-grown moist fruits before drying or shrinking begins
are here employed.)

I. LEGUMES.

	Number of seeds.	Char-acter of dry fruit.	Loss of weight after drying in air for weeks or months.				
			Stated in grains.		Stated as a percentage.		Stated as water-loss or water-percentage.
			Moist weight.	Dry weight.	Moist weight.	Dry weight.	
<i>Pisum sativum</i> (Pea)	7	...	250	50	100	20	80
<i>Guilandina bondu-cella</i>	2	...	400	95	100	24	76
<i>Phaseolus multi-florus</i> (Scarlet-runner)	4	...	300	75	100	25	75
<i>Faba vulgaris</i> (Broad Bean)	5	...	750	195	100	26	74
<i>Mucuna urens</i>	3	...	1000	280	100	28	72
<i>Canavalia obtusi-folia</i>	6	...	400	112	100	28	72
<i>Leucaena glauca</i>	24	...	100	30	100	30	70
<i>Entada polystachya</i>	14	...	800	240	100	30	70
<i>Cæsalpinia sepiaria</i>	5	...	100	32	100	32	68
<i>Cassia fistula</i>	95	Woody	5000	1650	100	33	67
<i>Vicia sativa</i>	10	...	15	5.6	100	37	63
<i>Cajanus indicus</i>	4	...	40	16	100	40	60
<i>Acacia Farnesiana</i>	20	...	150	60	100	40	60
<i>Andira inermis</i>	1	Woody	135	54	100	40	60
<i>Dioclea reflexa</i>	4	Woody	1800	738	100	41	59
<i>Vicia sepium</i>	3 or 4	...	6	2.5	100	42	58
<i>Ulex europæus</i>	4 or 5	...	2.5	1.1	100	44	56
<i>Poinciana regia</i>	40	Woody	3500	1575	100	45	55
<i>Cæsalpinia Sappan</i>	4	Woody	260	130	100	50	50

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II. CAPSULES.

	Char- acter of dry fruit.	Loss of weight after drying in air for weeks or months.				Stated as water-loss or water- percentage.
		Stated in grains.		Stated as a percentage.		
		Moist weight.	Dry weight.	Moist weight.	Dry weight.	
Momordica Charantia	500	75	100	15	85
Blighia sapida (Akee)	1730	346	100	20	80
Scilla nutans	10	2.4	100	24	76
Æsculus Hippocastanum (Horse-chestnut)	1 seeded	700	168	100	24	76
Iris foetidissima	170	42.5	100	25	75
Ipomœa tuba	100	25	100	25	75
Iris Pseudacorus	250	65	100	26	74
Gossypium barbadense	100	26	100	26	74
Primula veris (Primrose)	4	1.2	100	30	70
Datura Stramonium	360	108	100	30	70
Allium ursinum . . .	3 seeded	2.4	0.8	100	33	67
Thespesia populnea . . .	Inde- hiscent	230	76	100	33	67
Swietenia Mahogani (Ma- hogany)	Woody	5800	2030	100	35	65
Hura crepitans . . .	Woody	3200	1152	100	36	64
Hypericum Androsæmum	Inde- hiscent	3	1.1	100	37	63
Viola tricolor	3	1.2	100	40	60
Bignonia (near æquinoc- tialis)	Siliqui- form	1250	500	100	40	60
Arenaria peploides	8	3.3	100	41	59
Ravenala madagascari- ensis	Woody	700	294	100	42	58
Aquilegia (species of) . . .	Folli- cular	10	4.5	100	45	55
Canna indica	100	47	100	47	53

III. BERRIES, DRUPES, etc.

	Family.	Fruit.	Loss of weight when dried in air for weeks or months.				
			Stated in grains.		Stated as a percentage.		Stated as water-loss or water-percentage.
			Moist weight.	Dry weight.	Moist weight.	Dry weight.	
<i>Pyrus Malus</i> (Apple)	Rosaceæ	Berry	900	126	100	14	86
<i>Ribes Grossularia</i> (Gooseberry)	Ribesiaceæ	"	120	18	100	15	85
<i>Tamus communis</i>	Dioscoreæ	"	14	2.5	100	18	82
<i>Opuntia Tuna</i> (Prickly Pear)	Cactææ	"	800	144	100	18	82
<i>Citrus aurantium</i> (Orange)	Aurantiaceæ	"	2400	460	100	19	81
<i>Sambucus nigra</i> (Elder)	Caprifoliaceæ	"	3.3	0.7	100	21	79
<i>Lonicera Periclymenum</i> (Honey-suckle)	Caprifoliaceæ	"	4.8	1.2	100	25	75
<i>Monstera pertusa</i>	Araceæ	"	5.0	1.0	100	20	80
<i>Arum maculatum</i>	"	"	6.1	1.8	100	29	71
<i>Hedera Helix</i> (Ivy)	Araliaceæ	"	5	2	100	40	60
<i>Quercus Robur</i> (Oak)	Amentaceæ	Nut	60	24.0	100	40	60
<i>Prunus communis</i> (Sloe)	Rosaceæ	Drupe	30	8	100	27	73
<i>Sparganium ramosum</i>	Pandaneæ	"	1	0.45	100	45	55
<i>Barringtonia speciosa</i>	Myrtaceæ	Berry	9000	1350	100	15	85
<i>Areca Catechu</i>	Palmaceæ	"	250	80	100	32	68
<i>Cocosnucifera</i> (Coconut)	"	Drupe	60,000	18,000	100	30	70
<i>Acrocomia lasiospatha</i>	"	"	550	200	100	36	64
<i>Arenga saccharifera</i>	"	Berry	600	300	100	50	50
<i>Mauritia setigera</i>	"	"	1000	560	100	56	44
<i>Cocos plumosa</i>	"	Drupe	100	63	100	63	37
<i>Oreodoxa regia</i>	"	Berry	15	10.0	100	66	34
<i>Hyophorbe Verschafftii</i>	"	"	15.5	6.2	100	40	60

Note.—The total amount of water in these fruits can readily be ascertained by applying a small correction to the loss sustained when dried in air. As a rule the air-dried fruits would lose between 10 and 15 per cent. of their weight when exposed to a temperature of 100° C. The corrected result for the air-dried berry of *Tamus communis*, assuming that it lost 12 per cent. of its weight in the oven, would be as follows:—

Moist weight	100
Air-dried weight	18
Oven-dried weight	16
Loss when air-dried	82
Loss when oven-dried	84

The contents of the foregoing tables raise a number of interesting points, and it would be easy to devote some chapters to the details of the experiments, if space allowed and necessity required it. Indeed, not a few of these points will come under our notice when we discuss the relation of parts in the living or moist and in the dead or dried fruit. There are, however, some matters that call for immediate notice. It has already been explained in a note to the tables that a small minus-correction applied to the air-dried weight will give approximately the total water-contents, such as would be indicated by the loss of weight of the fresh fruit when exposed to a temperature of 100° C. The water remaining after drying in air is the water of hygroscopicity, which fruits possess in common with all other vegetable substances, whether living or dead (see Chapter VII).

Another point here claims attention. It is remarkable how much water fruits described as woody in the dry state contain in the full-grown living condition on the plant. Amongst the fruits that in the dried state specially merit the designation of "woody," one would certainly include the long pod of *Cassia fistula*, the large capsule of the Mahogany tree (*Swietenia Mahogani*), and the polycocous capsule of *Hura crepitans* (the Sandbox-tree). Yet each of these fruits, as will be seen in my tables, loses about two-thirds of its weight when allowed to dry in free air in the moist, green, full-grown condition, the water-loss, denoted by the decrease in weight, being respectively 67, 65, and 64 per cent. of the original weight. Although the woody fruits lose less water when dried in air than fleshy fruits, a glance at the tables will show that the difference is usually not great. If fleshy fruits may lose between 70 and 80 per cent. of their weight, woody fruits may lose between 60 and 70 per cent.

But many disturbing influences come into play and prohibit any precise general statement until their effect is determined. This is at once made evident when we perceive that the woody fruits of *Cassia*, *Swietenia*, and *Hura* lose about as much

The large amount of water in living, woody fruits.

Disturbing influences affecting the drying in air of fruits.

water when dried as does the Acorn (*Quercus*), the capsule of *Viola*, and the pods of *Vicia* and *Cajanus*. Then, again, it is apparent that several very different causes have combined to produce the same result in the Coco-nut, the Acorn, and the pod of *Cassia fistula*, all of which lose a similar amount of water, namely, from 60 to 70 per cent. of their weight. Some of these causes will be considered when we come to deal with the relation of parts in a fruit.

The effect of
sugars.

The development of sugars in the ripening berry makes a material difference in the weight of the fruit after it has been dried in air. Elder berries (*Sambucus nigra*), before the sugars are formed, lose about 87 per cent. of their weight, but with the production of sugar their weight during drying is diminished by only 78 or 79 per cent., the saccharine materials being especially hygroscopic and preventing the complete drying of the fruit. The berries of the Honeysuckle (*Lonicera Periclymenum*), which, when the sugars are formed, lose about 75 per cent. of their weight, behave in a similar fashion. In the same way the ripe fruits of the Gooseberry (*Ribes Grossularia*) cannot be dried properly in air on account of the abundance of the sugars. The congealed juice that encrusts the surface of the air-dried berry is very hygroscopic. The ripe fruit loses about 85 per cent. of its weight; but if the sugars are removed by washing, the air-dried materials make up only about 5 per cent. of the weight of the moist berry (see Note 10A of Appendix). The same behaviour is displayed by the berries of *Opuntia Tuna* (Prickly Pear), which, when air-dried, lose 82 per cent. of their weight, but if the sugars are removed by washing, the dry residue of 18 per cent. is reduced to 12 per cent. (see Note 10B of the Appendix).

The seeds of such sugary fruits often remain moist and sticky and require washing for their complete drying. Those of the Pomegranate (*Punica Granatum*), for instance, never dry properly unless previously washed. A good example of the influence of the sugars on the air-drying of fruits is afforded by the different behaviours of the husky coverings of the ripe

drupes of the Coco-nut (*Cocos nucifera*) and of *Cocos plumosa*. In the first case there is a loss of quite 80 per cent. In the second case, where the coverings contain a good deal of sugar, the loss is only about 55 per cent.

As with the sugars of berries, the presence of oil in the pericarp of fruits greatly retards the air-drying process. This explains why, in my experiments, the drupaceous berries of *Oreodoxa regia* (Palmacæ) lost only 22 per cent. of their weight. In the same way, fragments of the pericarp of the Cashew-nut (*Anacardium occidentale*), which contain a caustic oil in abundance, dry but slightly, losing less than 15 per cent. of their weight when exposed to the air.

In connection with the loss of weight sustained by fruits when dried in air, some curious considerations arise from the fact illustrated in the table below, that immature fruits contain more water than mature fruits. Although the data there given refer almost exclusively to immature fruits of nearly the maximum size that are characterised by incompletely developed seeds, they illustrate a process of change that runs through nearly the whole of the fruit's life-history, from the time of its occurrence as a young fruit, until, with maturity passed, the fruit dries up and loses its vitality. But in this respect, namely, in the progressive decrease of the water-contents as they pass from youth to maturity, and thence to the loss of vitality, fruits share the fate of all vegetable substances.

If we regard only the percentage of water in the whole or in the part of a plant, whether stem, leaf, root, fruit, or seed, we can construct a scale beginning with the young growth, containing, we will say 70 or 80 per cent. of water, and ending with the air-dried dead substance that holds only the water of hygroscopicity, amounting only to 12 or 15 per cent., the water which it derives from the air and which it gives up in the oven. Between the initial and terminal stages of this scale there is an ever-progressive decrease in the proportion of water that the living plant-substance yields up when drying to the air. But this progressive decrease in the proportion of the

The effect of oils.

Immature fruits contain more water than mature fruits.

In this respect they illustrate a principle characteristic of the vegetable world.

water-contents differs in character in the earlier and later parts of the period covered by the scale. In the first portion, where we are concerned with the living plant or its part, the decrease in the percentage of water is merely due to the fact that during the building-up processes involved in growth the solids increase more rapidly than the liquid constituents. In the second portion, when the plant or its part is dying and drying, there is an actual loss of water, and this goes on until the plant-substance, like all other dead vegetable materials, ceases to give up water to the air and retains only the water of hygroscopicity.

Such is the rôle played by water in the life of a plant, either entire or in part, as stated in terms of the decrease in the proportion of the water-contents. In active life this decrease, as just observed, is only relative, and is due to the more rapid increase of the solids. When the plant dies it is absolute, and involves the loss of all the water required for the processes of vitality. But between the period appropriated by the living plant or its part and the period associated with death and desiccation, there often seems to be an interval of varying length characterised by repose. This is the rest-period that appears to be claimed by all vegetable life, by the plant in its entirety, and by the plant in its smallest constituent parts. Though it is difficult to point to any plant or any part of a plant that does not seem to undergo this so-called rest-period, I am inclined to think that nature often merely cloaks, but does not suspend the processes of growth. With fruits such a period of repose, if it exists at all, must be very brief; and with the great majority of seeds, which soon lose their vitality on being dried, I should be disposed to believe that the period between the cessation of active growth and the commencement of loss of vitality must be very short.

Such are some of the considerations that present themselves when we reflect that the immature fruit holds more water than the ripe fruit. They illustrate the great significance that lies behind all experiments even of the simplest nature,

such as are represented in the following two tables. The story of the Acorn, viewed from the standpoint offered by the rôle taken by the water-contents, seems to be particularly suggestive, especially in connection with the tendency to vivipary at times displayed, a subject discussed in Chapter XIX. Some of the most fascinating problems bound up with plant-life lie behind the phenomena of the drying fruit; and none are more important than that connected with germination on the plant.

In this respect the story of the decrease in the water-contents of the Ivy berry (*Hedera Helix*), as it grows steadily from the autumn through the winter, finally dropping to the ground in the spring, and often with one or more of its seeds germinating, is particularly interesting. This progressive decrease is clearly shown in one of the following tables. But

TABLE SHOWING THE DIFFERENCE IN THE WATER-CONTENTS OF IMMATURE AND MATURE FRUITS, AS INDICATED BY THEIR LOSS OF WEIGHT WHEN DRIED IN AIR UNDER ORDINARY CONDITIONS.

(By mature fruits are meant those that are full-grown and moist, contain ripe seeds, and show no signs of drying. By immature fruits are usually meant those that have attained nearly the full size and weight, but have seeds with contents not set or incompletely developed. For the berries of *Sambucus nigra* another explanation is required, as is given below.)

	Average weight of moist fruit in grains.		Loss of weight when dried in air stated as a percentage.		Type of fruit.
	Immature.	Mature.	Immature.	Mature.	
<i>Iris Pseudacorus</i> . . .	200	250	85 per cent.	74 per cent.	Capsule.
,, <i>fetidissima</i> . . .	130	170	83 "	75 "	"
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	600	700	82 "	76 "	"
<i>Hura crepitans</i> . . .	3000	3200	86 "	64 "	"
<i>Phaseolus multiflorus</i> .	270	300	82 "	75 "	Legume.
<i>Faba vulgaris</i> (Broad Bean)	650	750	85 "	74 "	"
<i>Guilandina bonducella</i> .	340	400	81 "	75 "	"
<i>Hedera Helix</i> (Ivy) . .	1'7	5'5	79 "	63 "	Berry.
<i>Quercus Robur</i> (Oak) * .	10	60	77 "	68 "	Nut.
<i>Sambucus nigra</i> (Elder) †	3	3	87 "	78 "	Berry.

* The browning acorn is taken as the mature stage (see Chapters XIV and XIX).

† In the case of Elder berries the difference is due to the formation of sugars in the ripening fruit, as explained in an earlier page of this chapter.

the data there supplied only illustrates one of the features in a process that in the Ivy berry often terminates in germination on the plant. Matters more directly relevant to the subject of vivipary in this plant, especially those concerning the growth of the seed and its embryo, will be dealt with in detail in Chapter XIX.

The decrease in the water-contents of a growing fruit naturally involves the increase of the solid constituents. How fruits gain in solids as they grow is well brought out in the general table immediately preceding these remarks, and with

TABLE SHOWING THE GRADUAL DECREASE IN THE WATER-CONTENTS OF ACORNS (*QUERCUS ROBUR*) AS INDICATED BY THEIR LOSS OF WEIGHT IN DIFFERENT STAGES OF THEIR DEVELOPMENT WHEN DRIED IN AIR UNDER ORDINARY CONDITIONS. (The cupule is not included.)

Date of collection.	Condition of fruits.	Average weight of a fruit in grains.	Loss when dried in air, taking the moist fruit as 100.
Aug. 24, 1910	} Firmly attached by living tissue to cupule	10	77 per cent.
Sept. 13, "		32	74 "
" 20, "		46	72 "
" 27, "		50	65 "
Oct. 4, "	do.	55	61 "
" 11, "	Connection slight	51	48 "
" 18, "	Browned; fall at a touch	57	48 "
	After two months, when air-drying complete.	30	00 "
Sept. 4, 1908	Firmly attached to cupule	56	75 "
" 17, "	Still firmly attached	62	68 "
" 30, "	do.	62	54 "
Oct. 6, "	Connection slight; nuts browned.	71	51 "
" 14, "	Browned; fall at a touch	64	43 "
	After two months, when air-drying complete.	40	00 "

This table is only intended to illustrate the decrease in the water-contents. At the same time a rough idea can be formed of the progressive changes in the average weight of an acorn, which is all that the method of the experiment will allow. The acorns of each series were obtained from the same locality. It will be noticed that the acorns of 1908 were considerably heavier and larger than those of 1910. Ten fruits were used in each case. For other data relating to the ripening and drying of the fruit the reader should consult Chapters XIV, XIX, etc.

special detail for the Acorn and the Ivy berry in the two additional tables. These tables speak for themselves, and there is no necessity to push the subject further here.

TABLE SHOWING THE GRADUAL DECREASE IN THE WATER-CONTENTS OF IVY BERRIES (*HEDERA HELIX*) AS THEY DEVELOPED AND MATURED AT REDLAND, BRISTOL, DURING THE WINTER 1908-1909.

(The collections were made by my sister, Mrs H. Mortimer, from the same plant and weighed by her at once, the samples containing from forty to sixty berries. They were weighed again by the author some months after.)

Date of collection.	Condition of fruits.	Changes of weight of an average berry when dried in ordinary air-conditions.			
		Stated in grains.		Stated as a percentage.	
		Moist.	Dry.	Moist.	Dry.
Nov. 9	All green	1'69	0'36	100	21
" 18	"	2'86	0'61	100	21
Dec. 3	"	4'02	0'98	100	24
" 17	Two - thirds green, rest black	4'96	1'46	100	29
Jan. 9	All black	5'44	1'93	100	35
" 24	"	5'50	2'06	100	37
Feb. 21	"	4'10	1'64	100	40
Mar. 19	"	4'02	1'58	100	39
Observation at Salcombe, Devon.					
May 16	"	4'60	2'00	100	43

Note.—The reader is referred to Chapter XIX for other details respecting the growth of the seed and its embryo.

SUMMARY

(1) Some of the most interesting problems connected with plant-life lie behind the phenomena of the drying fruit.

(2) But a comparative study in this direction brings to the front preliminary considerations of importance, more especially those concerned with the lack of true adjustment which prevails in the general classification of fruits and with the comparison of fruits in the different stages of their history (p. 259).

(3) Observation on the drying of fruits shows us that when the systematist speaks of a berry as fleshy and indehiscent and a capsule as dry and dehiscent, he is contrasting a living with a dead fruit (p. 260).

(4) We come also to discover the fallacy that may lie in the distinction between succulent and dry fruits, especially when it implies

a contrast between a moist living fruit that has yet to dry and a fruit that has more or less completed the drying process and is to a greater or less degree devitalised (p. 260).

(5) The tabulated results of the author's observations on the drying of fruits in air indicate that nature does not recognise this distinction between moist and dry fruits, all mature living fruits being moist fruits. The contrast which the systematist draws between the fleshy drupe of *Prunus* and the dehiscent, dried, or drying fruit of *Datura* is not the contrast nature offers. Nature as interpreted through the balance tells us that the full-grown moist and living capsule of *Datura Stramonium* contains just as much water as the ripe drupe of *Prunus communis*, and that the dried and dead open capsule of the one could only be compared with the dead and shrivelled drupe of the other (p. 261).

(6) These misconceptions lead to others. Thus, it is usually implied that dry dehiscent fruits, like typical capsules and legumes, open only when they are ripe, an assumption that involves us in much confusion between the maturing, dehiscent, and drying stages of fruits. How much we may err in this respect is indicated in Chapter XIII, where it is also shown that ripe capsules and ripe legumes are all moist fruits as far as their water-contents are concerned, and that whilst the capsule dehisces in the living, moist state, the legume opens in the dried and dying condition (p. 262).

(7) Amongst the points brought out in the tables are the large amount of water in full-grown, living, woody fruits, and the manner in which the drying of fruits is retarded by the presence of sugars and oils (p. 265).

(8) Some curious considerations also arise from the fact that immature fruits contain more water than mature fruits. But this progressive change in the water-contents as the fruit passes from immaturity, when it contains, we will say, 80 per cent. of water, to maturity, when the amount would be about 70 per cent., and thence on to the drying-stage accompanying its loss of vitality, when it retains only the water of hygroscopicity, probably about 15 per cent., is characteristic of all vegetable matter (p. 267).

(9) At first during active life this decrease is only relative and is due to the more rapid increase of the solids. In the latter stage, when the plant dies, it is absolute and involves the loss of all the water required for the active processes of vitality. The occasional vivipary of the acorn on the Oak and of the seeds of the Ivy berry (*Hedera*) on the plant is in part an expression of the principle that the mature fruit contains less water than the immature fruit (p. 269).

(10) The increase in the solid constituents of a growing fruit as the water-contents decrease is well brought out in the tables, in one table for a variety of fruits, in another with special detail for the acorn and the Ivy berry (p. 270).

CHAPTER XIII

THE DEHISCENCE OF FRUITS

ONE is apt to associate the process of dehiscence with dryish fruits, neither very soft nor very hard, and justly so, because many opening fruits belong to this category. Both the capsule and the legume are classed amongst dry fruits; and the implication often is that their dehiscence is connected with the relief of strain produced by unequal contraction during the drying of the fruit. My observations indicate that this applies more especially to fruits like legumes, that often only dehisce after they have been considerably dried, and that as a rule it does not concern capsules. The incorrect conception seems to be due in the case of capsules to the tendency to regard as one and the same process the loosening of the cohesion between the valves or carpels, which may take place when the green fruit begins to mellow, and their subsequent drying, when the fruit is rapidly losing its vitality. The sudden relief of tensions generated by drying in the latter part of the dehiscence, resulting as it sometimes does in the forcible expulsion of the seeds, produces effects that often emphasise the influence of drying in the latter stages of the process, and is apt to favour the idea that dehiscence is merely a matter of desiccation.

Thus, in *Viola*, the breaking down of the cohesion between the valves is one thing, whilst the subsequent folding inwards of the edges as the valve dries up is another. Whether the "nipping" and forcible propulsion of the seeds are purposive or merely accidental can only be determined after an extensive

The capsule dehisces before drying, and the legume after drying.

Capsules dehiscing under moist conditions where drying is prevented.

Viola.

comparative study of different fruits in all their stages. That which concerns us here is the circumstance that *Viola* capsules will dehisce under moist conditions without any drying whatever, and without any of the display of the results of elastic tension which that process engenders. If we place a detached, full-grown green fruit in wet moss, the first stage of dehiscence, namely, the loosening of the cohesion between the valves, will be accomplished without any drying, whilst the curling in of the edges of the valves will be inhibited.

This is what happened in my experiments on the fruits of the Garden Pansy (*Viola tricolor*); and one may contrast with such results, where dehiscence takes place without any drying, those results for the same plant where drying plays a prominent part in the opening of the capsule, as given below.

THE DRYING AND DEHISCENCE OF A DETACHED RIPE CAPSULE OF VIOLA TRICOLOR, WEIGHING FOUR GRAINS, THE RESULTS BEING STATED IN PERCENTAGES.

Full-grown green fruit (4 grains).	Beginning to dehisce (2·8 grains).	Valves lying back (2·6 grains).	Valves folded on the seeds and dry (1·6 grain).
100	70	66	40

Æsculus Hippocastanum (Horse-chestnut) and *Iris*.

Again, if we take a number of full-grown but still closed capsules of *Æsculus Hippocastanum* (Horse-chestnut) and of *Iris Pseudacorus*, and place some in wet moss and others exposed to the free air on a table, we obtain the following results. In a few days several of those on the table will be found to be opening after losing 25 or 30 per cent. of their weight; whilst those in the wet moss which have not dried at all but have probably added to their weight will be also dehiscing. The detached capsules of *Iris fetidissima* illustrate the same thing more forcibly, since they dehisce in wet moss, but fail altogether to open when allowed to dry. Drying, therefore, though it develops strains, the relief of which ends in the dehiscence of fruits, is not a necessity for their opening. It is

essential in the latter stages, if the parts of the fruit are to acquire the elasticity concerned in the forcible expulsion of the seeds, but it is not necessary for seed-liberation. Seeing that most fruits liberate their seeds without forcibly discharging them in this manner, it may be doubted whether we should specially regard such violent propulsion as purposive, determined as it is largely by the degree of dryness of the air. However this may be, it is evident from the above experiments that other factors than those concerned with drying go to determine the dehiscence of fruits.

Though the phenomena are physical in origin, writes Pfeffer (*Physiology of Plants*, iii. 146-153), the development of the requisite physical conditions is a physiological problem. The required instability, when mechanical agencies of external or of internal origin may release the dehiscing organism, is produced by growth, the requisite tissue-strains and the conditions for their release being prepared by the vital activity of the organism. The distinction which he draws between internal and external agencies in the opening of dehiscent fruits coincides with one of the principal differences between the modes of dehiscence of legumes and many capsules, as indicated by my observations. Whilst in the one case the opening of the capsule is often brought about through the distension of its walls by the growth of its seed-contents, in the other the dehiscence of the legume is usually caused by the strain generated in the drying process. In the capsule the dehiscence, however arising, corresponds with the maximum growth of the fruit. In the legume it happens at a much later stage, namely, after its biological connection with the parent has been more or less severed, and when it has lost the greater part of its water by drying, and in consequence its vitality. Regarding the difference between the two processes from merely a physical standpoint, we can say that whilst the capsule dehisces and dries, the legume dries and dehisces. By removing a single letter we can at the same time express the biological distinction by saying that whilst the capsule dehisces and dies, the legume dies

Prof. Pfeffer
on de-
hiscence.

The author's
observations.

The capsule
dehisces and
dries. The
legume dries
and dehisces.

and dehisces. With the capsule, therefore, the mechanism of dehiscence is concerned with a living fruit. In the legume it has to do with a dead one.

The preliminary mellowing stage.

In both the green capsule and the green legume there is generally a preliminary mellowing stage, corresponding, as shown in Chapter XI, to the ripening of the berry ; but it may be transient or disguised by other changes, more especially with the legume. It marks the completion of active growth and indicates seemingly the commencement of the severance of the biological connection between the fruit and the parent. In this mellowing stage the green fruit often assumes a yellowish tinge or a paler hue, and its tense, turgid appearance gives place to one of relative flaccidity. Its firm, rigid walls become softer and more yielding, and the cohesion along the sutures is loosened. This is best exemplified in the capsule, though the same may be noticed in legumes, as in the Pea. But whilst with the capsule the immediate result is the dehiscence of the fruit, with the legume no such effect is produced at that stage, and dehiscence occurs at a much later stage as a relief from the tension produced from outside by the drying up of the pod.

Observations on the dehiscence of capsules on the living plant.

I will now refer to some of my observations on the opening of capsules on the living plant, and will begin with *Iris foetidissima*. This plant, growing as it often does in more or less shady woods, offers one a better chance of eliminating the drying factor than does *Iris Pseudacorus*, which frequents more exposed situations. Though the mellowing stage is not so easily recognisable as in the species last named, we can detect the approach of dehiscence in the lessened turgidity of the green fruit and in its paler hue. The capsules, when they display the earliest signs of their opening (a slight separation of the valves at and near the apex) are quite moist fruits and show no signs of drying. But, once begun, the process is rapidly completed by drying, and in a few days the valves stand well back, exposing the bright scarlet seeds. That the first rupture is due to some cause

Iris foetidissima.

acting from within, such as the pressure of the seed-contents, is highly probable. Full-grown fruits placed in water and in wet moss commenced to dehisce in a few days, whilst others left to dry on a table made no effort to open after prolonged drying.

With *Iris Pseudacorus* careful observation of the living plant convinced me that dehiscence as a rule occurs in moist, mellowing fruits, that is to say when the green capsule assumes a yellowish tinge. Although, as already observed, the detached fruits will dehisce in wet moss, this does not exclude altogether the participation of the drying factor in the plant's natural station by the water-side, where it is fully exposed to the sun. If fruits dehisced in my experiments without drying, some of them also opened after they had lost about 25 per cent. of their weight exposed on my table. Nature does not follow formularies in such matters; and though internal causes mainly determine the early dehiscence, we cannot entirely disregard the influence of external conditions. The stages in the history of the dehiscence of fruits normally maturing in September would seem to be as follows:—

Iris Pseudacorus.

- (1) The full-grown green capsule, firm, full, and turgid;
- (2) The capsule mellow, becoming yellowish and rather softer, which results in loosening the cohesion between the valves;
- (3) The dehiscence begins, determined by the pressure of the seed-contents, but aided by exposure to the sun and by buffeting in the wind;
- (4) The rapid drying of the fruit and the full exposure of the seeds.

The results of one method of proving that capsular fruits dehisce in the moist condition are given in the subjoined table for *Iris* and for the Horse-chestnut. Here we find that the fruit showing the first signs of dehiscence loses but slightly less in weight when dried in air than does the full-grown moist fruit with matured seeds that has not begun to open.

A proof that capsules dehisce in the moist condition.

TABLE SHOWING THE LOSS OF WEIGHT WHEN DRIED IN AIR OF FULL-SIZED, MOIST, CAPSULAR FRUITS, BOTH BEFORE DEHISCENCE AND IN THE EARLIEST STAGE OF DEHISCENCE, THE DEHISCING FRUITS BEING GATHERED IN THAT CONDITION FROM THE PLANT.

	Full-sized fruits before dehiscence.	Fruits beginning to dehiscence.
<i>Iris Pseudacorus</i>	74 per cent.	70 per cent.
<i>Iris foetidissima</i>	75 „	73 „
<i>Æsculus Hippocastanum</i>	76 „	69 „

Note.—The average was taken of from five to ten fruits in each case.

But it is often very difficult, by observing capsular fruits on the plant, to eliminate the drying factor; and the most we can often say in such cases is that dehiscence takes place in the living fruit before the drying is very evident. In the case of *Scilla nutans*, for instance, we find the full-grown green capsule in a condition of strain, not, however, on account of the pressure of the enclosed seeds, since they only partly fill the cells, but through the turgidity produced by active growth. Though green and moist, it ruptures with a “pop” when squeezed between the fingers. A little later the fruit becomes paler, looks a little dryer, and its turgid appearance has disappeared. If we press it gently, there is no longer an elastic resistance, and the valves, though still in position, are seen to be partially disconnected. The fruit has dehisced, although still green and fairly moist, and only the pressure of the finger reveals what has occurred. Here it seems impossible to separate the dehiscence from the early stage of drying; and yet the loosening of the cohesion between the valves was probably effected in the mellowing stage when the firm, turgid green fruit became softer and almost flaccid. On physiological grounds I would suppose that the dehiscence of a green fruit in active vitality could never be normally produced either by internal or external causes, and that dehiscence could only occur after the biological connection with the parent begins to be severed. This I take to be the mellowing stage of fruits,

Scilla nutans.

The normal dehiscence of an actively growing fruit impossible for physiological reasons.

pronounced in berries, much less evident in capsules, and often more or less disguised, or very slight, in legumes.

It is likely that the behaviour of the fruits of *Scilla nutans* is typical of many capsules but partially filled by their seeds. We will take the case of *Stellaria Holostea*. Here, as with fruits in general, the development of the fruit is far in advance of the seeds. In its early stage, when about the size of a small pea, the capsule is little more than an empty bladder, since the young seeds do not occupy one-tenth part of the cavity. But when the green fruit is full-grown, it is loosely but not entirely filled by its soft white seeds, so that there is no pressure on the capsular walls from within. Afterwards, as the fruit dries, the seeds shrink and only half fill it. The valves, though still in position, become disconnected at the edges, as a slight pressure of the finger will show; but there seems to be no reason why they should be sundered in the drying process, since they remain in position; and it would appear probable that the coherence between their edges was broken down, as in *Scilla nutans*, when the biological connection of the fruit with the parent first began to fail.

*Stellaria
Holostea.*

Assuming that the first preparation for dehiscence is accomplished when the capsule ceases active growth and begins to mellow, then we perceive that the next cause of the actual disconnection of the valves may vary according as the seeds completely or only partially fill the cavity. In the first case, as with *Iris*, the capsular walls, owing to the loosening of the connection between the valves, are no longer able to respond to the pressure of the seed-contents by increased growth. They yield at the weakened sutures and the fruit dehisces, the valves as they wither and dry falling back and exposing the seeds. On the other hand, when the capsule is not full of seeds, so that there is no distension or pressure on the walls from within, the cohesion between the valves is still loosened in the mellowing stage, but they remain in position during the early part or most of the drying.

The dehiscence of completely filled and partly filled ripe capsules.

A few remarks may now be made on some other capsules.

- Arenaria.** Those of *Arenaria peploides* behave like the fruits of *Stellaria Holostea* above described. Although detached capsules of
- Datura.** *Datura Stramonium* lost 18 per cent. of their weight in my experiments before they dehisced, it is highly probable that, like those of *Iris*, when kept in wet moss they would have opened without any drying at all. In the same way the moist
- Primula.** mature fruits of the Primrose (*Primula veris*), after lying one night on my table, were found to be dehiscent and to have lost about 20 per cent. of their weight. But observation of the capsules on the living plant led me to consider that the first stage in dehiscence begins still earlier in the drying process. It is singular that the normal opening of the Primrose capsule at the top may be prevented by making a hole in its base. Appended are the results of my observations on the dehiscence of detached mature capsules of *Primula veris* and *Datura Stramonium*, when allowed to dry on my table. Though obviously such experiments are not carried out under nature's conditions, their results will serve to illustrate the early opening of capsular fruits.

THE DRYING IN AIR AND DEHISCENCE OF DETACHED RIPE CAPSULES OF DATURA STRAMONIUM AND PRIMULA VERIS.

	Average weight in grains of a ripe moist fruit.	Loss of weight, the ripe unopened fruit being taken as 100.		
		Before dehiscence.	When dehiscence begins.	After the drying is complete.
<i>Datura Stramonium</i> . . .	35.0	100	82	30
<i>Primula veris</i>	3.5	100	80	30

Aquilegia.

In a species of *Aquilegia* growing in my garden the opening of the follicles took place shortly after the period of maximum growth. The green follicles are completely closed; but as they ripen they acquire a purplish tinge and gape open at the base before normal dehiscence occurs. In such mature fruits the cohesion at the ventral suture becomes very slight, and a slight increase of the tension due to some external cause would

bring about the separation. I found that the follicles just beginning to dehisce were usually the heaviest.

Dehiscence may take place in the most watery of capsules, as with those of *Momordica*, where 95 per cent. of the fruit (excluding the seeds) consists of water, and in the hardest and most ligneous of capsules, as with those of Mahogany (*Swietenia Mahogani*), where the woody walls hold only about 66 per cent. of water and are 10 millimetres or nearly half an inch thick. The dehiscence of the fruits of a species of *Momordica* observed by me in Jamaica (seemingly a cross between *M. Charantia* and *M. Balsamina*) was quite regular, and took place when the fruits were ripe and moist. After the seed-contents were removed, a ripe fruit not yet beginning to open lost 94 per cent. of its weight when dried in air, whilst a similar fruit just beginning to dehisce lost 91 per cent. The first stage in dehiscence seems to be due to the tension produced in the walls of the softening fruit by its contents. With the woody fruits of Mahogany the exact stage at which dehiscence occurs on the tree is not easy to determine; but one can get an approximate idea. The full-grown green fruits, which seem to average about four-fifths of a pound in weight (5600 grains or 363 grammes) lose about two-thirds of their weight when detached and allowed to dry for several months, but they begin to open when they have lost about one-fourth of their weight.

Contrast in the water-contents of capsules.

Momordica.

Mahogany.

DRYING IN AIR OF A DETACHED, GREEN, FULL-GROWN CAPSULE (NOT YET DEHISCING) OF MAHOGANY (*SWIETENIA MAHOGANI*), INCLUDING SEEDS.

Condition of fruit.	Weight in grains.	Percentage.
Green, full-grown, not yet dehiscing .	5900	100'0
The same fruit beginning to dehisce on my table	4370	74'1
The same fruit after drying for months	2030	34'4

Dehiscence will probably occur also if drying is prevented, as shown below.

These results for the drying of a detached fruit of Mahogany are, as far as dehiscence is concerned, very much the

same as those obtained for detached fruits of *Iris Pseudacorus* and *Æsculus Hippocastanum* (Horse-chestnut), which dehisced in my room after losing 25 or 30 per cent. of their weight. It has, however, been shown that in both these cases dehiscence occurred in wet moss when drying was prevented, and it is very probable that Mahogany capsules would behave in the same way.

In the above experiment the fruit was dried in the entire condition. Closely similar results were obtained in drying a fruit that had been taken to pieces. The original total weight of the green fruit was 5576 grains, and the weight after the drying-in-air was completed was 1996 grains, the proportions being as 100·0 to 35·8.

Ravenala.

The dehiscence of the fruits of *Ravenala madagascariensis* (Traveller's Palm), as observed by me in plants growing near the rest-house on the Grand Etang in Grenada, presents another type of the opening of capsular fruits. We are here concerned with a sub-drupaceous capsule displaying loculicidal dehiscence. Within the outer moist husk is a bony endocarp or "stone," which even in the fresh fruit requires a heavy blow to break it, and is 5 or 6 millimetres thick. The dehiscence of this fruit raises a number of questions which are dealt with in other chapters. Not the least important of them are the proportion of parts and their several water-contents, and especially the failure of the young seeds, which is here quite phenomenal.

Its dehiscence.

With regard to the failure of the young seeds, reference will also be made to the subject in Chapter XVI. Here I will merely allude to it in connection with the fruit's dehiscence. The full-sized seeds vary from 9 to 15 millimetres in length; but there is only room in each of the double spaces of the three compartments for from three to five, making a possible total ranging from eighteen to thirty seeds. But even this is often never reached. The fruit figured in Schumann's monograph below referred to probably did not contain more than fifteen seeds. Amongst those fruits examined by me there were not uncommonly only one to three full-grown seeds in each valve, or from three to nine or ten in all. All the rest of the fruit-cavity

is occupied by numerous aborted seeds, 3 to 5 millimetres long, and varying from twenty or thirty to forty or fifty in number.

This tremendous waste, not of ovules, but of seeds that could find no room for further development, plainly indicates the existence of a great tension within the living fruit. If the stony walls by their pressure are able to prevent the proper growth of all but a very few seeds, they are subjected in their turn to the opposing strain of the expanding seeds; and in the end the seeds are successful in rupturing the walls, though too late for the maturation of most of them. This is evidently what happens on the tree, since it is the moist fruits that are found dehiscing. The first stage in the dehiscence of *Ravenala* fruits is therefore due to the expansive force of the growing seed, and drying does the rest. One may note in passing that the genesis of the thick, tough walls of this and other capsular fruits may lie in its being a response to the expanding pressure of the growing seeds.

That drying is a potent factor in the completion of the process is shown in the behaviour of the "stones" of *Ravenala* when allowed to dry after being removed from ripe, unopened fruits. They begin to split loculicidally when they have lost about 15 per cent. of their weight, but some also split septically at the apex of the valves, the loculicidal dehiscence ultimately prevailing. The loss of water during the drying in air of the entire fruit may here be given, though the subject is also dealt with in tables given in Chapters XII and XIV.

RESULTS OF DRYING IN AIR A FRESH FRUIT OF RAVENALA
MADAGASCARIENSIS.

	Fresh fruit.		Air-dried fruit.		Loss of weight in drying.
	Weight in grains.	Percentage of entire weight.	Weight in grains.	Percentage of entire weight.	
Skin and husk . . .	268	37'2	49	16'3	81'7 per cent.
Stone with seeds . . .	452	62'8	252	83'7	44'2 "
Entire fruit . . .	720	100'0	301	100'0	58'2 "

The loss of weight of the stone without the seeds would be about 40 per cent.

Excellent illustrations of the fruits of *Ravenala* are given by Schumann in his monograph on the Musaceæ (*Das Pflanzenreich*, iv. 45). He, however, figures only the dry fruit, as his description of *eine holzige Kapsel* would also imply. The ripe fruit before dehiscence is yellowish and moist, and it is only when it dehisces, dries, and turns brown that the woody texture is disclosed.

The contrast above drawn in the case of such different kinds of capsular fruits as *Momordica*, with 95 per cent. of water, Mahogany, with about 66 per cent., and *Ravenala*, with about 62 per cent., leads one to compare these extreme examples with other capsules as regards their water-contents. The subject is discussed for fruits in general in the following chapter. The data tabulated below are merely intended to illustrate the great variation in the amount of water held by capsular fruits when full-grown, and before they begin to dehisce and dry, the seeds being for the convenience

THE WATER-CONTENTS OF FULL-GROWN CAPSULES BEFORE DEHISCENCE AND DRYING COMMENCE, THE SEEDS BEING EXCLUDED.

	Weight in grains of full-grown capsules, excluding seeds.	Water-contents stated as a percentage.	
		Loss when dried in air without heat.	Total, including the water driven off at 100° C. (Estimated: see below.)
<i>Momordica Charantia</i>	600	94·0 per cent.	95·0 per cent.
<i>Scilla nutans</i>	7	93·0 "	94·0 "
<i>Datura Stramonium</i>	220	87·0 "	89·0 "
<i>Iris Pseudacorus</i>	130	86·4 "	88·4 "
<i>Ipomœa tuba</i>	35	86·0 "	88·0 "
<i>Arenaria peploides</i>	1·7	84·6 "	87·0 "
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	440	84·0 "	86·3 "
<i>Primula veris</i> (Primrose) . . .	1·7	83·8 "	86·0 "
<i>Canna indica</i>	36	82·6 "	84·8 "
<i>Iris foetidissima</i>	70	78·7 "	82·0 "
<i>Aquilegia</i> (species of)	17	76·8 "	80·0 "
<i>Thespesia populnea</i>	150	76·3 "	79·3 "
<i>Swietenia Mahogani</i> (Mahogany)	4800	62·6 "	66·3 "
<i>Ravenala madagascariensis</i> *	700	58·2 "	62·5 "

* The seeds are here included, but their influence on the total result is small.

of comparison excluded, except in one case there explained. In spite of the contrast between the fruits of *Momordica* and *Scilla* on the one hand, and those of *Swietenia* and *Ravenala* on the other, the driest of these mature fruits contain a large amount of water.

Notes on the above table.—The total water of the fruit as given in the last column is estimated by applying a correction to the air-dried residue. Although the result is only approximate, the limits of error, as will be seen, are small. The water driven off in the oven after living vegetable substances have been air-dried is the water of hygroscopicity possessed in common by both living and dead matter (see Chapter VII). According to my observations, this varies usually from about 10 per cent. for air-dried, stony fruits to about 15 per cent. for loose-textured, air-dried fruits, such as ordinary legumes, capsules, and nuts, the seeds being excluded. Thus, in the case of *Momordica*, the air-dried residue of 100 grains of fresh material would weigh 6 grains. In the oven, exposed to a temperature of 100° C., this residue would at the most lose 15 per cent. of its weight and would be reduced to nearly 5 grains, so that the total water in the fresh material would amount to about 95 per cent. In the same way, if, as is probable, the air-dried Mahogany capsule lost 10 per cent. of its weight in the oven, the air-dried residue of 37.4 grains out of 100 grains of fresh material would be reduced to 33.7 grains, so that the total water held by a living Mahogany capsule, excluding the seeds, would amount to 66.3 per cent.

It will have been gathered from the preceding remarks, as well as from the indications afforded in the table just given, that when we speak of a capsule as a dry fruit, we have usually in our mind dehiscent capsules, which have been more or less completely severed from the parent as far as the biological connection is concerned. Dehiscent capsules now appear as dead or dying fruits; and although even the toughest and most ligneous among them hold a considerable amount of

Dehiscent
capsules,
being dead
or dying,
belong only
to the
herbarium.

water when full-grown and before dehiscence on the plant, as dehiscing fruits they give up the greater part of it to the air, only retaining what is common to both dead and living organised vegetable substances, the water of hygroscopicity. All dehiscing capsules, whether they originally possessed in the full-grown, unopened condition on the plant as much as 94 or 95 per cent. of water, as in *Scilla* and *Momordica*, or as little as 62 or 66 per cent., as in *Ravenala* and Mahogany, should be classed with dry fruits when they present themselves in the act of freeing their seeds on the plant. It is very questionable whether the expression "dry fruit" has any significance except for the herbarium. Consistently applied, it has no biological value, since the living connection with the parent plant has been severed.

Let us take the dry, dehiscing fruits of *Canna*, *Iris*, and *Datura*, which, as we observe them on the plant, certainly deserve that appellation, though they have lost their vitality. When full-grown on the parent and ready to dehisce, they contain (excluding the seeds) from 80 to 90 per cent. of water; and their soft seeds, as shown by actual experiment on those of *Iris Pseudacorus*, are able to proceed at once with germination without the interruption of a rest-period. Such are the fruits with which the student of the living plant is chiefly concerned. The dry, dehiscing capsule belongs only to his herbarium. So it is with legumes, as will subsequently be shown, and so it is with the shrivelling berry. All that is purposive ends when a fruit has passed its prime. The fruit dies, let it be a capsule, a legume, or a berry; and the mode of liberation of its seeds depends on structural characters that were developed when it was a part of a living plant, and could have had no possible concern with the escape of the seeds from a dead fruit. All appearances of adaptation to seed-dispersal in fruit-dehiscence are delusive and based on a one-sided view of the subject. We observe all those cases where Nature seems to give her aid and ignore the multitude of others that she seems

Structural characters cannot be concerned with the liberation of seeds from a dead fruit.

to leave alone. Nature, as we should read her story, is indifferent to all. The distribution of seeds by dehiscing fruits thus presents itself as determined by the laws controlling the disintegration of dead organised matter; and in this disintegration the loss of the water necessary for the fruit's vitality occupies an early stage. It is with the drying of fruits biologically severed from the parent plant that the discharge of seeds by capsules, legumes, and other similar fruits is usually connected.

As previously pointed out, the typical dehiscence of legumes occurs at or near the close of the drying process. (The opening can be easily prevented by placing the fruit in wet moss, the valves ultimately falling apart through the decay of the connecting tissues.) If, then, dehiscence takes place in a capsule in a living fruit, it takes place in a legume in a dead fruit; and all the objections urged in the case of a capsule against regarding the propulsive liberation of seeds as a special adaptation apply even more forcibly to the legume. Late dehiscence is evidently characteristic of all those numerous legumes, with which the reader will be familiar, where the dry valves spring apart suddenly (throwing the seeds often some distance) and then coil up spirally. It is likely, as in the capsule, that the first loosening of the connection between the valves takes place when the fully developed green legume begins to soften or mellow, a stage marking the beginning of the severing of the biological connection with the parent and the ushering in of the drying process. But though such a change is often more or less disguised in legumes, it may be recognised at times in the paler green colour, and more conspicuously in those cases where, as with *Cesalpinia sepiaria*, the green fruit assumes a yellowish tinge. The drying pod generally darkens or blackens, as in *Vicia*, *Lathyrus*, *Cesalpinia*, *Ulex*, etc.; but there are whole groups, as with *Canavalia*, where the fruit as it dries becomes lighter in colour and ultimately has a nondescript, parchment-like appearance.

The dehiscence of a legume is the dehiscence of a dead fruit.

Method of determining the stage at which dehiscence of legumes occurs, such as those of *Vicia*, *Ulex*, and *Cæsalpinia*.

As illustrating the dehiscence of typical legumes, I will take the behaviour of the pods of *Vicia sativa*, *Ulex europæus*, and *Cæsalpinia sepiaria*, as determined by the balance. The plan adopted was similar to that followed in the case of capsules like those of *Viola*. The total loss of weight by drying of the detached, full-grown green fruit was first ascertained and then the loss of weight during parts of the process. Thus with *Viola* capsules I found the loss of weight before and after dehiscence began. With the legumes I checked the total loss of weight during the drying of the green fruit by ascertaining the average loss of weight after and before the pod had blackened. By combined observation on these lines of the detached fruit and of the fruit on the plant it is not difficult to obtain an approximate result. With *Vicia* and *Ulex* the final loss of water in the closing stage of the dehiscence immediately resulting in the elastic opening of the pod was determined by placing the darkened or blackened, nearly dry pods, under a glass in the sun, when they would all dehisce in an hour, and the weights before and after the experiment were then compared.

The results given for the three typical legumes in the table below are closely similar. We there see that the full-grown moist pod on the plant loses on the average 59 per cent. of its weight before dehiscence occurs, and that the subsequent loss of weight is small, the total loss in drying amounting to about 62 per cent.

TABLE ILLUSTRATING THE STAGE IN THE DRYING PROCESS AT WHICH THE DEHISCENCE OF LEGUMINOUS PODS OCCURS.

	Average weight of a green pod in grains.	Changes in weight during drying, the full-grown moist pod being taken as 100.			
		Green.	After turning black.	Still closed.	After dehiscence.
<i>Vicia sativa</i>	15'0	100	50	39'0	37'6
<i>Ulex europæus</i>	2'3	100	50	45'0	43'0
<i>Cæsalpinia sepiaria</i>	110'0	100	...	38'0	33'0

One might mention a number of other legumes where, although the balance was not employed in this connection, it was evident that dehiscence occurred when the drying in air was far advanced, such as *Guilandina bonducella* and *Poinciana regia*, the last tardily dehiscent.

The transverse dehiscence of legumes into closed joints or articles also takes place towards the close of the drying process. I am most familiar with this form of opening in the case of *Entada scandens* and *E. polystachya*. In this genus, to employ the description employed by Grisebach in his *Flora of the British West Indian Islands*, the legume is "flat-compressed, the joints separating from each other and leaving a persistent, continuous border, the replum." The pods, when the drying is far advanced, break up on the plant into closed joints, each joint enclosing a single seed. With *Entada polystachya* this is generally preceded by the scaling off of the epidermis. If the epidermis is persistent, as happens at times, the pod remains entire. The ultimate liberation of the seed is affected by the decay of the joint.

The transverse dehiscence of *Entada* pods.

As far as the mode of dehiscence is concerned, the remarkable polycoccous capsular fruit of *Hura crepitans* might be almost described as composed of a number of single-seeded legumes arranged around and attached to a central axis. The rupturing of the cocci takes place in the last stage of the drying of the fruit. A fruit, seemingly dry, but displaying the earliest signs of the splitting of the cocci, was placed in a box and left in a warm corner. After the dehiscence was complete I found that the fruit had lost about 8 per cent. of its weight in the process. This fruit, which contained fifteen cocci, weighed 1233 grains, and I was able to estimate its weight in the green condition from the following data:—

The dehiscence of *Hura crepitans*.

Actual weight of a green fruit with	14	cocci =	3062.5	grains.
"	"	"	16	" = 3281.2 "
Estimated	"	"	15	" = 3172.0 "

This reliable estimate of its weight in the green, full-grown condition enabled me to complete the history of its dehiscence

by means of the balance. As shown in the results below tabulated, the stage in the drying process at which dehiscence occurred corresponds closely with that obtained for typical leguminous pods of the genera *Vicia*, *Ulex*, and *Cæsalpinia*, as before given.

DRYING AND DEHISCENCE OF A FRUIT OF *HURA CREPITANS*.
(See above for explanation.)

Full-grown green fruit (estimated).		On the point of dehiscing.		After dehiscence.	
Weight in grains.	Percentage.	Weight in grains.	Percentage.	Weight in grains.	Percentage.
3172	100	1233	38·9	1137	35·8

But the resemblance between a coccus of *Hura crepitans* and a leguminous pod is not merely concerned with the stage at which dehiscence occurs, but also extends to the mode of the dehiscence. Each woody coccus splits along the back more or less completely into two valves, whilst at the same time it detaches itself with violence from the central axis and carries the seed away for many yards. After the rupture each valve displays a very slight spiral twist, thus indicating that the mechanism of dehiscence is similar to that of the legume, which after its sudden opening shows two spirally twisted valves.

SUMMARY

(1) One is apt to associate the process of dehiscence with dry fruits, and both the capsule and the legume are usually classed among dry fruits; but the author's observations indicate that this association applies more especially to fruits like legumes that usually only dehisce after they have almost completed the drying process, and that as a rule it does not concern capsules. Whilst the legume dehisces after drying, the capsule dehisces before drying begins.

(2) The author's results bring him into line with the view expressed by Professor Pfeffer that whilst the phenomena of dehiscence

are physical, the development of the requisite physical conditions is a physiological problem.

(3) Yet the different behaviour of capsules and legumes illustrates the difference between external and internal causes in the dehiscence of fruits. Whilst with the capsule dehiscence takes place in the ripening fruit as a relief to the tissue-strains developed by growth, in the legume dehiscence usually presents itself as a relief to the tensions developed by drying. Whilst the capsule dehisces and dries, the pod dries and dehisces, the mechanism being concerned in the first case with a living fruit and in the second case with a dead one. Amongst the capsular fruits especially studied in this connection were those of *Æsculus*, *Arenaria*, *Datura*, *Iris*, *Primula*, *Scilla*, *Stellaria*, and *Viola*.

(4) Dealing particularly with capsules, it is considered that the first step in the relief of the strain produced by active growth is promoted by the loosening of the cohesion of the valves affected in the mellowing stage of the full-grown moist fruit. It is held that the normal dehiscence of an actively growing fruit is physiologically impossible, and that dehiscence could only occur after the biological connection with the parent begins to be severed in the mellowing process. The nature of the next stage depends on whether the seeds completely fill the fruit cavity, as in *Iris*, or only partially fill it, as in *Scilla* and *Arenaria*. In the first case the capsular walls, owing to the loosening of the connection between the valves, are no longer able to respond to the pressure of the seed-contents and gape widely during the subsequent drying process. In the second case the drying completes the loosening begun in the mellowing stage, but the valves remain more or less in position.

(5) Dehiscence may occur alike in the most watery of capsules, as in *Momordica*, where the fruit-case holds 95 per cent. of water, and in the hardest and most ligneous of capsular fruits, as with Mahogany (*Swietenia*), where the water-percentage is 66, the dehiscence being carried on in each case on the same regular plan as in *Iris* and in the Horse-chestnut (*Æsculus*). The dehiscence of the Mahogany fruit is especially described, as well as that of *Ravenala*, another type of woody capsule, in which last special questions are raised.

(6) The contrast just drawn between the water-contents of the pericarp or fruit-case of fleshy and woody capsules leads to the discussion of a number of observations on different fruits, and stress is laid on the point that even the driest-looking and most ligneous of capsules hold more than 60 per cent. of water in the full-grown living state. When, therefore, we speak of a capsule as a dry fruit, we really have in our minds the dry dehisced fruit that has lost its vitality. Dehisced capsules thus appear as dead or dying fruits; and the expression "dry fruit" has in their connection no biological significance

for the student, the dry dehiscent capsule belonging only to his herbarium. It is futile for him to look to the structural characters of a dead capsule for evidence of adaptation to the dispersal of seeds. The living fruit alone should be his study. The fruit dies, and the mode of liberation of its seeds depends on structural characters that were developed when it was part of a living plant and could have had no possible concern with the ultimate escape of the seeds from a dead capsule. All that is purposive ends when a fruit has passed its prime.

(7) In reference to the late dehiscence of legumes at or near the close of the drying process, as compared with the early dehiscence of capsules which occurs at or near the commencement of the same process, it is pointed out that if dehiscence takes place in a capsule in a living fruit, it occurs in a legume in a dead fruit, and that all the objections urged in the case of a capsule against regarding the propulsive liberation of seeds as a special adaptation apply even more forcibly to the legume.

(8) The late dehiscence of legumes is then illustrated by the typical cases of *Vicia*, *Ulex*, and *Cæsalpinia*.

(9) Finally, the transverse dehiscence of some legumes is briefly referred to; and the dehiscence of the polycocous capsule of *Hura crepitans* is described in detail; the behaviour of the opening fruit being that of a number of single-seeded legumes around a central axis.

CHAPTER XIV

THE PROPORTION OF PARTS IN FRUITS

THE relation in weight between the pericarp and the seeds in the different stages of a fruit's history now claims our attention. This involves not merely a comparison of parts in the various states, but a detailed examination of the shrinking process which the moist, full-grown fruit has to undergo in entering the air-dried state.

Amongst the first questions that offer themselves in an investigation of this kind is that concerned with the respective values of the moist and dry fruit for such comparisons. The moist condition is naturally the most important, since the fruit-covering or pericarp and the seed are still actively functioning, whilst in the dry condition the fruit-case is dead and the seed has its vitality suspended. It is true that the systematist often employs the last-named condition of the fruit; but he has been under the whip of necessity; and if by so doing he has at times confused the issues as regards the homology of fruits, he has been constrained by the circumstances of his investigation. Yet it behoves us all the more to keep the living fruit always in our mind. By so doing we can best hope to avoid those false analogies and deceptive contrivances which are so apt to be accepted as adaptive when we deal indiscriminately with dead and living fruits.

The subject, however, is a very complex one, and Nature herself does not always aid us by bringing the several processes concerned in the maturation of fruits and seeds into a final relation with each other. Thus, as already pointed out in

The respective values of moist and dry fruits.

Chapter XI., the seeds shrink in the ripening berry. Then, again, we shall see later on in this chapter how in the Acorn (*Quercus*) the seed often continues its growth after the fruit-shell has ceased to add to its weight and has begun to dry ; whilst with the Coco-nut, when the husk of the drying fruit is losing pounds in weight, the hard shell and the albumen increase considerably in amount.

The method of investigation as illustrated in the case of *Barringtonia speciosa*.

The method of investigation usually adopted may be best illustrated in the case of the large husky fruits of *Barringtonia speciosa*, the experiments covering many weeks. (The materials, it should be remarked, were allowed to dry in my room in Grenada, except in the early stage of the drying process, when they were exposed for a few hours daily in the sun.) The first step consisted in determining the shrinking ratio of the moist, full-grown fruit as shown by the difference in weight in the moist and dry conditions. There were three ways of obtaining this result :

- (1) By comparing the average weights of moist and dry fruits ;
- (2) By drying the moist fruit in the entire state ;
- (3) By drying separately the parts of the moist fruit, namely, the husky pericarp and the seed.

By employing these three methods the following results were obtained for *Barringtonia speciosa* :—

Method.	Shrinking ratio, taking the moist fruit as 100.	
Average of moist fruits (15 to 21 ounces), and of dry fruits (3 to 5 ounces)	100	22
Drying the entire fruit	100	16
Drying the fruit in parts	100	13

The shrinkage of the fruit in the entire condition.

On account of the considerable variation in the size and weight of the fruits of *Barringtonia speciosa* the results supplied by the first method could only be regarded as roughly approximate, and in consequence they were used merely as a check. The drying of the fruit in parts was deemed to give

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results in excess of what would happen under natural conditions which would be best imitated in the method of drying the entire fruit. One or two reasons led me, when accepting the result of the second method, to reduce it slightly, and the shrinking ratio of 100 to 15 for the fruit was finally adopted.

The next step was to determine the separate shrinking ratios for the pericarp and the seed of the moist fruit. In spite of its husky appearance, the pericarp, like the husk of the coco-nut, contains a very large amount of water. Two plans were followed here, as below described.

The shrinkage of the separate pericarp and seed of *Barringtonia speciosa*.

- (1) The relative weights of the husk and seed of the moist and dry fruits were obtained, and the results were applied to the shrinking ratio of the entire fruit as above ascertained. In this manner it was found that in the moist mature fruit the weight of the pericarp constituted about 80 per cent. of the weight of the entire fruit, whilst in the dry fruit it amounted to about 50 per cent. Since the fruit attains its full size far in advance of the seed, it was necessary to select moist fruits where the seed had attained the maximum weight.

Barringtonia speciosa.	Weight in grains.		Shrinking ratios.		Relation of parts.	
	Moist.	Dry.	Moist.	Dry.	Moist.	Dry.
Pericarp . . .	8000	750	100	9'4	80	50
Seed . . .	2000	750	100	37'5	20	50
Entire fruit . . .	10,000	1500	100	15'0	100	100

- (2) The actual shrinkage or loss of weight was obtained separately for the pericarp and seed of the moist fruit with the following results :—

Ratio of shrinkage for the pericarp 100 to 10.
 „ „ „ seed 100 „ 40.

Supplementary observations on individual fruits led me to the opinion that in the results of the first method the weight of

the moist seed was too great and its estimated shrinkage excessive, whilst it also appeared that in the dry fruit the pericarp is as a rule rather heavier than the seed. The requisite corrections were not great, but they brought the various results into harmony, and the final statement accepted was as follows :—

Barringtonia speciosa.	Shrinking ratios.		Relation of parts.	
	Moist.	Dry.	Moist.	Dry.
Pericarp	100	9·5	82	52
Seed	100	40·0	18	48
Entire fruit	100	15·0	100	100

Such is an example of the method that has been usually employed, alike for the green coco-nut, weighing some sixty or seventy thousand grains, and for the small berries and pods of the Elder (*Sambucus*) and the Gorse (*Ulex*), that weigh only two or three grains. Still, as I have before remarked, these results are all concerned with the drying fruit. The more I handle these “drying” data, which bulk very largely in my note-books and have taken up a considerable portion of the time occupied in the preparation of this work, the more my interest in them dwindles. Nature offers to us the living fruit, and it is there that the real biological interest lies. If she presents us also with the dead fruit—I am of course referring more particularly to the pericarp exclusive of the seeds—we ought to regard it much as a physician would regard a patient dying from natural decay, a process which in the fruit we should term “drying up.”

I will now proceed to deal with the results of my observations on the weight-relations of the pericarp and seeds in various types of mature fruits before any withering or loss of weight through drying occurs. In the following table the entire fruit is taken as 100, the proportional weight of the pericarp alone being given, that of the seeds representing the complement. This plan has been adopted with the object of letting the table tell its story by the aid of a single set of figures at the same time

The relative weights of pericarp and seeds in mature fruits before drying begins.

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arranged in numerical sequence and grouped according to the type of the fruit. If the reader desires particulars relating to the average weight of a fruit, number of seeds, etc., he will find them at the end of the chapter in the table containing the elements for the determination of the drying régime of fruits.

COMPARISON OF THE WEIGHT-RELATION OF THE PERICARP IN DIFFERENT TYPES OF FULL-GROWN FRUITS BEFORE DRYING BEGINS, THE WEIGHT OF THE ENTIRE FRUIT BEING TAKEN AS 100.

(The fruit is here regarded as made up of pericarp and seeds. The only families indicated are Leguminosæ by L. and Palmacæ by P.)

	Relative weight of the moist pericarp, the entire fruit being taken as 100.				
	Legume.	Capsule.	Berry.	Drupe.	Miscellaneous.
<i>Pyrus Malus</i> (Apple)	99
<i>Citrus Aurantium</i> —					
(a) Mandarin Orange	99
(b) Common "	98
<i>Citrus decumana</i> (Shaddock)	97
<i>Cocos nucifera</i> (Coco-nut)	P.	96*	...
<i>Prunus communis</i> (Sloe)	95	...
<i>Achras Sapota</i> (Sapodilla)	95	...
<i>Ribes Grossularia</i> (Gooseberry)	95	...
<i>Sambucus nigra</i> (Elder)	93	...
<i>Acrocomia lasiospatha</i>	P.	92	...
<i>Cocos plumosa</i>	P.	92	...
<i>Arenga saccharifera</i>	P.	90	...
<i>Psidium Guajava</i> (Guava)	90
<i>Momordica Charantia</i>	89
<i>Opuntia Tuna</i> (Prickly Pear)	89
<i>Tamus communis</i>	87
<i>Ravenala madagascariensis</i>	87
<i>Lonicera Periclymenum</i> (Honey-suckle)	86
<i>Cassia fistula</i>	L.	85
<i>Sparganium ramosum</i>	85	...
<i>Swietenia Mahogani</i> (Mahogany)	85
<i>Hura crepitans</i> (Sandbox-tree)	84
<i>Barringtonia speciosa</i>	82
<i>Poinciana regia</i>	L.	80
<i>Entada polystachya</i>	L.	75
<i>Cæsalpinia Sappan</i>	L.	75
<i>Theobroma Cacao</i> :	75

* The pericarp-proportion of 96 per cent. refers to the green coco-nut only when the husk has attained its greatest development, whilst the albumen and shell are but partly formed. If we imagined a fruit where the seed and pericarp reach their greatest development together, the pericarp-proportion would be about 80 per cent.; but nature, as shown later on in this chapter, does not supply such fruits.

COMPARISON OF THE WEIGHT-RELATION OF THE PERICARP—*continued.*

		Relative weight of the moist pericarp, the entire fruit being taken as 100.				
		Legume.	Capsule.	Berry.	Drupe.	Miscellaneous.
Areca Catechu (Areca-nut)	P.	74
Thespesia populnea	72
Ulex europæus (Gorse)	L.	70
Scilla nutans	70
Æsculus Hippocastanum (Horse-chestnut)	70
Monstera pertusa	66
Hyophorbe Verschafftii	P.	65
Oreodoxa regia	P.	64
Cæsalpinia sepiaria	L.	64
Canavalia obtusifolia	L.	62
Mucuna urens	L.	61
Andira inermis	L.	61
Pisum sativum	L.	60
Phaseolus multiflorus	L.	60
Arum maculatum	60
Hedera Helix (Ivy)	59
Datura Stramonium	58
Allium ursinum	56
Bignonia (near æquinocalis)	56
Iris Pseudacorus	55
Vicia sativa	L.	50
Faba vulgaris (Broad Bean)	L.	50
Guilandina bonducella	L.	50
Vicia sepium	L.	49
Artocarpus incisa (Bread-fruit)	49
Dioclea reflexa	L.	47
Cajanus indicus	L.	47
Leucæna glauca	L.	47
Primula veris (Primrose)	46
Mauritia setigera	P.	46
Acacia Farnesiana	L.	46
Aquilegia (species)	45 (follicle)
Iris foetidissima	43
Canna indica	39
Ipomœa tuba	35
Arenaria peploides	25
Quercus Robur (Oak)*	} A 48 } B 35 (nut) } C 25

* The peculiarity in the growth of the acorn is described later on in this chapter. Here it is sufficient to observe that A represents the pericarp-relation at the time when the seed and the fruit-shell cease to grow together. After this the growth of the pericarp is arrested and the seed alone increases in weight, so that the relative proportion of the pericarp decreases, as in B and C, until the growth of the seed is in turn arrested and the maximum weight of the fruit is attained. If in the A stage the fruit weighed 50 grains, in the B and C stages, when the shell would be hardening and losing its vitality, the weight would be increased to 55 and 60 grains respectively.

This table illustrates the relative proportions of the pericarp and the seeds in the weight of the full-grown living fruit, or, as we might term them, the moist relations. We should be handling a subject bristling with difficulties if we attempted at this stage of the inquiry to draw any inferences except such as are of a loose general nature from these data. Yet, scanty as they may seem, these numerical results represent a great amount of labour, since in several cases the ground was made secure by methodical observation of the fruit in its several stages. For instance, some scores of the fruits of the two species of *Iris* were examined, and some dozens of visits of observation were made, in the different seasons of three successive years, before I was satisfied with my investigation of the fruits and could safely fix upon the full-grown moist condition. An experience thus gained could be extended to fruits of a similar type ; but it would be unwise to make such an examination of the relative proportion of parts in a fruit without some acquaintance, either direct or indirect, with the fruit in its various stages on the plant. The more one is acquainted with the fruit and its parts and with the different states of its development, the more secure will be the ground on which to base a general conclusion.

One notices that the sixty-four fruits here named principally consist of legumes, capsules, and berries, the drupes being not so well represented. About one-sixth comprises fruits, all of them either berries or drupes, where the weight of the pericarp exceeds 90 per cent., or the weight of the seeds is less than 10 per cent of the entire fruit. The bulk of the fruits, where the seed-weight ranges from 10 to 60 per cent., and that of the pericarp from 90 to 40 per cent. of the entire fruit, is mostly made up of legumes, capsules, and berries ; and there is not much to choose between them in their arrangement in the scale. With drupes and berries "size," as interpreted here by "weight," does not appear to count for much in determining the place in the scale ; whilst with legumes and capsules the largest and

Remarks on
the table.

the heaviest fruits have usually the smallest seed-weight. Thus amongst the drupes, the Sloe (*Prunus communis*), weighing about 30 grains, and the Coco-nut (*Cocos nucifera*), weighing 60,000 grains, have much the same proportions. Coming near together amongst the baccate fruits are those of the Elder (*Sambucus nigra*), weighing 3 grains, the Gooseberry (*Ribes Grossularia*), weighing 100 grains, and the Shaddock (*Citrus decumana*), weighing 14,000 grains.

Although in this respect the capsules behave mostly like the legumes, the largest fruits having usually the greatest proportion of pericarp, one can point to cases where fruits widely different in size and weight have the same proportion in their parts. Thus in the capsules of the Blue-bell (*Scilla nutans*), weighing 10 grains, and in that of the Horse-chestnut (*Æsculus Hippocastanum*), weighing 700 grains, the proportional weight of the pericarp is the same. With the legumes those fruits possessing the greatest proportion of pericarp, to wit, those of *Cassia fistula*, *Poinciana regia*, and *Entada polystachya*, are certainly the largest; and this circumstance seems to be associated with the presence of much ligneous tissue. In fact, legumes like those of *Pisum sativum* (Pea) and of *Faba vulgaris* (Broad Bean), which have a thick, fleshy pericarp, are not conspicuously high in the scale. The same indication is supplied in a general way by the capsules, since the two largest and heaviest amongst them, those of *Swietenia Mahogani* and *Hura crepitans*, are not only the most ligneous, but rank amongst capsular fruits with the highest proportional weight for the pericarp, namely, 85 and 84 per cent. respectively.

It should again be observed that the weights and other particulars concerning the fruits in this table will be found in the last table in this chapter.

The history of the proportional and absolute weights of the pericarp and seeds of a fruit during its early growth, maturation, and drying now demands our attention. It is a familiar fact in the history of fruits and seeds that the pericarp or fruit-case is as a rule in its growth far in advance of the

The relative weights of pericarp and seeds in the different stages of a fruit.

seed. This often comes under our notice in green leguminous pods, as in the Pea (*Pisum sativum*), where, although the pod may be of full size, the immature seeds within are very small and quite out of proportion to the fruit containing them, the disproportion being subsequently removed by the rapid growth of the seeds in the ripening pod.

The circumstance that the earlier history of a fruit's development is mainly concerned with the fruit-case and the later with the seed is treated with some detail in a later page of this chapter. I will now therefore allude to that critical period in this sequence of events which may be pronounced the turning point in the history of the seed, that period when it has to make the choice between entering the resting state or germinating on the plant.

There are good grounds for holding that in most fruits the seeds, which, as before remarked, are far behind the fruit-case in the earlier stage of their growth, ultimately attain maturity about the same time as the fruit. In order that the pericarp and the seeds may reach their full development about the same time, it is necessary that in the ripening fruit the pericarp should considerably diminish and the seeds considerably accelerate the rate of their growth. But, as indicated by the proportion of the parts of a fruit in different stages, as determined by the balance, there are evidently cases where the seed proceeds with its development after the pericarp has not only completed its growth but has commenced to dry. In other words, the fruit-case begins to lose its vitality before the seed enclosed has attained its maximum development. This is shown in the Acorn (*Quercus*) and in the Coco-nut, and, as my observations suggest, probably in the fruits of *Barringtonia speciosa*. It would thus promise to be not infrequent with one-seeded fruits of these types.

Before giving the data on which these general inferences are based, I should remark that this subject only came into prominence during the elaboration of my data. It was the comparison of the results obtained for coco-nuts and acorns

Both the seeds and the pericarp usually reach maturity about the same time.

Yet there are fruits where the seed continues its growth after the pericarp has begun to dry.

that first opened my eyes to its importance. Although I can only claim to have broken the ground, the contents of the following table ought to be of interest. If figures can tell a story, these data plainly show the varying rates of growth of the pericarp and the seeds in the development of the fruit, besides illustrating their history in the drying stage when the pericarp has ceased to grow and begins to die. From this standpoint we have two types of fruits displayed in the table. The first, which is probably by far the commonest, is represented by the capsules of *Iris* and *Æsculus* and by the legumes of *Faba*, *Phaseolus*, and *Entada*. Here the time of the maximum growth of the seed roughly corresponds with that of the pericarp, the seed entering upon its rest-period when the fruit-covering begins to dry and lose weight. The second is represented by such closed fruits as the acorn or nut of the Oak (*Quercus Robur*), and by the berry of *Barringtonia speciosa* and the drupe of the Coco-nut Palm, the two last possessing husky pericarps. Here the seed continues to add to its weight and size after the pericarp has ceased to grow and has begun to dry.

The point in the case of the fruit of *Barringtonia*, however, needs further investigation; but the indications are very suggestive. Thus, in the table given below it is shown that the drying fruit, weighing 4000 grains, has a heavier seed than the full-sized moist fruit, weighing 9000 grains, that has not yet begun to dry. The same thing is brought out in the table illustrating the history of the fruit of *Barringtonia speciosa* given in Note 11 of the Appendix. It will be found there remarked under J that the seed has probably increased its weight whilst the husk has been drying.

It is quite possible that future investigators will discover that the differences between the two types of fruits represented in the following table are more in degree than in kind, and that even in the prevailing type the seeds may continue to add to their weight for a little while after the fruit-case has begun to lose its vitality and to dry. There are distinct

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TABLE SHOWING THE PROPORTIONS BY WEIGHT OF THE PERICARP AND SEEDS DURING THE DIFFERENT STAGES OF FRUITS, INCLUDING THE IMMATURE, MATURE, AND DRIED CONDITIONS.

(The weights are in grains. In the percentage columns the entire fruit is taken as 100.)

Plant-name.	Parts.	Green fruits with immature seeds.				Ripe fruits with mature seeds.					
		Less than half size.		More than half size.		Full size before drying.		Early drying stage.		Drying in air completed.	
		Weight.	Percentage.	Weight.	Percentage.	Weight.	Percentage.	Weight.	Percentage.	Weight.	Percentage.
Iris foetidissima (capsule) {	Pericarp	73	52	78	43	25	25	15	34
	Seeds	67	48	102	57	75	75	30	66
	Entire fruit	140	100	180	100	100	100	45	100
Iris Pseudacorus (capsule) {	Pericarp	77	77	98	70	135	54	86	48	16	25
	Seeds	23	23	42	30	115	46	94	52	49	75
	Entire fruit	100	100	140	100	250	100	180	100	65	100
Æsculus Hippocastanum (capsule, 1-seeded) {	Pericarp	218	84	468	78	490	70	400	66	68	40
	Seeds	42	16	132	22	210	30	200	34	100	60
	Entire fruit	260	100	600	100	700	100	600	100	168	100
Entada polystachya (legume) {	Pericarp	425	85	600	75	149	62
	Seeds	75	15	200	25	91	38
	Entire fruit	500	100	800	100	240	100
Faba vulgaris (5-seeded legume) {	Pericarp	170	85	455	65	400	50	240	40	48	24
	Seeds	30	15	245	35	400	50	360	60	152	76
	Entire fruit	200	100	700	100	800	100	600	100	200	100
Barringtoniaspeciosa (baccate, 1-seeded) {	Pericarp	1980	99	4800	96	7380	82	1880	47	702	52
	Seeds	20	1	200	4	1620	18	2120	53	648	48
	Entire fruit	2000	100	5000	100	9000	100	4000	100	1350	100
Cocos nucifera, Coco-nut (drupaceous) {	Pericarp	9,900	90	57,600	96	19,000	72	14,040	78
	Seeds	1,100	10	2,400	4	7,400	28	3,960	22
	Entire fruit	11,000	100	60,000	100	26,400	100	18,000	100
Quercus Robur, Oak (nut) {	Pericarp	13	65	18	57	20	44	17	30	5	19
	Seeds	7	35	14	43	26	56	40	70	21	81
	Entire fruit	20	100	32	100	46	100	57	100	26	100
Phaseolus multiflorus, Scarlet-runner (4-seeded legume) {	Pericarp	133	95	200	80	180	60	110	55	27	36
	Seeds	7	5	50	20	120	40	90	45	48	64
	Entire fruit	140	100	250	100	300	100	200	100	75	100

Note.—Although in selecting the fruits to form the same series those similar in character were chosen, minor inconsistencies occur, but the general trend of the data is to be relied on.

indications of this in the data given for *Faba vulgaris* and *Phaseolus multiflorus*.

The case of
the coco-nut.

In order to throw light on this matter, as concerning the coco-nut, I will give some of the results of observations made in Jamaica. Though the data tabulated below do not present a continuous record, the intervals can be readily filled up; and it may be added that the general trend of results illustrated in these tables is confirmed by indications supplied by a number of other fruits in addition to those for which the record is here given.

It will be seen from the tables that the drying of the full-grown green fruit is practically the drying of the husk alone, since it is likely that mould and other causes of decay usually come into play in nature before the completely air-dry condition is attained, as exemplified in column D. Indeed, planters hold that fruits kept too long do not usually dry up, but rot and decay. Whilst the drying of the husk is proceeding on the plant, remarkable changes take place in the shell and in the kernel. In a full-grown green fruit, as is well known, the shell is thin and the kernel soft and almost creamy. During the drying process the maturation of the seed proceeds. Whilst the husk is losing pounds in weight, the shell is becoming tougher and thicker, and the kernel solidifies and increases in quantity. But the increase of the kernel is much greater. Though in the green fruit its weight is rather less than that of the shell, it becomes 50 per cent. heavier as the seed ripens in the drying fruit. When, however, after many months of drying, the fruit has yielded all its water to the air, except the water of hygroscopicity, which, according to the principle laid down in Chapter VII., is common to both living and dead vegetable matter, the weight of the kernel is only about the same as that of the shell. Such a completely air-dried condition, as has been observed above, would be rarely attained in nature. This last stage is more fully discussed in the explanatory remarks that follow the tables.

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TABLES SHOWING THE RELATION OF PARTS BY WEIGHT IN DIFFERENT STAGES OF THE COCO-NUT (*COCOS NUCIFERA*). (Table I. is in grains; Table II. in grammes.)

I. GRAINS.

(Data obtained from individual nuts in different stages.)

Parts.	A.		B.		C.		D.	
	Weight.	Per-centage of entire fruit.	Weight.	Per-centage of entire fruit.	Weight.	Per-centage of entire fruit.	Weight.	Per-centage of entire fruit.
	Full-grown green fruit.		Fruit in the early stage of drying on the tree.		Fruit after drying for 2 to 3 months on tree (a ripe fruit.)		Fruit completely air-dried (see explanation of tables).	
Husk . . .	46,750	85'0	31,185	81'0	13,440	56'0	9410	57'2
Shell . . .	2,640	4'8	2,618	6'8	3,744	15'6	3480	21'1
Kernel . . .	2,200	4'0	3,080	8'0	5,952	24'8	3570	21'7
Water . . .	3,410	6'2	1,617	4'2	864	3'6
Total . . .	55,000	100'0	38,500	100'0	24,000	100'0	16,460	100'0
Relation of the total weights	100		70		44		30	

II. GRAMMES.

(The proportions given in Table I are here applied to a fruit assumed to weigh originally 4000 grammes, or nearly 9 lbs.)

Husk . . .	3400	85'0	2268	81'0	986	56'0	686	57'2
Shell . . .	192	4'8	190	6'8	275	15'6	254	21'1
Kernel . . .	160	4'0	224	8'0	436	24'8	260	21'7
Water . . .	248	6'2	118	4'2	63	3'6
Total . . .	4000	100'0	2800	100'0	1760	100'0	1200	100'0
Relation of the total weights	100		70		44		30	

Explanation
of the tables.

Though these tables largely explain themselves, a few explanatory remarks are necessary. The data in Table I were obtained from individual fruits, excepting those in column D, those fruits being selected which came from the same palm and gave results similar to those supplied by others in the same stage. In Table II the percentages shown in Table I are applied to a green, full-sized fruit of average weight. It is important to notice that whilst the first table is in grains, the second is in grammes. All the observations were made during the winter 1907-8 in Jamaica.

The contents of column D call for special remark. They represent the results of different experiments on the ordinary drying in air of the separate husk, shell, and kernel, applied to the fruit in the stage at which they reach their greatest development. Since the husk attains it in the green unripe fruit of full size, the drying experiment was made on the husk at this stage. In the same way and for the same reason the shell and kernel of the ripe fruit were subjected to the drying test. The following results were obtained :—

Loss of weight when dried in air of husk of green coco-nut,
80 per cent.

Loss of weight when dried in air of shell of ripe coco-nut,
7 per cent.

Loss of weight when dried in air of kernel of ripe coco-nut,
40 per cent.

To produce the completely air-dried coco-nut these losses had to be applied to the husk of the green fruit in column A, and to the shell and kernel of the ripe fruit in column C. The fruit typified in column D is therefore a coco-nut that has given up all its water to the air, or rather all the water that the air can absorb, the fruit retaining only what it would hold independent of its vitality. This completely air-dried fruit represents, accordingly, rather the result of a laboratory experiment than a process of nature, since, as previously remarked, we should only expect to find a coco-nut in this state under exceptional conditions. Such a fruit would most

The com-
pletely air-
dried coco-
nut.

probably have lost its germinative capacity, as may be inferred from my observations on the embryo of the coco-nut recorded in Chapter XVIII. But although these data are concerned with a dead fruit, they bring the completely air-dried fruit of the Coco-palm into line with other fruits in the same devitalised condition, such fruits only holding the water of hygroscopicity which is common to both living and dead organised vegetable matter. If we were asked what stage in the drying of a coco-nut corresponds to that of the dried-up apple, cherry, and currant as they hang in dry weather from the tree, we should point to the completely air-dried fruit of column D. The trade husked coco-nut, such as is sold in the English markets, would be drier than the ripe fruit of column C, but moister than that of column D. If kept under dry atmospheric conditions and secured against the attacks of mould, it would lose more water.

It would thus appear that what the planter calls a "ripe" coco-nut is a fruit that has lost in the ripening process rather over half its weight as a green nut. This process may be completed on the tree, or it may be continued in the stored, detached fruit which has been gathered in the early ripe condition. When we speak of the fruit as maturing its seed whilst it dries on the palm, we are not adopting the phraseology of the planter. For him a ripe nut is a fruit with a thick, solid, oily kernel; and in practice he is less concerned with the mode of ripening than with the characters indicating his ripe fruit. Thus, the statement in Simmond's *Tropical Agriculture* that the seed-nut must be "fully ripe and not aged" would be full of meaning to the planter, but it might be misinterpreted by one not familiar with the Coco-palm in its home.

However, the theoretical view advanced above that the seed grows whilst the fruit is drying is in accord with practical experience. Ripe nuts, it is advised in the work above named, should be allowed to dry for not less than a month after gathering before they are planted. If intended for "copra" they should not be broken up for four or six weeks after

A "ripe"
coco-nut.

The seed of
the coco-nut
grows whilst
the pericarp
is drying.

gathering. This implies that the maturation of the seed is continued after the early ripe fruit has been detached. It is during the period of storage, covering usually one or two months, that the oil in the kernel increases considerably in amount. The proportions of water and oil in the kernel vary in an inverse relation, the water gradually diminishing and the oil gradually increasing as the fruit matures. In an interesting compilation entitled *All about the Coco-nut Palm*, which was published at Colombo in 1885, the following are given as the proportions of water and oil in the kernels of young and ripe fruits as obtained by M. Lépine of Pondicherry:—

Young coco-nuts contained 90·3 per cent. of water and 2·3 per cent. of oil.

Ripe coco-nuts contained 53·0 per cent. of water and 30·0 per cent. of oil.

This increase of the oil in a stored coco-nut is a point emphasised by different writers in the book just quoted; and it is one on which stress is laid in a letter to me by Mr H. Matthes, a planter of "Bacolet," Tobago.

The use of the term "young" deserves a word of explanation. It is applied to the full-sized green fruit with shell and kernel but partially formed. The term "ripe" is applied to a fruit with a hard shell and a thick solid kernel. During the ripening process the husk loses a large amount of water, and in consequence the ripe fruit is much lighter in weight than the green fruit, though to the inexperienced eye its appearance may not be greatly changed.

As confirming my method, I have compared below the proportions of parts for young and ripe fruits as given in *All about the Coco-nut Palm* with my own results. The data are apparently all derived from M. Lépine, but they are concerned with a smaller variety of coco-nut than that experimented upon by me in Jamaica. Since the husk and shell are not distinguished by him in the young nut, I have followed the same plan in the subjoined table.

Decrease of
the water
and increase
of the oil.

Observations
of Lépine.

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COMPARISON OF THE PROPORTIONS OF PARTS IN COCO-NUTS AS OBTAINED BY LÉPINE AND GUPPY.

	Young fruit (Lépine).		Ripe fruit (Lépine).		Percentages obtained by Guppy.	
	Weight in grammes.	Percentage of entire fruit.	Weight in grammes.	Percentage of entire fruit.	Green.	Ripe.
Husk and shell	1760	81·9	766	53·0	89·8	71·6
Kernel . . .	90	4·2	434	30·0	4·0	24·8
Water . . .	300	13·9	250	17·0	6·2	3·6
Total .	2150	100·0	1450	100·0	100·0	100·0
	A.	B.	C.	D.	E.	F.

After allowing for variation in the proportion of parts in coco-nuts of different localities, it is easy to recognise in the young and ripe fruits of Lépine the green and ripe fruits of my tables. In both sets there is a marked increase in the absolute weight and in the relative amount of the kernel in the green (young) and ripe fruits. M. Lépine's fruits were evidently selected at random; but it is to be noted that his young fruit is about 50 per cent. heavier than his ripe fruit. The question cannot be further discussed here, but it should be added that the total amount of water in the coco-nut is dealt with in Note 27 of the Appendix, and that the subject of the embryo is treated in Chapter XVIII.

As another example of those cases where the seed continues to increase in size and weight after the pericarp has ceased to grow and is beginning to lose its vitality, I will take the fruit of the Oak (*Quercus Robur*). Here the subject is bound up with that of the occasional vivipary of the acorn, or, in other words, with its germination on the tree, a matter dealt with in Chapter XIX. My observations were made at Salcombe in Devonshire in the successive autumns of 1908-1911. The

The case of the Acorn (*Quercus Robur*).

method employed consisted in making observations systematically during the five or six weeks preceding the fall of the acorn from its cupule in October. On each occasion a number of fruits were gathered from the same two or three trees, and ten were selected for examination and experiment. The vital connection with the parent plant is maintained by the attachment of the base of the fruit to its cupule. When the acorn begins to "brown" this attachment to the cupule begins to loosen, the result evidently of the drying of the pericarp or shell. The "browning" and drying of the shell proceed until the biological union with the cupule is severed, when at a touch the acorn falls to the ground.

Explanation
of the table.

With regard to the table on opposite page it may be observed that the acorns of the experiment in 1908 were larger and heavier than those employed in 1910, a difference that will explain the divergencies in the absolute weights. The results of many observations are embodied and stated numerically; but there is much that of necessity finds no expression in the figures. A careful examination is needed before the data here tabulated can be used legitimately, and especially is it requisite that those making use of them should know a little of the acorn and its ways. As far as is consistent with its being a tabular statement, the author has endeavoured to make it as self-explanatory as possible. But he can hardly expect his readers, whilst perusing the dry array of numerical results, to invest them with the interest they created in his mind as they gradually disclosed their story in the course of a fascinating piece of investigation. That interest they can only acquire by going to the Oak themselves and by appealing to the balance in an inquiry that should at least cover two seasons. The secret of vivipary will lie behind the results of their observations.

To show how this table is to be employed I will take one of the entries, that of September 27, 1910. It is here indicated that in a freshly gathered acorn, weighing 50 grains, the shell or pericarp weighed 19 and the seed 31 grains. In other words, as stated in the next two columns, taking the weight of

THE PROPORTION OF PARTS IN FRUITS 311

TABLE ILLUSTRATING THE GROWTH OF THE ACORN (*QUERCUS ROBUR*) AS REVEALED BY THE BALANCE, DURING THE SIX WEEKS PRECEDING ITS DETACHMENT FROM THE CUPULE, FROM OBSERVATIONS MADE BY THE AUTHOR AT SALCOMBE, DEVONSHIRE, IN 1908 AND 1910. (The cupule is not included in these observations.)

Date when gathered.	Condition and state of attachment of the fruit to the cupule.	Average weight in grains of a single fruit and its parts (10 nuts in each case).			Relative weight of the pericarp and seed, taking the entire fruit as 100.		Loss of weight after drying in air at the ordinary temperature, stated as a percentage of the weight in the moist fruit.		
		Total.	Pericarp.	Seed.	Pericarp.	Seed.	Entire fruit.	Pericarp.	Seed.
1910.									
Sept. 13	Firmly attached by living tissue to the cupule; pericarp 2 mm. thick and moist	32	18·2	13·8	57	43	74·0	76·0	70·0
„ 20		46	21·6	24·4	47	53	72·0	76·4	67·8
„ 27	Attachment looser; beginning to turn brown	50	19·0	31·0	38	62	64·4	72·8	59·2
Oct. 4		55	19·3	35·7	35	65	61·0	68·7	56·8
„ 11	Easily detached, but still a slight biological connection; browning pericarp thinner and drier	51	15·3	35·7	30	70	47·4	62·6	41·0
„ 18	Falls at a touch from the cupule; well browned	57	17·1	39·9	30	70	47·7	57·5	43·5
„ 18	After keeping for some time and no longer losing weight, pericarp very thin, 0·3 mm.	26	19	81
1908.									
Sept. 4	Firmly attached to cupule; pericarp thick and moist	56	24·6	31·4	44	56	25·0
„ 17		62	29·1	32·9	47	53	32·3
„ 30	Attachment loosening; browning; pericarp thinner and drier	62	45·5
Oct. 6		71	18·1	52·9	25·5	74·5	48·6
„ 14	Vital connection severed; falls at a touch from the cupule	64	57·4
„ 14	After keeping for some months and no longer losing weight	35	18	82

the fresh fruit as 100, the shell makes up 38 and the seed 62 parts of the whole. When this fresh acorn is allowed to dry in ordinary air, until it ceases to lose weight and exhibits merely the usual hygroscopic variations regulated by the

atmospheric humidity, the shell or pericarp loses 72·8 per cent. of its moist weight, the seed 59·2 per cent., and the fruit in its entirety 64·4 per cent. Such are the indications given in the columns of this table for the acorn gathered at this date. When we compare them with those fruits collected earlier and later, we find that during the acorn's growth the seed steadily increases its weight and decreases its water-contents long after the pericarp has ceased to grow and has begun to dry.

This table will be noticed in different connections, but especially in relation to vivipary or germination on the plant in Chapter XIX. With these explanatory remarks I will now proceed to refer more in detail to the particular lesson which the data furnish us here respecting the development of the acorn on the tree, namely, the continued growth of the seed after the fruit-shell has begun to lose its vitality. This is not only the tale of the balance ; but it is the story that the acorn, as we handle it, conveys to us plainly enough in the increase in size, weight, and solidity of the seed, whilst the shell is becoming thinner and drier in the "browning" process.

The tendency of a seed in some cases to continue its growth after the fruit-case or pericarp has begun to lose weight and dry, in other words, to die, finds its final expression in the germination of the seed on the plant. To put it in another way, it is a step towards vivipary. It is not by a mere coincidence that I am enabled to bring into touch with the viviparous habit all the three plants that have before been mentioned as illustrating the normal growth of the seed after the pericarp has begun to dry and to lose its vitality. In the cases of the Oak and the Coco-nut Palm, the connection is more or less direct, whilst with *Barringtonia speciosa* the implication is only indirect.

Thus in Chapter XIX I have dwelt upon the tendency to vivipary displayed by the nuts of the Oak (*Quercus Robur*), as observed by me during successive years at Salcombe in Devonshire. That the coco-nut does occasionally "sprout" on the palm came under my notice in Fiji (*Plant Dispersal*, by

The connection between vivipary and the continued growth of the seed after the fruit-case has begun to dry.

H. B. Guppy, p. 472); and there is to be cited in this connection the well-known habit in the Pacific of suspending the ripe fruits from a tree by a strip of the husk and leaving them exposed to the weather until they germinate. Although there is no evidence of vivipary in the case of the fruits of *Barringtonia speciosa*, there are grounds for believing that the fruits of an allied species (*B. racemosa*), which are frequently found germinating in the floating drift of the Rewa estuary in Fiji, begin to germinate whilst hanging from the trees that abound at the water-side (*ibid.*, pp. 564, 575).

The discovery of this peculiarity in the growth of the acorn was made in this way. My attention was first directed to some anomaly in the growth by an impossible result produced by applying a shrinking ratio deduced from experiments on the drying of moist full-sized nuts gathered in the middle of September, 1908, to fruits of the same tree well dried after being kept some months. Since the moist fruits in question lost just two-thirds of their weight whilst drying, and since the dry acorns, gathered when ready to fall from the cupule, now weighed from 30 to 40 grains in each case, it followed from the application of the shrinking ratio that their original weight as moist fruits must have been between 90 and 120 grains. As a matter of fact, from the tree concerned I had rarely obtained moist nuts more than half this weight. Influenced also by other considerations, I made a note at the time that "it is not at present possible to obtain a satisfactory shrinking ratio for the moist green acorn, since the kernel apparently adds to its weight after the shell has ceased to grow and has begun to dry."

Strangely enough, although I had noticed on this and neighbouring trees that whilst the acorns were still attached to the cupule on the tree their seeds were in some cases splitting their shells and in rare instances actually protruding the radicle, the connection between the anomaly above described and the vivipary did not then present itself. So the matter rested for a year and more, until, having found that a similar anomaly in

The discovery that the seed of the acorn continues its growth after the shell has begun to dry.

the shrinkage of the coco-nut was satisfactorily explained by the growth of its seed after the husk had begun to dry, I began to examine in this light my data for the acorns of the autumn of 1908. The growth of the kernel after the shell had begun to lose weight and dry was unmistakably brought out in the results of my weighings, as is shown in the table. Further observation on the tendency to germination of the acorn on the tree was made in the autumn of 1909; and during September and October 1910 systematic weekly observations and experiments were carried out on neighbouring trees, leaving the original tree for the study of the viviparous tendency. The results told the same story; and their indications were emphasised by those of fresh experiments on the water-contents. It thus finally appeared that the tendency of the seed of the ripening acorn to increase in weight after the pericarp or shell has begun to dry finds its final expression in the splitting of the shell and in the germination of the seed, whilst the fruit is still attached to the cupule on the tree. It was the first step towards vivipary, and a sign diagnostic of the potentially viviparous habit of the oaks observed. Such is the history of my researches in this connection.

It is noteworthy that the observations made in 1908 are in one respect more significant than those of 1910 in showing how the seed of the acorn continues its growth after the shell or pericarp has begun to lose its vitality and to dry, since they were carried out with no special view in my mind. But it is to the more systematic observations of 1910 that I will now more especially refer, since the data there enable us to compute the water-contents as far as they are shown by the loss of weight of the materials when dried under ordinary air-conditions. During the period between the middle of September and the middle of October, the weight of the seed increased from about 14 to 40 grains, whilst its water-percentage decreased from about 70 to 40 per cent., thus indicating a very marked addition to the solids as it grew. But there was no such continuous growth of the shell

This peculiarity in growth represents the first step towards vivipary.

The drying of the shell in the ripening acorn.

or pericarp during this period ; and, as in the case of the seed, the two sets of observations for 1908 and 1910 tell a similar story. In the third week of September, when the shell had reached the height of its growth, it was moist, almost fleshy inside, and about 2 millimetres thick. After this it began to turn brown, lose weight, and to dry, signs of the severance of its vital connections that antedated those of the seed. Whilst the seed had been getting larger, heavier, and more solid, its shell had been getting thinner and drier, so that when the acorn was ready to fall from its cupule, its well-browned shell had lost more than half its original thickness and much of its water. Such are some of the changes in relation between the seed and shell of the acorn illustrated in the table. They are still more evident when we handle the ripening acorns on the tree.

On looking at the general table given on p. 303 showing the proportions by weight of the pericarp and seeds during the early growth, maturation, and subsequent drying of a variety of fruits, it will be noticed that as a general rule from the young fruit on the plant with immature seeds, to the withered-up fruit, as it lies on the ground, there is a continuous decrease in the proportion by weight of the pericarp, and a continuous increase in that of the seeds. In some fruits, it is true, as in the capsule of *Iris fœtidissima* and in the fruit of the Coco-palm, the proportional amount of the pericarp in the completely dried fruit is rather more than in the earlier drying stage, a result due to the seeds losing weight less readily at first, as explained below. But this does not seriously affect the general trend of the figures ; and it is very probable that in the majority of fruits of the type of the capsule and the legume the general decrease in the proportional weight of the pericarp, as the fruit grows, matures and dries, would not exhibit any such interruption.

It is a familiar fact of observation that the earlier history of a fruit's development is mainly concerned with the fruit-case and the later history with the seed. Nothing short of

The general principle that as the fruit grows, matures, and dries, the proportion of the pericarp decreases, and that of the seeds increases.

Illustrations of the principle.

handling and actual inspection can be more effectual than the data in this table in bringing out the fact that the growth of the fruit-case is for a long time far in advance of that of the seed. As typical of the behaviour of legumes I will take the pods of the Scarlet-runner (*Phaseolus multiflorus*) and the Broad Bean (*Faba vulgaris*), and as representing the capsules the fruit of *Iris Pseudacorus*.

In the young pods of the Scarlet-runner and of the Broad Bean, when less than half the mature size, the contrast between the large fruit-case and the diminutive, partially formed seeds is very striking. On the average the weight of the fruit-case would be about 90 per cent. of the total weight of the entire fruit. When the pods have attained maturity in the moist condition, the proportion is lowered to 50 or 60 per cent. ; and in the air-dried pods it is still further reduced to 25 or 35 per cent. From an early stage in the fruit's development until it hangs as a dried-up pod on the plant there is a continual decrease in the proportional weight of the pericarp or fruit-case. Up to the time of maturity this decrease is due to the active growth of the seeds. After maturity it arises from the larger water-contents and the consequently greater drying capacity of the fruit-case.

The capsules of *Iris Pseudacorus* give similar indications. Here also we notice in the columns of the table that there is a continuous decrease in the relative weight of the pericarp. When the young fruit is only two-fifths of the mature size, the proportion is as much as 77 per cent. ; and it attains the minimum of 25 per cent. in the completely air-dried fruit. If we had commenced with a still younger fruit, the proportion of pericarp would have been as much as 85 or 90 per cent. But it is obvious that this continuous decrease is brought about by different causes during the growing and the drying stages. In the early growing stage, when the seeds are small and their contents more or less unformed, the pericarp greatly predominates ; but as growth proceeds and the ripening stage is approached, the seeds rapidly add to their weight, and the

Phaseolus multiflorus
and *Faba vulgaris*.

Iris Pseudacorus.

proportion of the pericarp decreases up to the time of maturity. The subsequent decrease in the drying stage is due to the pericarp holding relatively more water than the seeds, and to its giving it up to the air more readily. It will be noticed in the table on p. 303 that when allowed to dry in the air, the pericarp of the moist mature fruit reduces its weight from 135 to 16 grains, a loss of as much as 88 per cent. of its weight, whilst in the full-grown soft seeds of the ripe fruit there is a reduction in weight from 115 to 49 grains, a loss of about 57 per cent.

We may here cite the case of the acorn, which acts quite in accordance with the principle that the proportional weight of the fruit-case is a continually decreasing quantity as the fruit develops, ripens, and dries. As high as 65 per cent. in an immature fruit only one-third of the mature size, the relative weight of the shell or pericarp is reduced rapidly, being 44 per cent. when the seed has attained its maximum size and weight in the moist condition, and as little as 19 per cent. in the air-dried acorn lying on the ground. These results are those given in the general table on p. 303.

The acorn.

It will be observed in the same table that a small divergence in behaviour is displayed by the fruit of *Iris fœtidissima* in the drying stage; and we notice it also in the fruits of *Barringtonia speciosa* and *Cocos nucifera* (Coco-nut). Here during the drying process, as previously remarked, there is a period when the loss in weight of the seed is checked and the loss in that of the pericarp proceeds very rapidly. In time, however, the seeds, like the pericarp, surrender their water to the air; and the temporary check is indicated by the circumstance that the lowest proportional weight of the pericarp is found, not in the completely dried state, as in *Iris Pseudacorus* and in *Æsculus Hippocastanum* (Horse-chestnut), but in the earlier stage of the drying process. The cause of this check to the drying of the seeds arises in *Iris fœtidissima* from the amount of saccharine material in the seed-coverings, and in *Barringtonia speciosa* and *Cocos nucifera* from the hindrance imposed on the seed-drying by the enveloping pericarp. The history of the

Small departures from the principle in *Iris fœtidissima*, *Cocos nucifera*, and *Barringtonia speciosa*.

pericarp relation in the husky fruit of *Barringtonia speciosa* is especially instructive. Here, as shown in the table in Note 11 of the Appendix, the pericarp proportion remains as high as 98 or 99 per cent. until the fruit has attained to one-third of the full size. When the fruit is half size, it is still as much as 96 per cent., and after this falls to 82 per cent. in the full-grown fruit, and to about 50 per cent. when the fruit is lying completely dry on the ground.

The significance of the fact that in the drying fruit the pericarp loses far more water than the seed.

Much significance lies in the circumstance that as the fruit dries on the plant the seeds form a larger proportion of the weight of the entire fruit. When the moist fruit dries the pericarp loses far more water than the seed, the result being that whilst the fruit-case dies the seed lives. If we were to strike a rough average from the data given in the table on p. 320, and more particularly from the results summarised for types at its end, we would say that whilst seeds as a rule lose half their weight during the drying process on the plant before entering the rest-period, the pericarp loses generally from 70 to 85 per cent.

And it is in the behaviour of the pericarp that fruits differ most.

It is, however, in the behaviour of the pericarp that fruits differ most, the seeds as a rule presenting much less contrast in this respect. Taking the averages below given, we find that the pericarp sustains the greatest loss of 86 or 87 per cent. in the case of typical fleshy or pulpy berries and typical moist capsules, the living capsule being essentially a more or less fleshy and watery fruit. The significance of this close similarity in behaviour has been already dealt with in Chapter XII; but it is of interest here to note again that ripe fruits seemingly so contrasted as those of the Apple, Gooseberry, (*Ribes*), Prickly Pear (*Opuntia*), on the one hand, and those of *Canna*, *Datura*, *Ipomœa*, and *Iris* on the other, yield up much the same amount of water as the fruit-case dries naturally on the plant. Next come fleshy drupes, typically represented by those of *Prunus communis*, which experience a loss of 75 per cent. Then we have the legumes with an average loss of weight of 72 or 73 per cent.; and last come the large woody capsules, exemplified by those of the Mahogany tree, *Ravenala*,

and *Hura crepitans*, where the average loss is rather over 60 per cent.

It is remarkable that when grouped on the basis of the loss of weight sustained by the pericarp during the drying process on the plant the fruit-types arrange themselves in a regular series, commencing with typical berries and capsules and ending with woody capsules and Palm fruits. This is shown in the following results which are taken from the summary at the end of the subjoined table.

Loss sustained by	fleshy capsules and pulpy berries	86 or 87	per cent.
„	„ fleshy drupes	75	„
„	„ legumes	73	„
„	„ woody capsules	63	„
„	„ Palm fruits	62	„

Seeds, as already remarked, are much more constant in behaviour. As indicated in the summary of the results of the table, if we exclude Palm seeds, they lose on the average about half of their weight, the seed proper of the Palm losing as a rule about a third of its weight.

The drupaceous and baccate fruits of Palmaceæ are often considerably affected by the presence of oil or of sugars in the pericarp. Thus, whilst the pericarp of the fruit of *Cocos nucifera* (Coco-nut) contains an abundance of water and loses about 79 per cent. of its weight in the drying, that of *Cocos plumosa*, which holds a large amount of sugar, loses only 37 per cent. So, again, with the fruits of *Areca Catechu*, the fruit-case experiences a loss of 77 per cent. of its weight; whilst the pericarp of those of *Oreodoxa regia*, which holds much oil, loses only 42 per cent.

If space permitted it the treatment of this subject might be greatly extended; but many points are dealt with in different parts of this work, and the elements for determining the drying régime of many fruits and seeds not specially discussed here will be found in the table at the end of this chapter. Numerous matters of lesser interest cropped up in this part of my inquiry; but it would be scarcely worth while, even if there

was no other reason against it, to burden these pages with recounting them. One which occurs to me as I write is the relations as regards weight and size between the placental axis or columella of certain capsules. In Note 17 of the Appendix I compare together in this respect the capsules of the Primrose, weighing about 4 grains, and of the Mahogany tree, weighing about 6000 grains, or 1500 times as much. Although this is a comparison of the small with the great, the balance is equally effective in both cases in determining the relation of parts.

THE PERICARP AND THE SEED.

TABLE COMPARING THEIR LOSS IN WEIGHT DURING THE DRYING AND SHRINKING PROCESS.

(The results are given in percentages, the moist pericarp and the soft, uncontracted seed of the ripe fruit being taken as 100. The data have been selected with the object of contrasting the behaviour of different types of fruits. They are all to be obtained by constructing the drying régime for each fruit from the elements given in the last table of this chapter; but the shrinkage of the seeds is also given in Chapter IX.)

Plant-name.	Type of fruit.	Loss in weight during the drying process, the moist condition being taken as 100, the dry weight being then given.	
		Pericarp.	Seed.
<i>Arum maculatum</i>	Berry	100 15	100 61
<i>Lonicera Periclymenum</i> (Honeysuckle)	"	100 19	100 60
<i>Opuntia Tuna</i> (Prickly Pear)	"	100 14	100 49
<i>Pyrus Malus</i> (Apple)	"	100 14	100 51
<i>Ribes Grossularia</i> (Gooseberry).	"	100 13	100 60
<i>Tamus communis</i>	"	100 10	100 64
<i>Prunus communis</i> (Sloe)	Drupe	100 25	100 53
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	Capsule	100 14	100 48
<i>Allium ursinum</i>	"	100 17	100 55
<i>Canna indica</i>	"	100 13	100 68
<i>Datura Stramonium</i>	"	100 11	100 63
<i>Ipomœa tuba</i>	"	100 14	100 31
<i>Iris foetidissima</i> } mean result {	"	100 16	100 36
" <i>Pseudacorus</i> } }	"	100 16	100 42
<i>Primula veris</i> (Primrose)	"	100 16	100 42
<i>Scilla nutans</i> (Bluebell)	"	100 7	100 67

THE PROPORTION OF PARTS IN FRUITS 321

PERICARP AND SEED.—TABLE OF LOSS IN WEIGHT—*continued.*

Plant-name.	Type of fruit.	Loss in weight during the drying process, the moist condition being taken as 100, the dry weight being then given.	
		Pericarp.	Seed.
Hura crepitans (Sandbox-tree)	Woody capsule	100 34	100 45
Ravenala madagascariensis	Woody capsule	100 39	100 65
Swietenia Mahogani (Mahogany)	Woody capsule	100 37	100 26
Acacia Farnesiana	Legume	100 35	100 50
Cæsalpinia sepiaria	"	100 24	100 46
Cajanus indicus	"	100 38	100 42
Canavalia obtusifolia	"	100 20	100 41
Cassia fistula	"	100 31	100 40
Dioclea reflexa	"	100 31	100 49
Entada polystachya	"	100 25	100 45
Faba vulgaris	"	100 12 5	100 40
Guilandina bonducella	"	100 14	100 33
Leucæna glauca	"	100 22	100 37
Mucuna urens	"	100 14	100 50
Phaseolus multiflorus	"	100 15	100 40
Poinciana regia	"	100 45	100 45
Ulex europæus	"	100 41	100 49
Vicia sativa } mean result	"	100 32	100 47
" sepium }			
PALMACEÆ.			
Acrocomia lasiospatha	Drupe	100 34	100 68
Areca Catechu	Berry	100 23	100 58
Cocos nucifera (Coco-nut)*	Drupe	100 21	100 53
Cocos plumosa	"	100 63	100 63
Hyophorbe Verschaftii	Berry	100 15	100 87
Mauritia setigera	"	100 55	100 57
Oreodoxa regia	"	100 58	100 81
SUMMARY OF SOME OF THE RESULTS.			
Average for fleshy and pulpy berries	Six kinds	100 14	100 57
" typical fleshy capsules	Eight kinds	100 14	100 51
Typical fleshy drupe (Prunus)	One kind	100 25	100 53
Average for legumes	Fifteen kinds	100 27	100 43
" woody capsules	Three kinds	100 37	...
" Palm fruits	Seven kinds	100 38	100 67

* This result applies to a dry, waterless coco-nut.

The régime
of the drying
fruit.

The régime of the drying fruit as indicated by the loss of weight of the pericarp and the seeds can be numerically formulated for nearly sixty plants from the data given in the following table. If we wish to extend the inquiry by distinguishing in the case of the seed between the seed proper and its coverings in this drying process, the data for several of these plants will be found in Chapter IX. Should one desire to go further and differentiate in these respects not only between the seed-coverings and the seed proper, but also in the case of albuminous seeds between the behaviour of the albumen and the embryo, the requisite data for plants like *Cassia fistula*, *Poinciana regia*, etc., will be found in the same chapter.

In the first place, regarding the fruit as made up of pericarp and seeds, we can extract from the table all the elements necessary for determining its drying régime, namely :

- (a) The weight of the moist fruit ;
- (b) Its loss in the drying process ;
- (c) The proportion of pericarp in the moist and dry fruit.

In the same way, for the seed we should require :

- (a) The weight of the moist seed ;
- (b) Its loss in the drying process ;
- (c) The proportion of the coats in the moist and dry seed.

The subject can only be illustrated here by a few examples. If the reader desires to work out the régime of other plants, he will find in the table the requisite data.

THE PROPORTION OF PARTS IN FRUITS 323

ILLUSTRATIONS OF THE DRYING RÉGIME OF FRUITS AND SEEDS ON THE PLANT.

(The data concerning the proportion of the pericarp to the seeds will be found in the next table, whilst those relating to the proportions between the seed and its coverings are given in Chapter IX. By referring to the table the elements for other plants will be found.)

			Weight in grains.		Loss of weight stated as a percentage.		Relative weight, taking the entire fruit or seed as 100.	
			Ripe moist.	Dried.	Ripe moist.	Dried.	Ripe moist.	Dried.
<i>Guilandina bonducella</i>	Legume	Pericarp	200	28·4	100	14·2	50	30
		Seeds (2)	200	66·3	100	33·1	50	70
		Entire	400	94·7	100	23·7	100	100
	Seed	Coats	61	17·7	100	29	61	58
		Kernel	39	15·6	100	40	39	42
		Entire	100	33·3	100	33·3	100	100
<i>Canavalia obtusifolia</i>	Legume	Pericarp	248	50·4	100	20·3	62	45
		Seeds (6)	152	61·6	100	40·5	38	55
		Entire	400	112·0	100	28·0	100	100
	Seed	Coats	11·3	2·7	100	24	45	27
		Kernel	13·7	7·3	100	53	55	73
		Entire	25·0	10·0	100	40	100	100
<i>Iris Pseudacorus</i> (see footnote, p. 324)	Capsule	Pericarp	137·5	16·3	100	11·9	55	25
		Seeds (65)	112·5	48·7	100	43·3	45	75
		Entire	250·0	65·0	100	26·0	100	100
	Seed	Coats	0·72	0·14	100	20	40	20
		Kernel	1·08	0·58	100	54	60	80
		Entire	1·80	0·72	100	40	100	100
<i>Primula veris</i> (Primrose)	Capsule	Pericarp	1·84	0·3	100	16·3	46	25
		Seeds	2·16	0·9	100	41·7	54	75
		Entire	4·00	1·2	100	30·0	100	100
<i>Æsculus Hippocastanum</i>	Capsule	Pericarp	490	67·2	100	13·8	70	40
		Seeds (1)	210	100·8	100	48·0	30	60
		Entire	700	168·0	100	24·0	100	100
	Seed	Coats	73·5	28	100	38·1	35	28
		Kernel	136·5	72	100	52·8	65	72
		Entire	210·0	100	100	47·6	100	100

ILLUSTRATIONS OF THE DRYING RÉGIME OF FRUITS, ETC.—*continued.*

			Weight in grains.		Loss of weight stated as a percentage.		Relative weight, taking the entire fruit or seed as 100.	
			Ripe moist.	Dried.	Ripe moist.	Dried.	Ripe moist.	Dried.
<i>Ipomœa tuba</i>	Capsule	Pericarp	35	5	100	14'3	35	20
		Seeds	65	20	100	30'8	65	80
		Entire	100	25	100	25'0	100	100
	Seed	Coats	7'3	2'3	100	31'5	44	46
		Kernel	9'2	2'7	100	29'4	56	54
		Entire	16'5	5'0	100	30'3	100	100
<i>Swietenia Mahogani</i> (Mahogany)	Capsule	Pericarp	5100	1869	100	37	85	89
		Seeds	900	231	100	26	15	11
		Entire	6000	2100	100	35	100	100
	Seed	Coats	8'4	0'74	100	9	60	20
		Kernel	5'6	2'96	100	53	40	80
		Entire	14'0	3'70	100	26	100	100
<i>Cassia fistula</i>	Legume	Pericarp	4250	1320	100	31'1	85	80
		Seeds	750	300	100	40'0	15	20
		Entire	5000	1620	100	32'4	100	100
	Seed	Coats	2'63	0'6	100	22'8	26'3	15
		Kernel	7'37	3'4	100	46'1	73'7	85
		Entire	10'00	4'0	100	40'0	100'0	100
	Seed	Coats	2'63	0'60	100	22'8	26'3	15
		Albumen	5'37	2'64	100	49'2	53'7	66
		Embryo	2'00	0'76	100	38'0	20'0	19
Entire	10'00	4'00	100	40'0	100'0	100		
<i>Arum maculatum</i>	Berry	Pericarp	4'2	0'61	100	14'5	60	30
		Seeds (3)	2'8	1'42	100	50'7	40	70
		Entire	7'0	2'03	100	29'0	100	100.
<i>Pyrus Malus</i> (Apple)	Berry	Pericarp	993	136'4	100	13'7	99'3	97'4
		Seeds (10)	7	3'6	100	51'4	0'7	2'6
		Entire	1000	140'0	100	14'0	100'0	100'0

Note that in some cases, as in *Iris Pseudacorus*, there is a slight difference between the loss of weight of the entire seed, as given under the fruit and under the seed. This is due to the aborted seeds being included in the first case.

THE PROPORTION OF PARTS IN FRUITS 325

TABLE CONTAINING THE ELEMENTS FOR THE DETERMINATION OF THE DRYING RÉGIME OF FRUITS AND SEEDS AS ILLUSTRATED IN THE PAGES PRECEDING.

(The only natural orders indicated are the Palmacæe by P. and the Leguminosæ by L. before the plant's name. Further details will be found in Note 28 of the Appendix for those plants where N. follows the name.)

	Type of fruit.	Average weight of a moist fruit in grains.	Number of seeds in fruit tested.	Weight-relation of the pericarp, taking the entire fruit as 100.		Loss of weight of fruit when air-dried, taking the moist fruit as 100, the dry weight being then given.
				Moist fruit.	Dry Fruit.	
Pyrus Malus (Apple), N.	Berry	900	10	99.3	97.4	100 14
Citrus Aurantium (Common Orange), N.	,,	2400	5	99.3	98.3	100 19
Citrus Aurantium (Mandarin Orange)	,,	1900	5	99.0
Citrus decumana (Shaddock), N.	,,	14,000	80-85	97
P. Cocos nucifera (Coconut), N.	Drupe	60,000	1	96	78	100 30
Ribes Grossularia (Gooseberry), N.	Berry	120	40	95	80	100 15
Prunus communis (Sloe), N.	Drupe	30	1	95	90	100 27
Achras Sapota (Sapodilla), N.	Berry	1000	5	95
Sambucus nigra (Elder), N.	,,	3.5	3 or 4	93	60	100 21
P. Acrocomia lasiospatha, N.	Drupe	550	1	92	85	100 36
P. Acrocomia sclerocarpa .	,,	...	1	...	89	...
P. Cocos plumosa, N. . .	,,	100	1	91.6	91.6	100 63
P. Arenga saccharifera, N. .	,,	600	1	90	80	100 50
Psidium Guajava (Guava) .	Berry	600	300	90
Momordica Charantia, N. .	Capsule	500	15	89	51	100 15
Opuntia Tuna (Prickly Pear), N.	Berry	800	90	89	70	100 18
Tamus communis . . .	,,	14	4 or 5	87	50	100 18
Ravenala madagascariensis, N.	Capsule	700	10 or 12	87	80	100 42
Lonicera Periclymenum, N. (Honeysuckle)	Berry	5	5	86	66	100 25
L. Cassia fistula	Legume	5000	95	85	80	100 32.4
Sparganium ramosum, N. .	Drupe	1	1	85	84	100 45
Swietenia Mahogany (Mahogany), N.	Capsule	5800	60	85	89	100 35
Hura crepitans (Sandbox-tree), N.	,,	3000	14	84	80	100 36
Barringtonia speciosa, N. .	Berry	9000	1	82	52	100 15
L. Poinciana regia, N. . .	Legume	3500	40	80	80	100 45
L. Entada polystachya, N. .	,,	800	14	75	62.5	100 30
L. Cæsalpinia Sappan . . .	,,	260	4	75	75	100 50
Theobroma Cacao, N. . .	Berry	7000	45	75

TABLE CONTAINING THE ELEMENTS, ETC.—*continued.*

	Type of fruit.	Average weight of a moist fruit in grains.	Number of seeds in fruit tested.	Weight-relation of the pericarp, taking the entire fruit as 100.		Loss of weight of fruit when air-dried, taking the moist fruit as 100, the dry weight being then given.
				Moist fruit.	Dry fruit.	
P. Areca Catechu (Areca-nut), N.	Berry	250	1	74	53	100 . 32
Thespesia populnea . . .	Baccate capsule	230	13 or 14	72	45	100 33
L. Ulex europæus	Legume	3	4 or 5	70	66	100 43
Scilla nutans	Capsule	10	20	70	20	100 25
Æsculus Hippocastanum, N. (Horse-chestnut)	„	700	1	70	40	100 24
Monstera pertusa, N.	Berry	5	1	66	30	100 20
P. Hyophorbe Verschafftii	„	15.5	1	65	24	100 40
P. Oreodoxa regia, N. . . .	„	15	1	64	56	100 66
L. Cæsalpinia sepiaria . . .	Legume	100	5	64	48	100 32
L. Canavalia obtusifolia . . .	„	400	6	62	45	100 28
L. Canavalia gladiata, N. . .	„	...	6	...	45	...
L. Canavalia ensiformis, N. . .	„	...	14	...	44	...
L. Mucuna urens	„	1000	3 or 4	61	31	100 28
L. Andira inermis	„	135	1	61	53	100 40
L. Pisum sativum (Pea) . . .	„	250	7 or 8	60	20	100 20
L. Phaseolus multiflorus (Scarlet-runner) . . .	„	300	4	60	36	100 25
L. Phaseolus (tropical species)	„	...	3	...	34	...
Arum maculatum	Berry	7	3	60	30	100 29
Hedera Helix (Ivy)	„	5	3	59	52	100 40
Datura Stramonium	Capsule	300	600	58	24	100 30
Bignonia, near æquinoctialis, N.	Siliquiform capsule	1240	55	56	38	100 40
Allium ursinum	Capsule	2.4	3	56	29	100 33
Iris Pseudacorus	„	250	80	55	25	100 26
L. Vicia sativa	Legume	15	10	50	40	100 37
L. Vicia sepium	„	6	3 or 4	50	40	100 42
L. Faba vulgaris (Broad Bean), N.	„	800	5	50	24	100 26
Artocarpus incisa (Bread-fruit)	Aggregate	12,000	60	50
L. Guilandina bonducella . . .	Legume	400	2	50	30	100 24
L. Dioclea reflexa	„	1800	4	47	36	100 41
L. Cajanus indicus	„	40	4	47	45	100 40
L. Leucaena glauca, N. . . .	„	100	24	47	35	100 30
Primula veris (Primrose), N.	Capsule	4	62	46	25	100 30
P. Mauritia setigera, N. . . .	Berry	1000	1	46	45	100 56
Aquilegia, N. . . .	Follicular capsule	10	100	46	24	100 45
L. Acacia Farnesiana	Legume	150	20	46	40	100 40
Iris foetidissima	Capsule	180	40	43	34	100 25
Canna indica, N. . . .	„	100	24	39	11	100 47
Ipomea tuba	„	100	4	35	20	100 25
Arenaria peploides	„	8	10-12	25	9	100 41
Quercus Robur (Oak), N.	Nut	60	...	35	19	100 40

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TABLE SUPPLEMENTARY TO THE PRECEDING AND RELATING ONLY TO THE PERICARP-RELATION OF THE AIR-DRIED FRUIT, THAT FOR THE MOIST LIVING FRUIT BEING NOT ASCERTAINED, EXCEPT IN THE CASE OF COCOS, WHERE TWO SPECIES FROM THE PREVIOUS TABLE HAVE BEEN ADDED FOR THE PURPOSE OF COMPARISON.

(See the preceding table for explanation. N.=Note 28 of the Appendix.)

	Type of fruit.	Average weight of a dry fruit in grains.	Weight-relation of the pericarp, taking the entire dry fruit as 100.
L. <i>Abrus precatorius</i> (4 or 5 seeds) .	Legume	8	25
L. <i>Albizia Lebbek</i> (7 or 8 seeds), N.	"	38	55
<i>Anacardium occidentale</i> (Cashew)	Nut	95	66
P. <i>Bactris</i> (species of), N. . . .	Drupe	170	67
L. <i>Bauhinia</i> (18 seeds)	Legume	300	78
<i>Cakile æqualis</i> , N.	Lomentaceous siliqua	0'7	71
" <i>maritima</i> , N.	do.	0'9	70
P. <i>Caryota</i> (species of) with 2 seeds, N.	Drupe?	80	26
P. <i>Cocos schizophylla</i> ? N. . . .	"	500	65
" <i>nucifera</i> (Coco-nut), N. . .	"	16,000	78
" <i>plumosa</i> , N.	"	63	91'6
L. <i>Cynometra</i> (species of) with 1 seed	Legume	200	26
P. <i>Elæis guineensis</i> , N.	Drupe	120	85
L. <i>Erythrina corallodendron</i> (7 or 8 seeds), N.	Legume	40	41
L. <i>Erythrina indica</i> (10 seeds) .	"	140	35
<i>Gossypium barbadense</i> (16 seeds) N.	Capsule	31	28
<i>Gossypium hirsutum</i> (23 seeds) N.	"	50	24
<i>Hibiscus esculentus</i> (10 carpels) N.	"	100	30
<i>Kleinhovia hospita</i> (5 seeds) .	"	1'6	50
P. <i>Licuala grandis</i>	Berry	10	42
P. <i>Livistonia</i> (species of)	"	25	49
<i>Moringa pterygosperma</i> (15 seeds)	Siliquiform capsule	170	62
P. <i>Prestoea montana</i>	Berry	18	30
<i>Ricinus communis</i> (Castor-oil), N.	Coccous capsule	12	50
<i>Rumex</i>	Nut	0'08	30
P. <i>Sabal umbraculifera</i>	Berry	10	44
<i>Saccoglottis amazonica</i> (2 seeds)	Drupe	330	94
<i>Scirpus maritimus</i>	Nut	0'07	50
<i>Terminalia Catappa</i> , N.	Drupe	110	95
<i>Viola tricolor</i> (40 seeds)	Capsule	1'5	50

SUMMARY

(1) This chapter deals with the weight-relations between the pericarp (fruit-case) and the seeds in the different stages of a fruit's history, and it involves a special inquiry into the drying of the mature fruit.

(2) After pointing out that for purposes of comparison the fruit in the moist living condition is far more important than in the dried dead state, the author illustrates his method of investigation by taking the fruit of *Barringtonia speciosa* (p. 294).

(3) The relative weights of pericarp and seeds in sixty-four mature fruits before drying begins are then discussed, and the results of the author's observations are tabulated (p. 297)

(4) With regard to the influence of the type of fruit on this relation, it appears that fruits possessing the greatest proportion of pericarp, that is to say, where the weight of the fruit-case is more than 90 per cent. of that of the whole fruit, are either berries or drupes (p. 299).

(5) In determining the weight-relation, "size" counts for little with drupes and berries. Thus about 2000 drupes of *Prunus communis* (Sloe) make up the weight of a single green fruit of the Coco-nut Palm, and nearly 5000 Elder berries (*Sambucus nigra*) are required to weigh down an average fruit of the Shaddock (*Citrus decumana*). Yet the proportions of pericarp and seeds are much the same in the two cases. With legumes the largest and heaviest fruits have the smallest seed-weight, a rule usually but not always applicable to capsules also (p. 300).

(6) The history of the weight-relations between the fruit-case and the seeds in different stages of the fruit's development is then dealt with, and it opens up a study of the growing, ripening, and drying fruit (p. 301).

(7) It is observed that whilst in the younger fruits the growth of the fruit-case is far in advance of that of the seeds, both fruit-case and seeds usually reach maturity about the same time.

(8) Yet there are fruits where seeds continue their growth after the fruit-case has begun to dry. This is exemplified in the fruits of the Coco-nut Palm (*Cocos nucifera*), of the Oak (*Quercus Robur*), and probably also of *Barringtonia speciosa*. The cases of the two first-named are discussed with much detail, the results largely of the indications of the balance. That of the coco-nut, which was studied by the author in the West Indies, is first dealt with, and it is shown that the seed grows markedly whilst the husk is drying. That of the acorns of the Oak, which was investigated by the author in Devonshire, is treated at length, and it is established that the seed of the acorn continues its growth after the shell has begun to dry (pp. 301-314).

(9) This occasional tendency of a seed to continue its growth after the fruit-case or pericarp has begun to dry, or, in other words, to die, finds its final expression in the germination of the seed on the plant. To put it in another way, it is a step towards vivipary.

(10) Reference is then made to the principle established by the results tabulated in this chapter, that as the fruit grows, matures, and dries, the proportion by weight of the pericarp decreases and that of the seeds increases. This is merely stating in other words the familiar fact of observation that the earlier history of a fruit's development is mainly concerned with the fruit-case and the later history with the seed. As illustrating this principle for the legumes, the pods of the Scarlet-runner (*Phaseolus multiflorus*) and of the Broad Bean (*Faba vulgaris*) are specially discussed, the fruits of *Iris Pseudacorus* being taken for the capsules, whilst the acorn is also referred to. Small departures from this rule are noticed in the cases of the coco-nut and of the fruits of *Iris fœtidissima* and *Barringtonia speciosa* (p. 315).

(11) Attention is then called to the significance of the fact that in the drying fruit the pericarp loses far more water than the seed, the result being that whilst the fruit-case dies the seed lives. Whilst on the average the pericarp of the moist fruit loses between 75 and 80 per cent. of its weight, the seed as a rule loses only half its weight (p. 318).

(12) When we compare the different fruit-types we find that it is in the behaviour of the pericarp in the drying process that most variation is displayed, the seeds being much more constant in this respect. Thus on the average fleshy capsules and pulpy berries lose 86 per cent. of the weight of the moist pericarp when drying on the plant, fleshy drupes 75 per cent., legumes 73 per cent., woody capsules 63 per cent., and palm fruits 62 per cent (p. 318).

(13) A method of numerically formulating the drying régime of fruits is then described and illustrated, and in a special table are given the elements of this determination for nearly sixty plants (p. 322).

CHAPTER XV

THE RELATION BETWEEN THE NUMBER OF SEEDS AND THE WEIGHT AND SIZE OF THE FRUIT

The relation between the number of seeds and the weight of a fruit,

THE relations between the number and weight of the seeds on the one hand and the total weight of the fruit and the proportional weight of the pericarp on the other offer an interesting study. Although we shall at first treat the subject on its own ground, it will soon be perceived that in so doing we are ignoring important determining influences. Foremost among such influences stands that connected with the abortion of ovules before and after fertilisation, this distinction in time with regard to fertilisation being pregnant with results as regards the future of the fruit. But the subject of the failure of ovules and seeds is dealt with in Chapter XVI., and here it will be only incidentally noticed as we proceed with the discussion.

(α) in the living fruit.

The living fruit, that is to say, the green, moist, full-grown fruit with large, soft, uncontracted seeds, first claims our attention. This is but natural, and indeed the main interest of the withered or air-dried fruit should chiefly lie in its ability to aid us in our studies of the living fruit. Although the data below tabulated are scanty, their acquisition has often involved a good deal of labour, and a large amount of material had usually to be gone over to get a few results. It is necessary, for instance, to select only full-grown moist fruits that show no signs of drying; but of these a large number have frequently to be rejected on account of defective seed-development, or of a lack of uniformity in the size of the seeds.

TABLE SHOWING THE RELATION BETWEEN THE NUMBER OF SEEDS IN CAPSULES AND LEGUMES, AND THE PROPORTIONAL WEIGHT OF THE PERICARP IN FULL-GROWN FRUITS BEFORE DRYING BEGINS.

	Number of seeds.	Number of fruits examined.	Average total weight of a fruit in grains.*	Proportions of pericarp and seeds, taking the weight of entire fruit as 100.		Average weight of a seed in grains.	Ranges.	
				Pericarp.	Seeds.		Pericarp proportions.	Total weight of fruits in grains.
<i>Æsculus Hippocastanum</i> (capsule).	1	8	650	72	28	182	64-78	450-900
	2	6	920	67	33	150	61-75	600-1140
<i>Canna indica</i> (capsule).	13	1	65	46	54	2.7
	19	1	85	41	59	2.6
	23	1	100	39	61	2.7
	25	1	108	37	63	2.7
<i>Iris</i>	37-50	2	161	62.5	37.5	1.4	60.2, 64.7	137, 186
<i>Pseudacorus</i> (capsule).	67-77	4	265	54.0	46.0	1.9	50-60	246-288
	84-86	2	353	55.5	44.5	1.9	51.4, 59.5	350, 357
<i>Iris foetidissima</i> (capsule).	27	1	132	46.0	54.0	2.6
35	1	172	44.6	55.4	2.7	
	39	1	196	44.1	55.9	2.8
	43	1	207	41.1	58.9	2.8
<i>Casalpinia Sappan</i> (legume).	3	1	216	74.5	25.5	18.3
4	1	240	75.6	24.4	14.8	
	5	1	272	74.9	25.1	13.6
<i>Dioclea reflexa</i> (legume).	3	1	1341	46.8	53.2	2.8
4	1	1814	47.3	52.7	2.39	
<i>Guilandina bonducella</i> (legume).	1	2	260	68.0	32.0	81.0
2	2	330	56.0	44.0	73.0	
<i>Pisum sativum</i> (legume).	5	1	199	61	39	15.4
	6	1	167	64	36	10.0
	6	1	138	58	42	9.7
	7	1	198	62	38	10.9
	9	1	290	57	43	13.9

* In the case of single fruits the actual weight is given.

† The average length of the 3-seeded pods is 127 millimetres, and of the 4-seeded pods 152 millimetres.

‡ Two sets of pods are here represented, the first and last belonging to one season, and the others to another season.

For capsules with a few large seeds, the behaviour of that of the Horse-chestnut (*Æsculus Hippocastanum*) would probably be typical. Out of the original six ovules, not more than two or three develop into mature seeds; and fruits with a single

Capsules and legumes.

seed are not infrequent. The capsules with one and two seeds are best suited for comparison in this respect. In passing from the single to the double-seeded fruit of full size and showing no signs of dehiscence or drying, fruits with the seed or seeds in soft white coverings and the embryo normally developed, we find

- (1) An increase of about 40 per cent. in the total weight of the fruit ;
- (2) A decrease in the proportional weight of the pericarp from 72 to 67 per cent ;
- (3) A decrease of about 18 per cent. in the weight of each seed.

With many-seeded capsules, as with those of *Canna* and *Iris*, we also find that a marked increase in the total weight of the fruit and a gradual decrease in the relative weight of the pericarp accompany the additions to the number of seeds, but the average weight of a seed seems usually to remain unchanged. All these are merely indications, and appeal for confirmation will be made subsequently to results estimated from the dry fruits.

The data for the living legume are too scanty, and will have to be supplemented by results obtained from dried fruits.

We now come to the question of the use of the dried or withered fruit in determining the relation between the number of seeds and the proportional weight of the pericarp. Naturally such an investigation is far easier with dried or withered fruits than with moist mature fruits that have not begun to lose weight in drying. We can furnish ourselves from the plant with abundant materials in all stages of drying, and where further drying is needed it can be readily accomplished at home. But the case becomes very different when we make use of moist fruits. Here it is necessary to select only those fruits which a previous study has shown to have reached their maximum growth, but have not yet begun to dry ; and this is not always so easy as it seems. Then, again, the question as

(b) In the dried fruit.

to which of the two sorts of fruits offers the best materials, the moist or the dry, has to be answered with another query as to whether the two results would be really comparable and would possess a biological importance similar in degree and in kind.

As far as the dry fruit is concerned, it is requisite to remember that we are here actually determining the relation between a resting seed with its vitality suspended and a dried-up and dead fruit-case. Whether it is a shrivelled berry or a shrunken drupe, as in *Ribes* and *Prunus*, or a dried dehiscing pod, as in *Vicia*, or a withered capsule, as in *Iris* and *Canna*, or a woody dry capsule, like that of the Mahogany (*Swietenia*), that on account of the abundance of ligneous tissue retains the form of the moist fruit, makes no difference. The mere retention of form in some dried fruits, as in certain kinds of legumes and capsules, and its complete loss in others, as in most drupes and berries, are merely accidents in the history of the fruit. The investigator does not recognise the distinction between moist and dry fruits in the living condition. For him all fruits are moist in the living state; and if, after the drying up and death of the fruit-case, the form of the living fruit is to some degree preserved, he will avail himself of the circumstance only in so far as it assists him in his studies of the living condition.

It would therefore appear that the moist and the dry fruit are not mutually comparable, and that the only comparison of any biological value is one which enables us to reconstitute the living fruit, when the only materials at our disposal are its dried-up remains. The loss in weight which the pericarp and seeds of the living fruit undergo when dried in ordinary air-conditions can be ascertained by experiment, and the results can be applied to the dry fruit. These shrinkage ratios, being constant for the same species and independent of the size of the fruit, do not, when applied, interfere with the progressive scale of the weight-relations between the pericarp and the seeds. In this sense, therefore, the data supplied by the dry

The data supplied by dried-up fruits are only of service when referred to the living condition.

fruit can be utilised ; and as long as the means of converting them are available, the actual conversion may be at times dispensed with.

The dry legumes of *Leucæna glauca* and *Albizzia Lebbek*.

The validity of this use of the dry fruits is brought out in the two following tables, which contain the results of observations in Grenada on a considerable number of the dry legumes of *Leucæna glauca* and *Albizzia Lebbek*. In the first table the results for the dry legumes are alone given. In the second table these results are compared with those for the moist fruits as far as the relative weights of the pericarp and seeds are concerned. It should, however, be added that whilst the shrinking ratios for the legumes of *Leucæna glauca* have been ascertained by experiment, those for *Albizzia Lebbek* have been

A.—TABLE COMPARING THE RELATION BETWEEN THE NUMBER OF SEEDS AND THE WEIGHT, LENGTH, AND PERICARP PROPORTIONS OF THE DRIED LEGUMES OR PODS OF LEUCÆNA GLAUCA AND ALBIZZIA LEBBEK.

	Number of seeds in a pod.	Number of pods examined.	Average length of a pod in millimetres.	Average weight in grains.			Average weight of a seed in grains.	Proportional weight of pericarp and seeds, taking the entire pod as 100.		
				Entire pod.	Pericarp.	Seed contents.		Pericarp.	Seeds.	Entire pod.
<i>Leucæna glauca</i>	10-12	6	114 mm.	12.7	4.9	7.8	0.72	38.6	61.4	100
	13-17	11	130 "	14.8	5.2	9.6	0.68	35.1	64.9	100
	20-21	7	173 "	24.6	8.7	15.9	0.77	35.4	64.6	100
	22-26	9	195 "	29.0	10.1	18.9	0.78	34.8	65.2	100
<i>Albizzia Lebbek</i>	1	10	142 "	8.80	6.52	2.28	2.28	74.1	25.9	100
	2	14	180 "	13.70	9.11	4.59	2.29	66.5	33.5	100
	3	13	193 "	17.78	11.22	6.56	2.19	63.1	36.9	100
	4	13	218 "	22.75	13.99	8.76	2.19	61.5	38.5	100
	5	12	228 "	27.45	16.80	10.65	2.13	61.2	38.8	100
	6	10	236 "	31.52	18.99	12.53	2.09	60.2	39.8	100
	7	8	251 "	35.20	19.58	15.62	2.23	55.6	44.4	100
	8	8	262 "	39.77	22.30	17.47	2.18	56.1	43.9	100
	9	9	254 "	40.07	22.05	18.02	2.00	55.0	45.0	100
	10	11	290 "	49.39	26.92	22.47	2.24	54.5	45.5	100
	11	8	282 "	51.26	28.50	22.76	2.07	55.6	44.4	100
	12	10	294 "	59.42	34.43	24.99	2.08	57.9	42.1	100

B.—TABLE COMPARING THE RELATION BETWEEN THE NUMBER OF SEEDS AND THE WEIGHT OF THE ENTIRE FRUIT AND ITS PARTS IN THE MOIST AND DRY CONDITION FOR THE LEGUMES OF *LEUCÆNA GLAUCA* AND *ALBIZZIA LEBBEK*.

(The shrinking ratios for the last-named have been estimated as explained in the remarks below.)

	Number of seeds in a pod.	Average weight in grains of entire pod.		Relative weights, taking the entire pod as 100.			
		Moist.	Dry.	Pericarp.		Seeds.	
				Moist.	Dry.	Moist.	Dry.
<i>Leucæna glauca</i>	10-12	41·8	12·7	53·4	38·6	46·6	61·4
	13-17	47·6	14·8	49·6	35·1	50·4	64·9
	20-21	79·3	24·6	49·8	35·4	50·2	64·6
	22-26	93·2	29·0	49·2	34·8	50·8	65·2
<i>Albizzia Lebbek</i>	1	31·78	8·80	82·1	74·1	17·9	25·9
	2	47·91	13·70	76·1	66·5	23·9	33·5
	3	61·28	17·78	73·2	63·1	26·8	36·9
	4	77·86	22·75	71·9	61·5	28·1	38·5
	5	93·82	27·45	71·6	61·2	28·4	38·8
	6	107·28	31·52	70·8	60·2	29·2	39·8
	7	117·37	35·20	66·8	55·6	33·2	44·4
	8	135·87	39·77	65·7	56·1	34·3	43·9
	9	133·25	40·07	66·2	55·0	33·8	45·0
	10	163·85	49·39	65·7	54·5	34·3	45·5
	11	170·90	51·26	66·7	55·6	33·3	44·4
	12	200·19	59·42	68·8	57·9	31·2	42·1

The shrinking ratios employed for *Leucæna glauca* are 100-22 for the pericarp, and 100-40 for the seeds; the pericarp thus losing 78 per cent. of its weight in the drying process, and the seeds 60 per cent.

The ratios used for *Albizzia Lebbek* are 100-25 for the pericarp, and 100-60 for the seeds.

estimated, as I had no opportunity of experimenting on the living fruits. On the average, in moist mature legumes of this character the pericarp loses about 75 per cent. of its weight during the drying process, whilst the weight of the seeds is diminished by about 60 per cent.; and these are the ratios applied to the dry *Albizzia* pods. The estimate for the moist fruit thus obtained cannot be far wrong, and since any error would uniformly affect all the results, the relations between them would be unaffected.

Inferences to be drawn from the tabulated results above given.

We find the answer to the question suggested by the columns of Table A as to the relative values of the data afforded by moist and dry legumes in the contents of Table B. Here we see that although the relative proportions by weight of pericarp and seeds are on different planes, the pericarp being proportionately lighter and the seeds proportionately heavier in the dry than in the moist fruit, the progressive changes of relation are the same in both. We thus arrive at the following conclusions with regard to the relations between the number and weight of the seeds, the weight and length of the pod, and the relative proportions of the pericarp, in the living legumes of *Leucæna glauca* and *Albizzia Lebbek*.

(a) It is only in the few seeded pods of each plant that the legumes follow the principle of capsules, where not only a marked increase in the weight and size of the entire fruit, but a gradual decrease in the relative weight of the pericarp accompanies the additions to the number of seeds.

(b) But this principle has a limit in each case. In *Leucæna glauca* it is restricted to the shorter pods with less than a dozen seeds. In *Albizzia Lebbek* it is confined to the shorter pods with less than seven seeds. Beyond these limits in both cases, as the seeds increase in number and the pods increase in length, the relative proportions of the pericarp and the seeds remain about the same.

(c) The average weight of a single seed varies but little, whatever may be the number of seeds or the length of the legume. A slight increase of weight is indicated in the case of the longer pods of *Leucæna glauca*; but I do not imagine that this small difference would have been sustained if the materials had been more abundant.

The indications of other dried legumes.

The weight-relations of the pericarp in some other dried legumes, as shown by those of *Vicia*, *Ulex*, and *Erythrina* in the following table, give no very definite results, the tendency of the decrease in the relative weight of the pericarp, as the fruits increase in size and weight and the seeds in number, being but slight. However, in *Guilandina bonducella*, which has

usually one or two large seeds in each pod, there is a decided repetition of the behaviour of capsules in these respects, thus supporting the conclusion derived from the legumes of *Leucæna glauca* and *Albizzia Lebbek* that it is the pod with few seeds that is most likely to follow the principle of the capsule.

But even in such a case this seems only to apply to legumes with a few large seeds. More often it would be difficult in small pods containing only a few seeds to discover any such relation. Thus there is certainly but little to be made out of the results for *Abrus precatorius* given in the following table, in the columns of which data for larger legumes, like those of *Canavalia obtusifolia*, will be found, which are equally indeterminate in their indications. Doubtless the scantiness of the materials is partly responsible for this ; but we might have looked for some more consistent results than are given for dry legumes in the subjoined table. There are evidently some disturbing influences at work that cause this irregularity in the relations between fruit and seed in these legumes. These influences, as will subsequently be shown, are connected with the failure of seeds and the abortion of ovules.

One disturbing cause is needlessly brought into action when we employ indiscriminately legumes that have dried on the plant and those that have dried in an experiment. A serious effect may be thus produced, a matter discussed in Note 16 of the Appendix. This influence has, however, been avoided in my own results by using for each plant only fruits dried in the same way.

Coming to the evidence of dried capsules, like those of *Iris Pseudacorus* and *Iris fetidissima*, we find the features of the moist capsule reproduced in the following table. As the fruit increases in size and weight and in the number of its seeds, the proportion of the pericarp steadily decreases, but, unlike the moist fruits, there is an increase in the weight of the individual seed. Other types of capsules, such as those illustrated by the siliquiform fruits of *Moringa pterygosperma*, seem to follow the same rule.

TABLE SHOWING THE RELATION BETWEEN THE NUMBER OF SEEDS AND THE PROPORTIONAL WEIGHT OF THE PERICARP IN DRY LEGUMES AND CAPSULES.

(In the case of all the legumes and of the *Moringa* capsules the fruits had dried on the plant ; whilst the *Iris* capsules were allowed to dry slowly in my room.)

Plant.	Number of seeds in a fruit.	Number of fruits examined.	Average length of a fruit in millimetres.	Average weight in grains.			Average weight of a seed in grains.	Proportional weight of pericarp and seeds.		
				Entire fruit.	Pericarp.	Seed contents.		Pericarp.	Seeds.	Entire fruit.
Vicia sepium (legume).	4 or 5	8	30	2'36	0'93	1'43	0'33	39'4	60'6	100
	7-12	4	35	3'99	1'55	2'44	0'27	38'9	61'1	100
Ulex europæus (legume).	4	3	14'7	1'23	0'83	0'40	0'10	67'6	32'4	100
	5	5	...	1'24	0'82	0'42	0'08	66'1	33'9	100
Erythrina corallo-dendron (legume).	6	3	14'7	1'47	0'93	0'54	0'09	63'6	36'4	100
	3 or 4	2	...	13'3	5'7	7'6	2'2	42'9	57'1	100
Guilandina bonducella (legume)*	5 or 6	4	...	27'3	11'7	15'6	2'8	42'9	57'1	100
	7-9	5	...	41'6	17'0	24'6	3'1	40'9	59'1	100
Iris Pseudacorus (capsule).	1	6	...	53'3	20'8	32'5	32'5	39'0	61'0	100
	2	5	...	88'0	27'2	60'8	30'4	30'9	69'1	100
Iris foetidissima (capsule).	37	1	...	36'2	14'2	22'0	0'60	39'2	60'8	100
	50	1	...	43'3	14'6	28'7	0'57	33'7	66'3	100
	63	1	...	62'3	16'3	46'0	0'70	26'2	73'8	100
	74	1	...	70'0	17'0	53'0	0'72	24'3	75'7	100
	85	1	...	80'0	20'0	60'0	0'71	25'0	75'0	100
Moringa pterygosperma (siliquiform capsule).	96	1	...	93'3	23'0	70'3	0'73	24'7	75'3	100
	19-35	5	...	32'4	12'6	19'8	0'72	38'9	61'1	100
Abrus precatorius (legume).	40-55	5	...	58'7	17'9	40'8	0'90	30'5	69'5	100
	12	1	228	13'1	8'4	4'7	4'0	64'1	35'9	100
Canavalia obtusifolia (legume).	16	1	266	17'8	11'0	6'8	4'3	61'8	38'2	100
	3	1	...	5'6	2'0	3'6	1'2	35'7	64'3	100
	4	1	...	8'0	2'2	5'8	1'4	27'5	72'5	100
	4	1	...	7'2	1'65	5'55	1'4	22'9	77'1	100
	4	1	...	7'3	1'8	5'5	1'4	24'7	75'3	100
Canavalia obtusifolia (legume).	5	1	...	9'0	2'7	6'3	1'3	30'0	70'0	100
	5	1	...	9'0	2'1	6'9	1'4	23'3	76'7	100
	6	1	...	13'3	5'4	7'9	13'2	40'6	59'4	100
	6	1	...	12'3	5'7	6'6	11'0	46'3	53'7	100
	8	1	...	15'6	6'0	9'6	12'0	38'5	61'5	100
	8	1	...	14'6	6'3	8'3	10'4	43'1	56'9	100

* These pods were all gathered in the dried dehiscing condition at the same time from the same plant.

Summing up the indications of the influence of the number of seeds on the proportion of parts in capsules and legumes, we find that the capsule, as illustrated by the fruits of *Iris*, *Canna*, and *Æsculus*, in response to the augmentation of the number of seeds acquires a relatively lighter pericarp. The fruit increases in size and weight; but this increase is due more to the seeds than to the fruit-case. The legume, as typified by the fruits of *Leucæna glauca* and *Albizzia Lebbek*, follows the principle of the capsule in the few-seeded pods; but in the many-seeded fruits it preserves a fairly constant relation between the weight of the pericarp and the seeds, the pod increasing regularly in length and weight as the seeds increase in number. But the other results obtained for legumes often give no definite clue to any such relations, except in the case of pods with a few large seeds, as in *Guilandina bonducella*, where the principle of the capsule is indicated by both the moist and the dry fruits. This lack of relation is partly due to insufficiency of materials; but in the case of small pods with a few seeds, like those of *Abrus* and *Ulex*, there is evidently some disturbing cause which largely counteracts the display of a connection between the number of seeds and the size of the pod. The circumstance of the growth of the legume being linear, rather than tangential, as in the capsule, may help to explain why the first-named is more irregular in its behaviour. For this reason also the legumes would be more liable to be affected by the abortion of ovules and the failure of seeds.

As regards the alterations in the average weight of a seed with the accession to the number of seeds and with the increase in the weight and size of the fruit, the results seem to justify the following conclusions:—

(a) In the case of many-seeded capsules, like those of *Iris* and *Canna*, we find that as the fruit increases in size and the seeds in number, the seeds of *Iris* increase their weight, whilst those of *Canna* remain unchanged. But when a capsule matures only one or two large seeds, as with the Horse-

Summary of the indications of the influence of the number of seeds on the fruit in the case of capsules and legumes.

The degree of constancy of the weight of a seed in fruits of different size and weight.

chestnut (*Æsculus Hippocastanum*), the seeds of the two-seeded fruits are smaller and lighter than those of the single-seeded fruits, in this case the decrease in weight being about 18 per cent.

(b) With regard to legumes the indications supplied by the 126 dry pods of *Albizzia Lebbek* are particularly valuable, all of them being obtained at the same time from the same tree. Here the seeds range in number from 1 to 12; and for each number of seeds from 8 to 13 pods were employed. Here it will be seen that whilst the legume doubles its length, and increases its weight sevenfold, the average weight of a seed changes but little. The extreme range of the variations amounts to only about 13 per cent. of the average weight of the seed, the variations themselves being evidently fortuitous in character. The testimony of the legumes of other plants named in the tables cannot carry much weight, because the materials are insufficient. But I would gather from the cases of *Ulex europæus* and *Abrus precatorius* that with small pods the seeds keep their weight as they increase in number and the pods increase in size.

The study of the relation between the number of seeds and the proportions of the fruit opens up a difficult problem.

And now, before leaving this subject of the relation between the number of seeds and the weight and size of the fruit and its parts, it is necessary to point out that, however suggestive the indications may be, we have not yet discovered an end of the thread of this tangled problem. Yet these figures may serve to direct our efforts in the right direction. Thus the first question they will lead us to put will be the very pertinent one relating to the causes and nature of the variation in the number of seeds in the fruits of the same individual plant. If the relative size of the fruit is determined on fixed principles by the number of seeds, it would be natural to inquire what determines the number of seeds.

But several subsidiary questions arise when we peruse the columns of the tables. Why, for instance, does a single-seeded pod differ from other many-seeded pods on the same

plant in the exceptional proportion of its pericarp? In the single-seeded fruits of *Albizzia Lebbek* the large size of the pod in relation to the solitary seed is very conspicuous. But those interested in the subject will call to mind other leguminous plants displaying fruits of the same character. Let us take, for example, the pods of *Cytisus Laburnum* and of *Sophora tetraptera*. Occasionally they contain only a single seed; and in such cases it will not be necessary either to measure or to weigh them in order to perceive that, as compared with the typical many-seeded fruits, the size of the pod is quite disproportionate. However, if we rip open one of these single-seeded legumes, and examine the interior carefully, we make a discovery. There is, it is true, only one seed, but we can discern with a lens the remains of all or most of the missing ovules that existed in the ovary before pollen was applied to the stigma. Here, then, is the clue.

But this opens up another subject for inquiry which is discussed with some detail in the next chapter, namely, the abortion of ovules and the failure of fertilised ovules or of young seeds. Much depends in the history of the fruit on whether the original pollination of the stigma resulted in the fertilisation of the ovules, or merely served to stimulate the growth of the fruit. In the first event there would be produced a normally seeded fruit, but in the second event only a seedless one. It is, however, the partial failure of the ovules or seeds that will afford the most suggestive materials for study. If some of the ovules only are fertilised, important alterations in the form of the fruit may result; but the character of the change in shape will be determined by the situation of the aborted ovules, whether at the extremities of the fruit, or in the midst of the other ovules. Changes in shape much less marked will occur, if the fertilised ovules or young seeds fail early in their development. If the seed fails at a later stage in its growth, but little effect is produced on the fruit.

A problem bound up with questions relating to the abortion of ovules and the failure of seeds.

SUMMARY

(1) The relation between the number of seeds and the weight of the fruit, more especially for legumes and capsules, is then investigated, increase of size being connoted by increase of weight. In this connection the question is raised as to the stage in which the fruit offers the best materials for such a study, whether as a moist, mature living fruit on the plant, or as a dried fruit of the herbarium. The answer supplied is that dried-up fruits are only of service when referred to the living condition, since a fruit with living pericarp and actively functioning seeds cannot be compared with one where the fruit-case is dried up and dead, and the seeds are in a state of suspended vitality. The comparison can only be made with dried fruits by reconstituting the living condition.

(2) To determine this relation, however, we are often compelled by the whip of necessity to appeal to the dry fruit; and the author tabulates the results of a large number of observations on dried as well as on moist fruits.

(3) Summing up the indications of the influence of the number of seeds on the proportion of parts in capsules, like those of *Æsculus*, *Canna*, and *Iris*, he finds that the fruit, in response to the increase in the number of seeds, whilst becoming larger and heavier, acquires a relatively lighter pericarp. The legume, as typified by the pods of *Albizzia Lebbek* and *Leucæna glauca*, on which extensive observations were made, follows the principle of the capsule in few-seeded pods. However, in many-seeded pods, as the seeds increase in number and the fruit increases in length and weight, the legume preserves a fairly constant relation between the pericarp and the seeds.

(4) The indications afforded by other legumes often give no very definite results. This is due in part to the insufficiency of the materials, but partly also to the influence of some disturbing cause which specially affects small pods with few seeds, like those of *Abrus* and *Ulex*, and seems to make each plant a law to itself with regard to the size and weight of the legume and the number of the seeds. This influence is apt to upset all small sets of observations.

(5) It is in the abortion of ovules and failure of seeds that the cause of this disturbing influence is to be found; and it is pointed out that the legume would be more likely to be affected than the capsule in this respect, since its growth is mainly in one dimension, while with the capsule the growth is tangential rather than linear.

(6) As regards the alterations in the average weight of a seed as the seeds increase in number and the fruit increases in size and weight, the indications for the legume are that the seed's weight is but little

changed. For capsules the results obtained vary. Thus, with *Iris*, we find that as the fruit increases in size and the seeds in number, the seeds add to their weight and size, whilst with *Canna* they remain unchanged. But when a capsule matures only one or two large seeds, as with the Horse-chestnut (*Æsculus*), the seeds of the double-seeded fruits are smaller and lighter than those of the single-seeded capsules.

(7) However, the study of the relation between the number and size of seeds and the proportions of the fruit opens up a difficult problem. Questions concerned with the variation in the number of seeds in the same plant at once present themselves, and these cannot be answered without an inquiry into the abortion of ovules and the failure of young seeds. Much depends in the history of the fruit on whether the original pollination of the stigma resulted in the fertilisation of the ovules or merely served to stimulate the growth of the pericarp. These matters are dealt with in the succeeding chapter.

CHAPTER XVI

THE ABORTION OF OVULES AND THE FAILURE OF SEEDS

The history
of the in-
vestigation.

I FIRST took up this subject quite accidentally in Tobago whilst determining the proportional weight of the pericarp in the dry beaded pods of *Erythrina corallodendron*. Since the pronounced moniliform habit presented a disturbing influence, I was led on to examine its nature, and thus the inquiry commenced. A few weeks afterwards I made a detailed investigation in Grenada of the failure of ovules in the dry legumes of *Albizzia Lebbek*, and the inquiry developed. The investigations were continued in England and subsequently in Turks Islands. From the beginning my usual plan of following indications was adopted, forming crude hypotheses as I went along and dropping them as soon as they had lost their usefulness. Many points of course remain undetermined, and the contents of the present chapter can only be offered as a contribution to the study of a difficult but highly interesting subject.

Each fruit examined told its own story in its own way and threw new light on some point of the subject. Thus, after I had first learned from the legumes of *Vicia* that all the ovules begin to respond to the fertilisation of the ovary, the capsules of *Primula* gave the same testimony, but in a different fashion, and further elucidated the matter. The pods of *Albizzia* and the capsules of *Iris* and *Allium* afforded valuable data relating to the influence of the early failure of ovules and of very young seeds on the form of the fruit, the first named giving me the

hint that in the form of a fruit we have the history of the ovule rather than of the seed.

Regarding the beading of legumes many fruits supplied evidence both direct and indirect. Not only was special appeal made to characteristic moniliform pods like those of *Sophora* and *Erythrina* and to the less marked, though normal, contractions of the legumes of *Albizzia*, but help was also received from legumes like those of *Poinciana regia*, where the contraction of the pod is the exception and not the rule, and from pods like those of *Vicia* and *Ulex*, where the symmetry of the fruit is not affected by the failure of ovules and of very young seeds. The indications again of fruits of other types, like those of *Iris*, gave valuable data in this connection. Scarcely a fruit examined failed to assist in the elucidation of the problem. One of the earliest notes in my journal relating to this subject was to the effect that there was evidently a very early stage of ovule-abortion in the case of pods of *Erythrina corallodendron* which expressed itself in the narrowest constrictions of the fruit, but left no trace of the ovule itself. This has served to lighten up the background of the inquiry from the commencement to the end.

I made a special study of the legumes of *Vicia sativa* and *V. sepium* as concerns the abortion of ovules and the failure of young seeds. In the first case the legumes are long and narrow. In the second case they are short and relatively broad. The pods of *Vicia sativa* average 43 or 44 millimetres in length and about 5 millimetres in breadth, and possess as a rule eleven mature seeds and one aborted ovule or undeveloped seed. The pods of *Vicia sepium* average about 31 millimetres in length (range 25 to 36 millimetres) and 6 millimetres in breadth, four or five seeds being usually matured. In both species the average number of ovules in the flower is about the same, namely, twelve, the range being ten to sixteen in both plants.

With both species all the ovules begin to enlarge and to turn green after fertilisation of the ovary. At first about 0.3

The failure
of ovules in
Vicia sativa
and
V. sepium.

millimetre in size, they all attain a size rather less than a millimetre. It is after this stage that the differences between the two fruits are displayed, and in describing them I will make use of my average results. In the case of *Vicia sepium* four of the original twelve ovules now begin to fail and shrivel, the rest proceeding with their growth until about 1.5 millimetre across, when three more fail, and ultimately only five become mature seeds. On the other hand, with *Vicia sativa* nearly all the twelve ovules give rise to mature seeds, only one as a rule failing either in the early or later stage above described. I may add that such a study should be made on moist green pods in different stages, since the dry fruit could tell us but little of the history of the ovules.

Now this conspicuous difference in the history of the ovules is associated with considerable contrast in the growth of the pods, the pod of *Vicia sativa*, where nearly all the ovules form mature seeds, becoming long and narrow, and that of *Vicia sepium*, where many of the ovules fail, becoming short and broad, so that the ripe fruits differ greatly in appearance. At first sight one would be inclined to connect the shorter pod of *Vicia sepium* with the greater failure of the ovules, since in both species the original number of ovules is the same. But on closer investigation we find that the contrast in length cannot be so easily explained. In the first place, the ripe pod of *Vicia sepium* is but partially filled by its seeds, whilst that of *V. sativa* is nearly or completely filled. If the pod of the first named had been quite full of seed, the argument would have had some cogency; but as it happens, large unfilled spaces occur at the two ends of the seed-cavity due to the failure of the ovules chiefly in those situations. We thus get an indication of the independence of the size of the pod as far as concerns the number of seeds.

From this it would follow that the same dimensions of the legume are in the main retained in the few-seeded and in the many-seeded pods of *Vicia sepium*. Further inquiry indeed shows that this is in a general sense the case, such differences

as occur indicating only a slight increase in length of the pod as a result of a great increase in the number of seeds, and affording but scant basis on which to found an explanation of the differences in length between the pods of these two species. Thus the rule which we would apply to explain the differences between the two species largely fails when we apply it to the individuals of one of them; and we are accordingly debarred from using this argument in explaining the fact that the long pod of *Vicia sativa* has many seeds and few failures and the short pod of *V. sepium* many failures and few seeds.

Using legumes of the same set of plants of *Vicia sepium* and selecting a few at random, I found that a pod where all the twelve ovules had developed into mature seeds, a very rare event, had the same length as a pod where only five seeds had matured. So again a four-seeded pod and a nine-seeded pod had the same dimensions. In the aggregate, however, there is a tendency in the pod to increase its length as the seeds increase in number; but it is quite insufficient to explain the difference in length between the pods of these two plants. Thus ten pods of *Vicia sepium* containing four or five seeds had an average length in the dry state of 30 millimetres, whilst five pods containing from seven to twelve seeds had an average length of 35 millimetres. Here the doubling of the number of seeds only resulted in the increase of the pod's length by one-sixth.

There are two other points to notice in connection with the legumes of these two species of *Vicia*. In the first place, it will have been remarked that the aborted ovules, or more correctly speaking the seed-failures, are complementary to the matured seeds, the two going to make up the complete set of the original ovules. This is well brought out in the results tabulated below; and on referring to the general table for ovular abortion in fruits given later in this chapter, it will be seen that this principle is characteristic of fruits of all kinds.

In the next place, there is as a rule no "beading" to be observed in these fruits of *Vicia*, a character which is associated in moniliform pods with failure of the ovules. This is in part due to the fact that the failure of the growing ovule or young seed usually takes place in these pods at the extremities of the seed-cavity and not in the middle. But this only partly explains the absence of contractions, since much also depends on the structure of the pod itself.

TABLE SHOWING HOW THE ABORTED OVULES AND THE SMALL IMPERFECT SEEDS OF *VICIA SEPIUM* COMBINE WITH THE MATURED SEEDS TO FORM THE ORIGINAL COMPLEMENT OF THE OVULES (12).

(Twenty-four pods were examined. In a few cases the aborted ovules and imperfect seeds are differentiated, the results being given in the last two columns.)

Mature seeds.	Aborted ovules and imperfect half-sized seeds.	Total.	Aborted ovules.	Imperfect half-sized seeds.
2	10	12		
2	10	12		
3	8	11	6	2
3	8	11	3	5
3	7	10		
4	9	13		
4	9	13		
4	9	13		
4	7	11		
4	7	11		
4	7	11		
4	6	10		
5	7	12		
5	7	12	4	3
5	7	12	3	4
5	6	11	3	3
6	7	13	4	3
6	7	13	3	4
6	6	12	4	2
7	4	11		
8	4	12		
9	3	12		
11	0	11		
12	0	12		
		Av. 11.7		

All the ovules begin to enlarge and to turn green after the fertilisation of the ovary. Some of them fail before they attain a size of a millimetre and are termed aborted ovules. Others proceed further with their growth, but fail when about half-size (1.5 millimetre). The original size of the ovule is about 0.3 millimetre, their number averaging twelve.

TABLE SHOWING HOW THE OVULES THAT FAIL TO PRODUCE SEEDS IN THE CASE OF *VICIA SATIVA* COMBINE WITH THE MATURED SEEDS TO FORM THE ORIGINAL COMPLEMENT (12) OF THE OVULES BEFORE FERTILISATION OF THE OVARY.

(Ten pods were examined. All the remarks on the size, behaviour, and original number of the ovules of *Vicia sepium*, as given at the foot of the preceding table, here apply.)

Mature seeds.	Aborted ovules and imperfect half-sized seeds.	Total.
11	0	11
11	1	12
10	1	11
11	1	12
9	1	10
12	2	14
11	2	13
10	3	13
12	1	13
11	1	12
		Av. 12·1

To no fruits have I paid more attention to the relation between the failure of the ovules and the form and size of the fruit than to the legumes of *Albizzia Lebbek*. All my materials were obtained from one tree in Grenada ; but the observations were restricted on account of the season to the dry pods. These legumes well illustrate the commencement of the moniliform habit, but the contraction is rarely so marked as to merit that epithet.

The first thing to notice is the relation between the number of seeds and the length of the fruit. It will be observed from the results tabulated below that there is a progressive increase in the pod's length from the single-seeded to the twelve-seeded fruit ; but, as also indicated in the pods of *Vicia sepium*, the increase in length is relatively small, since the twelve-seeded legume is only about twice the length of the single-seeded fruit. Thus we obtain here another indication of the independent growth of the fruit-case as regards the seeds.

The failure of ovules in *Albizzia Lebbek*.

TABLE ILLUSTRATING IN THE CASE OF THE DRY LEGUMES OF *ALBIZZIA* *LEBBEK* THE RELATION BETWEEN THE NUMBER OF SEEDS AND THE LENGTH OF THE POD.

Number of seeds in a pod.	Number of pods examined.	Average length of a pod.		Range of length in inches.
		millimetres	inches	
1	10	142	5.6	4.9-6.5
2	14	180	7.1	6.3-8.5
3	13	193	7.6	6.3-8.7
4	14	218	8.6	7.2-9.8
5	13	224	8.8	7.0-10.3
6	10	236	9.3	7.6-10.5
7	8	251	9.9	8.5-11.3
8	8	262	10.3	9.0-11.4
9	10	254	10.0	8.4-11.1
10	11	290	11.4	10.0-12.5
11	8	282	11.1	10.1-12.3
12	10	295	11.6	10.8-13.2

These data are included in a table in Chapter XV., where the relations between the length and weight of the pod and the number of seeds are compared. The slight difference in three of the results is due to an additional pod being employed in the above table.

But it is around the early abortion of the ovules after the fertilisation of the ovary that our interest in the fruits of *Albizzia Lebbek* chiefly centres. With this feature in the history of these legumes are associated the contractions in the pod's width, which frequently give a fantastic shape to the fruit, as illustrated in the figures outlined in a later page. The legumes readily lend themselves to such an inquiry. The aborted ovules are conspicuous in the dry pod and present themselves as little black bodies 0.2 millimetre in size, attached to the end of the funicles, which are usually well preserved. The term aborted ovule is here applied, as in *Vicia*, to ovules that fail soon after the fertilisation of the ovary. Ovules that did not abort in this early stage as a rule advanced sufficiently far in their growth to be designated seeds. It will be subsequently shown that the failure of seeds advanced in growth has little or no influence on the fruit. As the result of a large number of observations the following inferences were formed.

In the first place, the complementary value of the aborted ovules with regard to the seeds is to be noticed. I had no opportunity of examining the flowers of this tree; but it is evident from what follows that, as in *Vicia*, the ovules average about twelve in number. So we find that whilst the one-seeded pods have usually about eleven aborted ovules, the twelve-seeded pods have none. With the intermediate pods we accordingly find the same relation. Thus a four-seeded pod displays about eight ovules and an eight-seeded pod about four ovules. This complementary relation is well displayed in the following table.

TABLE SHOWING THE COMPLEMENTAL RELATION IN THE CASE OF TWENTY-TWO LEGUMES OF ALBIZZIA LEBBEK BETWEEN THE NUMBER OF SEEDS AND THE OVULES THAT FAIL.

(See previous remarks for further explanation.)

Number of seeds.	Aborted ovules.	Full complement.	Number of seeds.	Aborted ovules.	Full complement.
1	11	12	5	8	13
1	11	12	5	7	12
1	11	12	6	7	13
2	10	12	7	4	11
2	9	11	8	4	12
2	8	10	8	4	12
3	10	13	9	3	12
3	9	12	10	2	12
4	9	13	12	0	12
4	8	12	12	0	12
4	8	12	13	0	13

Pods with thirteen seeds are rare, probably not 1 per cent. in frequency. Those with two to four seeds are most numerous, the single-seeded pods being infrequent.

Another important result was elicited by these observations, namely, that the shape of the pod of *Albizzia Lebbe* is not affected by the failure of a seed when it is well advanced in growth. Thus if a seed fails in the body of the pod when it is only one-third or one-half of the mature size, no narrowing of the fruit occurs. The form of the pod thus gives an epitome of the history of the ovules, but not of the seed. (I am assuming here that, as in *Vicia*, *Ulex*, etc., all the

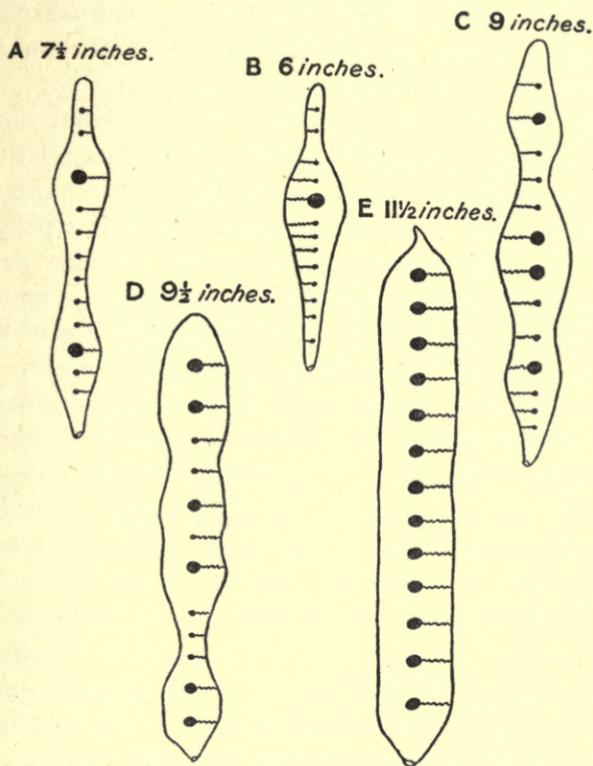
ovules share at first in the results of the fertilisation of the ovary ; and it is to those that fail early that the epithet of "aborted" is applied.) It is the early failure of the ovule that alone determines the contraction of the legume, and it is the number of such contiguous ovules that determines its amount.

The external form of the legume of *Albizzia Lebbek* therefore at once gives a clue as to the number of ovules that have aborted early and the number that have advanced to the seed-stage ; but it tells us nothing of whether the seed inside is fully formed or only half or a third of the normal size, the opening of the pod being required for that purpose. The form of the pod, therefore, depends on the fate of the ovules in an early stage of their history after the fertilisation of the ovary. After that is determined the ultimate form of the pod is fixed, and is not affected even if all the seeds fail before attaining half their normal size.

With the early failure of the ovules are connected, as before remarked, the contractions of the pod, which may be so slight as merely to give a sinuous margin to the fruit, or so marked as to produce almost a beaded shape. The moniliform tendency is displayed when the failure takes place in the body of the fruit. When the ovules abort at the ends the pod acquires tapering extremities. Now, as respects the narrowing of the body of the fruit, I find that the extent of the contraction depends on the number of contiguous ovules that fail. Thus a typical many-seeded pod, 35 millimetres broad in the seeded portion, has its width reduced to about 30 millimetres where a single ovule fails, to about 25 millimetres where two contiguous ovules abort, and to about 12 millimetres where three or four ovules fail. As a rule, when the space between the seeds is 12 to 15 millimetres broad there is no aborted ovule. When the inter-seminal space amounts to from 20 to 22 millimetres in width there is a single aborted ovule. When it is 30 to 35 millimetres there are two contiguous aborted ovules ; when 45 to 50 millimetres, three contiguous ovules, and so on.

The following outline-figures will serve to illustrate the foregoing remarks.

ALBIZZIA LEBBEK



These figures illustrate the relation between the contractions of the legumes and the failure of ovules shortly after the fertilisation of the ovary, the contraction being greatest when contiguous ovules abort, and least when only one fails.

All the figures are greatly reduced, but on the same scale. The seeds are indicated by large black spots, and the ovules by small black ones. In these diagrams it is assumed that the pod can be seen through. The seeds and ovules are, of course, arranged alternately on the two valves.

Many of the features of the legumes of *Albizzia Lebbek* are exhibited by the irregularly moniliform pods of *Cytisus Laburnum*, though here the ovules do not fail early but proceed

*Cytisus
Laburnum.*

a little with their growth and abort as young seeds. When all the ten ovules form mature seeds, or advance considerably in growth, the pod is regular in form and displays no constrictions; but more often three or four of the seeds fail in a very early stage, and when contiguous produce a marked constriction in the mature fruit. The club-shaped single-seeded pods, where all the ovules fail except one near the distal end, are very remarkable.

Reserving my treatment of beaded legumes for a later page, it may be here added that important data relating to this subject are supplied by the legumes of *Ulex europæus* and *Entada polystachya*. The examination of the *Ulex* pods brought out the fact that early abortion of the ovules never even provokes a tendency to moniliform contraction, and that the form of the pod, fixed soon after the fertilisation of the ovary, remains unaffected by the early failure of the ovules. This no doubt results from the structural characters of the pericarp.

Ulex
europæus.

The legumes of *Entada polystachya* also gave their indications. Here there is no early failure of the ovules after the fertilisation of the ovary; but all advance considerably in growth, and when failure occurs it is the young seed about a fourth of the normal size that aborts. Here the fruit consists of a series of joints each containing a single seed and held together in the dry state by the "replum," a stout stem-like border that would of itself prevent any constriction of the pod. The usual absence not only of a seed but of any trace of an ovule in the two terminal joints leads one back to an earlier condition of things, when additional ovules existed that are now doubtless only represented by rudiments in the ovary, and disappear altogether in the fruit.

Entada
polystachya.

The behaviour of legumes with one or two seeds is well represented by the fruits of *Guilandina bonducella*. The ovary here possesses two ovules, and it would seem that as a rule half of the pods mature one seed and the rest two seeds. In the first case the second seed usually attains a diameter of 4 or 5 millimetres before aborting, the mature size being about 25

Guilandina
bonducella.

millimetres. We can thus perceive, as explained with regard to *Albizzia* pods, why no effect is produced on the form of the fruit by the failure of one of the seeds. Had the ovule failed in an early stage the effect might have been noticeable. But even then, as in the case of *Ulex* pods, it is probable that there would have been no constriction in the pod's width, a result due to the structure of the pod itself.

Capsular fruits now claim our attention ; and it may be said of them, as of the legumes, that the mature seeds, the young seeds that fail before they attain any size, and the ovules that abort early, make up the full complement of the ovules in the flower. This is well brought out in the average results given in the table preceding the summary of this chapter, and one need scarcely labour the point here. They all behave, for instance, like the fruits of *Arenaria peploides*. The primal complement of twelve ovules in this case can almost always be recognised in the fruit, whether the fruit only contains five or six seeds or as many as ten, the failures making up the balance. All the ovules of the unfertilised ovary can be thus accounted for. They are potentially seeds from the beginning. The occurrence of rudiments of ovules in the flower raises quite another question, which will be dealt with in a later page.

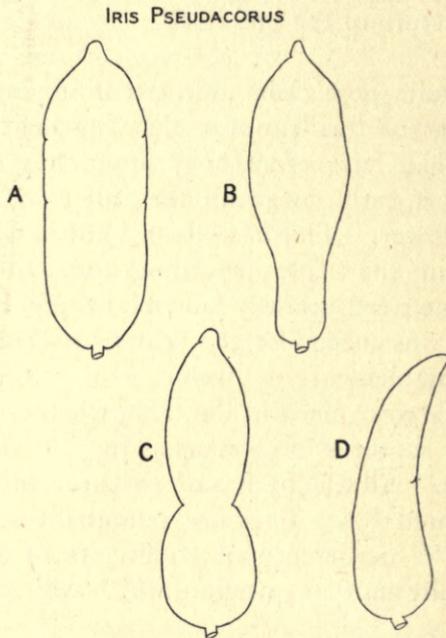
The failure
of ovules in
capsules.

As an example of the influence of the failure of ovules on the form of capsules, I will first take that of *Iris Pseudacorus*. Here there are two rows of ovules in each of the three compartments of the fruit ; and they all begin to enlarge after the fertilisation of the ovary. If most of the ovules in each of the two rows mature as seeds, the seeds are closely packed and overlap each other and are irregularly wedge-shaped ; but if the ovules in only one of the rows become seeds, whilst those of the other row fail, then the seeds assume a disc-like form.

Illustrated
by those of
Iris Pseuda-
corus.

Failure of some of the ovules is, however, a normal event, and much depends on their number and on their situation. Thus the average result given in the table at the end of the

chapter for a fruit possessing 120 ovules is that 80 mature as seeds, 30 fail soon after the preliminary enlargement due to fertilisation, and 10 fail after they have attained a fourth or a third of the size of the normal seed. In the typical oblong fruit 9 or 10 ovules soon abort at the bottom of each



Outline-figures of the capsules of *Iris Pseudacorus* showing the effect on the shape of the partial failure of the ovules and young seeds in different parts of the fruit, as described in the text.

- A=a typical regular fruit.
- B=a club-shaped or bulbous fruit.
- C=a fiddle-shaped fruit.
- D=a curved or arcuate fruit.

compartment. The occasional early failure of nearly all the ovules in the lower third of the young fruit gives the mature capsule a bulbous or club-like shape. I found such fruits frequent in one locality. An outline-figure of one of them is given above. If this became the rule, the bulbous form would become a specific constant. Should the early failure

of the ovules and of the young seeds be principally restricted to the centre of each compartment, the fruit-walls collapse in the middle and we get a fiddle-shaped fruit, as shown in the figure.

Then, again, if the failure of the ovules and young seeds takes place mainly in one loculus, whilst the seeds in the other two for the most part develop normally, the mature fruit then assumes a curved or arcuate shape, the concavity corresponding to the compartment in which the failures are situated. Sometimes in arcuate fruits two loculi or compartments correspond to the concave side; and then it will be found that seeds are lacking in the centre of each of the two loculi concerned. If the third compartment had been similarly affected, a fiddle-shaped fruit would have been produced. However, the essential feature of the arcuate type of fruit is a full set of seeds on the convex side, associated with extensive abortion or failure of the ovules and very young seeds on the concave side. Such are some of the commoner types of deformation of these capsules; but lesser irregularities arising from the same cause are numerous.

Irregular forms of the capsule, such as are frequent with *Iris Pseudacorus*, are not so common with *Iris foetidissima*. The fruits of the last named are useful in illustrating the fact that there is always a variation in the original number of ovules in each compartment of capsules of this type. The variation is not large, but it is sufficient to indicate a possible initial disturbing influence that would affect the symmetry of the plurilocular capsule. There are here appended the results obtained from four flowers of *Iris foetidissima* for the three loculi.

Iris foetidissima.

A	:	18	+	18	+	20	ovules
B	:	20	+	22	+	22	„
C	:	17	+	17	+	21	„
D	:	16	+	16	+	18	„

Respecting the distribution of aborted ovules in the several compartments of a plurilocular capsule, I obtained the following

*Scilla
nutans.*

data for *Scilla nutans*. Here each of the three loculi of the ovary contain from ten to twelve ovules, and each of the three compartments of the fruit on the average seven or eight seeds. As a rule early failure of the ovules and of the young seeds takes place with fair uniformity in the different compartments. Fruits displaying such variations in the number of seeds in each of the loculi as five, eight, seven, were frequent ; whilst those where the divergence was greater, such as three, eight, six, were infrequent. Out of a large number of fruits examined, none ever displayed a complete failure of the seeds in one compartment.

*Primula
veris.*

I will now take the capsules of *Primula veris*, in which most of the abortions of ovules and of the failures of young seeds take place around the base of the placental column. A typical ovary contains on the average about ninety white ovules. Of these all at first respond to the stimulus of the pollen, but only about sixty mature as seeds. Of the remaining ovules about twenty-two abort early when still uncoloured, whilst the rest (eight) turn green and advance a little in their growth before they too fail. Thus in *Primula* capsules we have a colour-indication which enables us to distinguish between the early failures of the ovules and the later failures of the young seeds, the first white, the second green like the growing seeds.

*Allium
ursinum.*

In *Allium ursinum* we have a three-celled ovary, each cell containing two ovules. Of the six ovules only three on the average mature as seeds, and often only two or even only one. In all cases the ovules that abort early and the seeds that soon fail combine with the mature seeds to make up the original complement of six ovules in the flower. The ultimate form of the fruit is, as might be expected, very variable, and irregularities almost appear to be the rule. Regular fruits have a seed in each cell ; but it is not uncommon to find two seeds in one cell, one seed in another, and none in the third, and then the shape is very irregular. However, all the ovules begin to enlarge after the fertilising process and at the same time all the cells enlarge as well ; but when the

two ovules in a cell fail early, the growth of the cell does not proceed far. Here it is evident that the initial growth of the fruit is determined by the fertilising process, but its later growth depends on the seed.

In *Aquilegia* each carpel contains on the average thirty ovules, of which twenty-five mature as seeds, four abort early, and one fails after proceeding a little further in its growth. Most of the aborted ovules usually occur in a clump at the lower end of the follicle. This may be connected with the fact that in the flower the ovules at the base of each carpel are exposed by the gaping of the carpellary walls, and remain exposed during much of the ripening of the fruit.

Aquilegia.

The tremendous waste of ovules, or rather of young seeds, in the sub-drupaceous capsule of *Ravenala madagascariensis* has already been alluded to in Chapter XIII. in connection with the dehiscence of the fruits. Of the plants with many-ovuled flowers included in the table near the close of this chapter there is not one that comes near *Ravenala* in this respect, five-sixths of the ovules at a very moderate computation failing to mature as seeds. It would seem, however, that nearly all of them first reach an early stage of seed-growth. One cannot help thinking that this large sacrifice of seeds is due to the great pressure exercised by the growing seeds upon each other within the stony, and for a long time unyielding, walls of the endocarp. When dehiscence at length occurs, the fruit-cavity is seen to be full of aborted seeds, 2 to 5 millimetres in size, with only a few large matured seeds.

*Ravenala
madagas-
cariensis.*

Although the beading of legumes is well marked in some genera, as in *Erythrina* and *Sophora*, a slight tendency to the moniliform type is frequently displayed in other leguminous genera with long pods, such as *Faba*, *Genista*, *Phaseolus*, *Poinciana*, etc. Though abnormal in such cases, it is due to the same influences that operate in the typical moniliform pod, namely, the early abortion of ovules and the early failure of seeds in the body of the fruit. In some other cases, as in those of the Laburnum and of *Albizzia*, the tendency is pronounced ;

*The beading
of legumes.*

but here the structural characters of the fruit act as final checks. In short broad pods like those of *Ulex* there is no constriction as a result of the failure of the ovules. The same remark applies to those of *Vicia*; but here the absence of any contraction of the legume is due chiefly to the failures occurring usually at the ends of the fruit. When several ovules and young seeds fail at the ends of a legume, we have tapering extremities. Such failures do not necessarily lead to shortening of a legume. An unusually short fruit is associated with an unusually small number of ovules in the flower.

Poinciana
regia.

Length in a legume is one of the pre-disposing causes; and in such a case even a dense ligneous texture, as in *Poinciana regia*, may not be sufficient to suppress the tendency. Here the failure of seeds that have advanced in their growth seems to have but little influence; but if a few contiguous ovules abort soon after fertilisation, or if a few contiguous seeds fail in a very early stage, a slight constriction of the pod is produced, the place of the seeds being occupied by ligneous material. Thus in a legume of *Poinciana regia*, where the space of four seeds was thus filled up, the width of the legume was reduced from 48 to 40 millimetres.

Erythrina
corallo-
dendron.

Coming to the typical moniliform legumes, I will begin with those of *Erythrina corallo-dendron*, which first led me to undertake this inquiry. Here there is a distinct relation between the beading of the pod and the failure of very young seeds; but this is not the whole of the matter, since the narrowest constrictions show no trace either of ovule or of seed. Here it may be that we have an indication of the influence of rudiments of ovules in the flower which disappear altogether in the fruit. In the accompanying diagram I have represented a typical seven-seeded dry pod about 115 millimetres long. At A, E, and F the constrictions are very narrow, 2 millimetres or less, and there is no trace of either seed or ovule. The other constrictions (B, C, D) are broader (2.5 millimetres to 3 millimetres), and here aborted seeds 1-1.5 millimetres long occur, the length of the constricted portion being regulated by the number

of contiguous seeds that have failed. These seeds when they aborted in the living fruit could not have been more than a sixth of the normal length, and when the failure took place the pod was probably about a third of its length when mature.

The above results of my examination of the pods of *Erythrina corallodendron* would lead one to infer that the narrowest constrictions, where not a trace of ovule or seed is to be recognised, are concerned with a much earlier stage of abortion, and this is also indicated by the terminal pointed beak. One may suppose that there were rudiments of ovules in the flower that were unable to respond to the fertilisation of the ovary, thus restraining the response of the ovary in those places to the stimulus of fertilisation. In this connection we have to bear in mind that the fruit as well as the seed is a product of pollination.

The flower in the case of the seven-seeded pod above described probably displayed thirteen ovules in its ovary, which I imagine would be typical for the species. Doubtless there were the rudiments of six or seven other ovules in the ovary, taking the beak of the fruit into consideration; and the primal complement of ovules was therefore probably twenty, though the other seven ovules need never have passed beyond the primordial stage. In other words, to adopt Dr Goebel's standpoint with regard to rudimentary organs in plants, the assumption of a primal complement of ovules larger than that of existing flowers does not require us to assume that all of them "functioned" as mature ovules. Such were some of the speculations that passed through my mind when I examined the first moniliform pods; and they have been exceedingly helpful to me ever since.

The moniliform pods of *Sophora tomentosa* were examined in the moist condition. A typical legume contains six or seven seeds separated from each other by narrow necks which often enclose shrivelled aborted seeds 1 to 3 millimetres long, the length of the neck depending on the number of aborted seeds, as indicated in the accompanying figure. We seem to be only concerned here with the failure of young seeds; but still earlier

*Sophora
tomentosa.*

failures are indicated when seeds, though actually in contact, are separated in a sense by a slight contraction of the pod, suggesting, as I would suppose, the existence of a rudimentary ovule in the flower which has disappeared in the fruit. The constriction of legumes is so generally associated with the early failure of

**ERYTHRINA
CORALLODENDRON**



Diagram of a seven-seeded dry pod, showing also six aborted seeds in the broader necks: drawn to a true scale.

**SOPHORA
TOMENTOSA**



Diagram of a portion of a green pod, showing the effect of failure of the seeds on the form of the fruit. The pod has not begun to dry, and the seeds are soft and large: drawn to a true scale.

ovules and young seeds that one would be scarcely justified in regarding a slight contraction as belonging to another order of things. Single-seeded fruits are spindle-shaped and contain the remains of at least six or eight seeds that failed in an early stage of their growth. When examining these pods I had no opportunity of inspecting the flowers; but I should imagine that the average ovular complement would be twenty, though

liable to considerable variation. The number of seeds in a pod varies from one to ten.

The development of the seedless fruit has a most important bearing on the relation between the form of many fruits and the failure of the ovule. The germination of the pollen-tube, writes Dr Jost in his *Lectures on Plant Physiology* (English edition, 1907, p. 370), has an exciting influence on the development of the fruit, so that fruits may be formed where degenerate ovules fail to become seeds. Again, Dr Pfeffer writes that the penetration of pollen-tubes may act as a stimulus to growth of fruits without any fertilising influence being exercised (*Physiology of Plants*, ii. 173). We have here a means of explaining some of the curious forms of fruits. But much will depend on whether the ovules habitually fail in the same part of the young fruit, or whether their failure is occasional and not restricted to one situation. In the first case we have a persistent effect produced on the fruit's shape which requires a specific or a generic value, as in *Anemone*. In the second we have inconstant variation of the fruit's form, such as I have described in the instance of *Iris Pseudacorus*.

The indication of the seedless fruit.

It would, however, be rash with the scanty data at my disposal to push this view very far. Yet the ovules that fail in a *Primula* or an *Iris* capsule appear to be in quite a different category from the ovules that fail in the fruits of the Oak or of the Coco-palm. In the first case it would seem that the ovules were actually fertilised and afterwards aborted. In the second case it would appear that the ovules were incapable of being fertilised, since they persistently fail. Lord Avebury would regard such persistently functionless ovules as carrying us back to the time when, in the ancestors of the plant, all the ovules developed into seeds (*Seedlings*, Internat. Sci. Ser., pp. 241 and 243). Professor Bower holds a similar view with reference to the abortive ovules in the beak of a fruit of *Anemone nemorosa*, regarding them as "the imperfect representatives of a plurality of ovules in the ancestry" (*The Origin of a Land-Flora*, 1908, p. 127). It should, however, be pointed

The functionless ovule.

out that this would not follow if we accept the standpoint taken by Dr Goebel in his *Organography of Plants* (i. 61), that functionless organs in plants are not necessarily the vestiges of former completely developed ones, and that many more primordia are laid down than become functional.

Many points remain to be determined before we can safely generalise in these matters. It is of importance, for instance, to ascertain by microscopical examination why, with the same complement of about twelve ovules in the flower, ten or eleven seeds are matured in *Vicia sativa* and only half that number in *Vicia sepium*. Then, again, it would be necessary to learn if the ovules that fail in the acorn, coco-nut, and similar fruits, have the same microscopical characters as the ovules that complete their development.

Nearly all the data included in the following table are from my own observations, with the chief exception of those relating to *Convallaria*, which are taken from Lord Avebury's book on seedlings. Although with many-ovuled flowers there is great variation as to the number of ovules that mature as seeds, as many as 80 or 90 per cent. failing in *Ravenala* and as few as 17 per cent. in *Aquilegia* and *Lychnis*, yet a rough average shapes itself for several of the capsules here dealt with. Thus with *Iris*, *Primula*, *Scilla*, *Stellaria*, and *Arenaria* about two-thirds of the ovules mature as seeds, and of the remainder the greater number (about 25 per cent. of the ovular complement) abort soon after fertilisation, whilst the residue advance a little in their growth and fail as young seeds. With leguminous plants the same rule prevails, though the data are insufficient for a numerical statement. Here also a large proportion of the ovules develop into seeds, but a considerable number fail, and of the failures most are concerned with the abortion of the ovule soon after fertilisation.

In nearly every case the number of the ovules in the flower has been directly determined; but in the cases of *Ravenala* and *Opuntia* it has been estimated from the total of mature seeds and of seed-failures.

Some indications of the following table.

TABLE SHOWING THE AVERAGE PROPORTION OF FAILURES OF SEEDS.
(See below for explanation.)

	Range of number of ovules in a flower.	Average number of ovules in a flower.	Seeds matured.		Failures of ovules and young seeds.		A. Failures of ovules.		B. Failures of young seeds.	
			Number.	Percentage.	Number.	Percentage.	Number.	Percentage.	Number.	Percentage.
<i>Iris Pseudacorus</i> , C.	90-160	120	80	67	40	33	30	25	10	8
,, <i>fetidissima</i> , C.	50-65	60	34	56	26	44	18	31	8	13
<i>Primula veris</i> , C.	70-100	90	60	67	30	33	22	24	8	9
<i>Scilla nutans</i> , C.	25-38	33	22	67	11	33	8	25	3	8
<i>Stellaria Holostea</i> , C.	9-12	11	7	64	4	36
<i>Arenaria peploides</i> , C.	10-13	12	8	66	4	34	2	17	2	17
<i>Entada polystachya</i> , L.	...	15	10	67	5	33	5	33
<i>Allium ursinum</i> , C.	6	6	3	50	3	50	2	33	1	17
<i>Ulex europæus</i> , L.	10-13	12	6	50	6	50	4	33	2	17
<i>Vicia sepium</i> , L.	10-15	12	5	42	7	58	4	33	3	25
,, <i>sativa</i> , L.	10-15	12	11	92	1	8
<i>Albizzia Lebbek</i> , L.	10-13	12	5	42	7	58	7	58
<i>Lychnis diurna</i> , C.	...	300	250	83	50	17
<i>Silene maritima</i> , C.	100-180	150
<i>Ravenala madagascariensis</i> , C.	...	60	10	17	50	83	50	83
<i>Quercus Robur</i> , N.	6	6	1	17	5	83	5	83
<i>Æsculus Hippocastanum</i> , C.	6	6	2	33	4	67
<i>Convallaria</i> , B.	6	6	1	17	5	83
<i>Opuntia Tuna</i> , B.	...	100	80	80	20	20
<i>Prunus communis</i> , D.	2	2	1	...	1	...	1
<i>Aquilegia</i> (a single carpel)	23-35	30	25	83	5	17	4	13	1	4

The percentage results given represent the proportion of the average number of ovules, as stated in the second column.

The data given in the last two columns, A and B, distinguish between the failures of ovules and the failures of young seeds.

The fruit-type is indicated by the capital letter after the plant-name: B, berry; C, capsule; D, drupe; L, legume; N, nut.

SUMMARY

(1) The subject of the failure of ovules and its influence on the form of the fruit was first taken up in connection with moniliform legumes, and the inquiry was extended to other fruits. Each fruit examined told its own story, and although many points remain undetermined, the data obtained go to support the following conclusions.

(2) In the first place, all the ovules begin to respond to the fertilisation of the ovary. This is equally true when it concerns the legume, as in *Vicia* and *Ulex*, and when it concerns the capsule, as in *Primula* and *Iris*.

(3) In many-ovuled flowers failure of a proportion of the ovules is a normal occurrence after the first enlargement due to the stimulus of fertilisation. In the case of plants with capsular fruits, it frequently happens, as in the case of *Arenaria*, *Stellaria*, *Primula*, *Scilla*, and *Iris*, that only two-thirds of the original complement of ovules develop into mature seeds. Of the ovules that fail, the greater number abort soon after fertilisation, whilst the remainder proceed a little with their growth and fail as young seeds. The same principle applies to plants with legumes, most of the ovules generally maturing as seeds, whilst of the remainder the majority abort early.

(4) It is shown that all the ovules conspicuous in the flower can be accounted for in the fruit, the complete ovular complement being made up by the ovules that abort soon after fertilisation, the seeds that fail in an early stage, and the seeds that proceed to maturity.

(5) It is in the legume that the influence on the form of the fruit of the failures of ovules and young seeds is generally most evident, a marked constriction resulting when the failures are contiguous in the body of the fruit, the degree of constriction being determined by the number of contiguous failures. The same principle applies to capsules, but not usually to the same extent. Yet in fruits like those of *Iris* and *Allium* great changes in the shape of the fruit may be thus brought about. In both legumes and capsules, however, but little effect is produced on the fruit's shape by the failure of seeds far advanced in growth. The form of the fruit is determined much earlier in its development. In a word, in the form of the fruit we have the history of the ovule rather than of the seed.

(6) Dealing especially with beaded legumes, it is first pointed out that abnormal constrictions of pods that are usually symmetrical, as in *Faba*, *Phaseolus*, and *Poinciana*, are due to the same influences that operate in the moniliform pod, namely, those concerned with the early abortion of ovules and the early failure of seeds. Even woody legumes, such as those of *Poinciana regia*, may exhibit constrictions due to the same causes.

(7) Next come those legumes, as with *Albizzia Lebbeck* and *Cytisus Laburnum*, where extensive failures of the ovules and young seeds habitually occur, producing a marked tendency towards the moniliform habit, but not sufficient to justify their being characterised as beaded legumes.

(8) As examples of the typical moniliform legume those of *Erythrina corallodendron* and of *Sophora tomentosa* are taken. Whilst the remains

of ovules and of young seeds are generally found in the constricted portions, it is shown that in certain cases no such remains exist, and it is argued that here we are concerned with only rudimentary ovules in the flower.

(9) Special stress is laid on the important indications given by the seedless fruit, where the fruit develops under the stimulus of pollination but the seeds fail. In the effects of failure of the ovules and young seeds on the fruit's shape a distinction is drawn between the constant failure of ovules in fruits, like those of *Quercus* and *Cocos nucifera*, and the normal failure after fertilisation of a certain proportion of the ovules in many-ovuled flowers, such as those of *Iris* and *Primula*. In the one case a persistent effect is produced on the fruit, in the other case an inconstant one.

(10) Much remains to be determined before one could safely generalise in these matters. It will be necessary to distinguish between the primal complement of ovules in a flower and the complement on which the systematist bases his distinctions. Of the second all are "functionable." Of the first many may never have passed beyond the primordial stage and may always exist as rudiments in the flower. Thus the carpels of *Anemone* are described as one-ovuled, yet the beaked form of the fruit has received its impress from other functionless ovules which the systematist does not recognise.

CHAPTER XVII

SEED-COLORATION

Inquiry
mainly
directed to
the con-
ditions of
coloration.

SEEDS, as is well known, display a great variety of hues, ranging from white and pale colours to deep green, black, brown, and red. Many seeds have a neutral or nondescript colour, which it is not easy to describe ; but probably brown in its numerous shades and mixtures is the most frequent. Whilst handling seeds so much, the colours naturally attracted my attention ; but seed-coloration involves so many points, physical, chemical, and biological, that a general treatment of the subject would be quite beyond my powers, and I will therefore mainly confine my remarks to a consideration of the conditions in which seeds acquire their colouring.

Not specially
adapted.

Matters relating to adaptation to means of dispersal will also be outside the field of discussion, but for quite another reason. The fancy is apt to detect similarity and adaptive purpose where in its ignorance accident alone could reign ; and it is too ready to forget that in the nature of things the whole organism is but a mass of adaptation, not only the cell-aggregate, but the cell itself. Adaptation to the conditions of life is the very essence of existence ; and we are not justified in singling out and designating as specially adaptive any character that happens to catch the eye, whilst ignoring all the rest. Adaptation goes without saying in this world of ours.

Seed-colours
in a native
garden in
Jamaica.

In the matter of seed-coloration puzzles surround us, especially in the tropics. Thus in the cultivated patch of a Jamaican native you may see growing side by side *Canavalia*

ensiformis with white seeds and *Canavalia gladiata* with red seeds, two plants by some considered as varieties of one species. (This association of white with coloured seeds is found also with our Scarlet-runner (*Phaseolus multiflorus*), where, besides the usual form with dark mottled seeds, there is a form with white seeds.) Looking around us in this bush-garden, we notice a great variety in the colours of the seeds, particularly with leguminous plants, some of which have been planted for ornamental or useful purposes, whilst others owe their presence there to birds. Growing over a neighbouring bush we notice *Abrus precatorius*, displaying in its opening pods the familiar bright red seeds with a black spot. Forming a shade for the young Cacao plants, we observe small trees of *Erythrina corallodendron*, exhibiting in their moniliform pods seeds strikingly similar in coloration to those of *Abrus precatorius*, though larger in size. Amongst the shrubby growths at the borders of the patch we see *Cesalpinia sepiaria*, the "Wait-a-bit" of the Jamaicans, showing dark mottled seeds in its dehiscent pods. Single trees, such as *Adenanthera pavonina* and *Blighia sapida*, are scattered about, the first-named displaying in its pods the beautiful large scarlet seeds used for necklaces, the second being the well-known Akee, from the branches of which hang bright red fruits, showing, as they open on the tree, shining black seeds partly exposed in their yellow arils. Hanging from a vine in the branches of one of these trees are the long dry fruits of the Loofah (*Luffa acutangula*), with their black seeds falling out; whilst on a neighbouring fence we see suspended the yellow fruits of *Momordica Charantia* (another cucurbitaceous plant), which, as they open, display their seeds in bright red soft coverings. However, when we turn to the fruit trees, the species of *Citrus* and *Anona*, the Sapodilla (*Achras Sapota*), and the Star Apple (*Chrysophyllum Cainito*), we miss the brightly coloured seeds, and find in their place whitish or brown seeds.

If the above illustration exhibits the variety in hue of tropical seeds, it also makes evident the difficulties attending such inquiries, and it at the same time shows the necessity of

Seed-colours
that dis-
appear
before the
fruit is ripe.

first considering the "How" of seed-coloration before one can attempt to think of the "Why." One of the first things that struck me in this connection was the circumstance that many a pretty hue in seeds comes and goes in the fruit before its seeds are exposed (by its dehiscence or its breaking down) to the air. This is well seen in *Abrus precatorius* and *Adenanthera pavonina*, where the scarlet coloration of the normal resting seed is preceded by a pretty rose-pink colour in the soft unripe seed. The seeds of *Ravenala madagascariensis* (the Travellers' Palm), when wrapped in their bright blue arils in the closed capsular fruit, are very different-looking objects from the same seeds in the opening fruit, when the aril has become a dirty brown. Then, again, on cutting open a young fruit of *Barringtonia speciosa*, one is a little startled to find seeds, half an inch in size and not much more than bags of fluid, coloured deep red, a hue which they lose altogether as the seed matures in the centre of the fruit. One of the most striking cases of seed-coloration is seen in the germination of the yellow seed of *Guilandina bonduc*, which, as the hard shell swells with the absorption of water, assumes a chocolate-brown hue. Such a seed, when the swelling process has affected one-half of its surface, is half yellow and half chocolate brown, and presents thus a conspicuous contrast in coloration.

Seeds colour
in the closed
fruit.

From the various cases of seed-colouring just noticed, it is obvious that it would be futile to look for an explanation before we learn more of the conditions attending and preceding the coloration of seeds. One of the most important conditions lies in the circumstance that seeds assume to a greater or less degree their permanent colours in the closed fruit before they are exposed to the air either by its dehiscence or decay. This is not absolutely essential for coloration, but it is as a rule essential for normal colouring. I have handled a great many immature seeds, and have found that generally such seeds colour defectively when removed as soft seeds from the green fruit. Those seeds that are white when immature and deep brown or black when mature often suffer least by being

allowed to colour in the detached state. However this may be, the point I wish to lay stress upon is that seeds are coloured in the closed fruits. Though that condition may not be absolutely essential for the development of colour, it is the protection which nature supplies to the plant-embryo, and it is under such circumstances that seeds acquire their hues.

It is to this general condition that attention will be first directed ; and afterwards inquiry will be made as to whether the colouring takes place in the green or in the ripe fruit, or in the drying fruit, or during all stages. Then other matters will be dealt with, such as the relation between the coloration and the drying and shrinkage of the seed.

With regard to the general question, it has already been shown in Chapter XI that in the case of berries, such as those of *Berberis*, *Arum maculatum*, and *Tamus communis*, coloration takes place within the moist fruit, and the same rule applies to fleshy fruits of the Apple and Sapodilla types and to other moist fruits. The seeds of *Momordica* acquire their colours in the most watery of fruits, the yellowish-brown seed being enclosed in a bright red soft covering. It is well to notice, however, that not all fleshy fruits have coloured seeds, to wit, those of *Citrus* and *Cucumis* ; but coloration seems to be more general in such cases, and when it occurs it takes place inside the moist fruit. (a) Berries.

In the same chapter it was noted that in dehiscent capsules, as illustrated by those of *Æsculus Hippocastanum* (Horse-chestnut) and *Iris Pseudacorus*, the seeds colour before the fruit opens, the coloration being well advanced in the first case, but in the second it only reaches the early stage of "browning." Capsules, as has been shown in Chapter XIII, often dehisce at an earlier stage than other types of dehiscent fruits, such as leguminous pods. In such cases it often happens that the seed-coloration is not complete when the fruit opens, the seeds deepening in hue after the dehiscence. Under unusual conditions the seeds may not begin to colour until the fruit dehisces. Thus, the immature soft seeds of the Mahogany, (b) Capsules.

according to my observations, retain their white hue until the capsule opens, when they begin to brown, a circumstance probably to be connected with the hard ligneous character of the fruit, the walls of which are 10 millimetres or nearly half an inch thick.

On the other hand, there is no difficulty in showing that with capsules and with similar fruits the absence of colouring before the fruit opens is the exception and not the rule. In baccate capsules, like those of *Thespesia populnea*, as already pointed out in Chapter XI, the white soft seeds of the green fruit, as they harden, become first purplish and then brown long before they are freed by the decay of the dried-up fruit. But here in Devonshire one has not to walk far to find the same indications in the plants growing around. The seeds of *Iris fetidissima* acquire their orange colour, those of *Scilla nutans* become shining black, those of *Allium ursinum* become deep reddish brown, and those of *Arenaria peploides* take on a similar hue, whilst the capsule is still moist and green and long before dehiscence occurs. So, again, the seeds of *Stellaria Holostea* and of *Primula veris* redden and brown before the capsule opens; whilst the seeds of *Aquilegia* assume their black hue in the moist unopened follicle. The common weeds around one's house in the tropics follow the same rule. In the cases of *Argemone mexicana*, *Datura Stramonium*, and *Portulaca oleracea* the soft white seeds become more or less black in the closed capsule whilst the fruit is still green and moist. The seeds of *Sesuvium*, a genus of beach plants, behave in precisely the same way. With *Ricinus* also the soft white seed hardens and colours in the green closed coccus.

In Chapter XI we found the same behaviour in the seeds of leguminous pods, as exemplified by those of *Cæsalpinia sepiaria* and *Ulex europæus*. But in legumes the coloration of the seeds is often more complete when dehiscence occurs than it is in capsules, because, as established in Chapter XIII, the fruit opens at a later stage of the drying process. It has already been indicated that the seeds of capsules often deepen

their hue after the fruit opens ; whilst in leguminous pods the seed colouring is practically complete when dehiscence takes place. With Leguminosæ this is the general rule whether the pod regularly dehisces, or breaks up into joints, or liberates the seeds by its decay. As further illustrations may be mentioned *Abrus precatorius*, *Acacia Farnesiana*, *Adenanthera pavonina*, *Canavalia gladiata*, and *C. obtusifolia*, *Dioclea reflexa*, *Entada*, *Erythrina*, *Guilandina*, *Leucæna*, *Mucuna*, *Phaseolus*, *Poinciana regia*, *Vicia*, *Vigna luteola*, etc.

With regard to the question whether seed-coloration is confined to one or all of the three states of the fruit, the green, the ripe, and the drying, there are so many different determining conditions between one fruit and another that a careful investigation is requisite before one can venture to reply. One would infer after watching the seeds of *Vicia* darkening in the drying and blackening pod, or the Horse-chestnut seeds as they brown in the drying capsule, that drying is necessary for their colouring. Here we should undoubtedly be wrong. On the other hand, we would conclude after observing the process of seed-colouring in the Blue-bell (*Scilla nutans*) that the seeds acquire their shining black hue in the moist green capsule. Here we should most probably be right. That the coloration of the seeds does frequently take place in the closed capsule whilst it is still green and moist has indeed been clearly shown a page or two back. But the subject is very complicated, and Nature seems to have done her best to make observation difficult and immediate inferences hazardous, more especially with legumes. Here experiment and observation must go hand in hand.

In the first place, I will take the colouring régime of the seeds of *Scilla nutans* as disclosed by my experiments on the fruits of the living plant. When I experimented on these capsules in the summer of 1908, I was not aware that similar experiments had been made by Lubimenko on the pods of certain leguminous plants, *Pisum sativum*, *Colutea arborescens*, and *Lathyrus latifolius*, the results of which have since been published

Does seed coloration take place in the green, ripe, or drying fruit?

Experiments of Lubimenko on the conditions in the interior of leguminous pods.

in a paper entitled "Étude physiologique sur le développement des fruits et des grains" (*Comptes rendus*, August 24, 1908). They are not concerned with the coloration of seeds, but they are interesting from the light they throw on the conditions in which it takes place. Selecting very young pods on the living plant with their sides still in apposition, he removed part of them by longitudinal sections, and found that they soon formed a new suture, closed themselves in, and developed normally. When, however, pods more advanced in growth and with their inner surfaces no longer in contact were experimented on, different results were obtained. By cutting out portions of the sides of the pods so as to bring the young seeds into direct communication with the outer air, it was ascertained that the growth of the seeds was arrested, the fruits falling off in about a week. The conclusions arrived at were that for the normal development of the seed a confined atmosphere (*une atmosphère confinée*) is needed, and that one of the functions of the pericarp is to maintain the internal air at a certain stable composition. The green parts of the pericarp, it is observed, decompose in light the carbonic acid arising from the respiration of the seeds and prevent its accumulation inside the fruit. Even in darkness the gas is kept within certain limits by its slow diffusion from the fruit.

As regards the failure of young pods when the seeds are exposed to the air through windows cut through the pericarp, it may be surmised that capsules with their cells or loculi distinct from each other would be rather more suitable for such experiments. When an opening is made in the side of an ordinary legume the whole contents are exposed to the outside air, whilst in a capsule, by confining the experiment to only one of the cells, the rest of the fruit would be relatively unaffected.

My own experiments on the green capsules of living plants of *Scilla nutans* occupied the period between the middle of June and the beginning of August, and were limited to one cell only in each fruit, the other two being left untouched. The cell was so incised that the seeds in it were freely exposed

to the air. Though checked by plants in pots kept indoors, the results as described below were all obtained from plants growing in a hedgerow and exposed to the ordinary weather-conditions. In the early stage, when the young seeds are little more than bags of fluid, they are pearly white. As the seeds mature and their contents solidify, they become successively dull white, yellowish, reddish brown, and finally shining black. The colouring stages and the maturation are completed in the green moist capsule before dehiscence. When the fruits were incised in the middle of June the seeds exposed were soft pearl-like bodies, which, if detached and allowed to dry, shrank to a mere skin. By the beginning of August the exposed seeds had reached the brown stage, the last but one of the stages of the colouring process ; but with the exception of the difference in hue and their rather smaller size they were normal hard matured seeds. In the other two closed cells of each capsule experimented on, the seeds during this period acquired the typical black colour and were normal in their other characters. The experiment did not seem to affect the rate of the changes in the seeds of the other two uncut cells ; and when the capsules of other plants around were dehiscing, these two cells were doing the same, displaying normal black seeds that contrasted in their hue with the brown seeds exposed in the incised cell. The upshot of these experiments is that the exposed seeds developed normally, with the exception of their failure to acquire the final black colour, for which enclosure in the fruit seems requisite.

The foregoing experiment on the seeds of *Scilla nutans* will serve to illustrate the complexity of the processes involved in seed-coloration. I will now proceed to discuss more at length the conditions under which seeds colour in leguminous pods, and in the first place I will take the blackening and black mottling of seeds. One of the chief points which we will endeavour to determine will be the connection between the coloration of the seed and the drying of the pod. Though the two processes are so frequently associated, it is quite

The blackening and black mottling of leguminous seeds.

possible that the association is in a sense accidental, and that, as in the berry and capsule, seed-coloration may occur in the green moist legume.

Vicia sepium
and *Vicia*
sativa.

The seeds of *Vicia sepium* and *Vicia sativa*, which are usually mottled with black spots on a dark green or greyish-green ground, will first serve to illustrate this point. After examining a considerable number of their seeds, one might think that these plants produced in each case three kinds of seeds as far as coloration is concerned. There are first the greyish or greenish-grey seeds, then the seeds with the same green or grey ground-colours, but mottled with black spots, and then the seeds that are almost uniformly black, the mottled seeds being the most frequent and the most typical. A closer inspection soon makes it clear that the seemingly uniform black colour really arises from an intensification of the mottling, and that, in fact, all three kinds have the same ground-colour, the differences being due to the variation in the extent of the mottling. In one seed it is almost absent; in the typical seed it is well developed; and in another it is so dense that the mottled patches largely coalesce.

Their
mottled
seeds.

In both these species of *Vicia* the soft seed of the green pod is green, with an embryo of a darker green. When the blackening and drying of the pod is well advanced these seeds gradually shrink, harden, and become duller or paler in hue, and then the black mottling appears, the shrinking of the pod ushering in the earlier changes. Long before the dehiscence of the pod the typical characters of the resting seed have been formed, and the embryo exchanges the dark green hue of the unripe soft seed for the dull yellowish colour that is so characteristic of the resting state of seeds.

With regard to the conditions under which the dark coloration of the seeds of these two species of *Vicia* occurs, the following remarks may be made. On the plant the drying and blackening of the pod precede the mottling of the seeds, which belongs to the latter stage of the shrinking and hardening process. But it appears to be essential for the develop-

The con-
ditions in
which the
mottling of
Vicia seeds
takes place

ment of the black mottling of the seeds that the pods should be left undisturbed on the plant. No mottling took place in any of my experiments on detached green pods with soft green seeds, whether the pod was allowed to dry in air or was placed in wet conditions, as in water or in wet moss. Experimenting on the soft green pre-resting seeds, I found that when totally submerged in water they failed to mottle and that when allowed to dry in air they did so very imperfectly. But when a soft green seed was placed on the surface of water so that a portion was exposed, in the course of a few days the exposed portion displayed mottling, whilst the under submerged part remained green. These results seem to signify that mottling occurs under conditions intermediate between those to which the air-drying seed and the submerged seed are subjected, such as would be presented in the confined conditions of the closed green pod.

These indications of the *Vicia* seeds will become more significant when we come to consider those of other leguminous seeds. It is more difficult than usual in their case to dissociate the coloration of the seeds from the drying of the pod ; but the data go to show that the seeds of *Vicia* are capable of hardening and of acquiring their dark coloration in the moist green pod. In this case the drying of the pod might be regarded as interfering with the completion of the blackening process ; and in this way the dark mottling would present itself as the result of a check in the progressive blackening of the seed. We would thus take it that *Vicia* seeds are mottled because they have failed to become uniformly black.

More determinate results are offered in the blackening of the large, soft, white pre-resting seeds of two other leguminous plants, *Mucuna urens* and *Dioclea reflexa* ; and I will let each tell its own story.

With *Mucuna urens*, where the immature seeds in the green pod are white, the soft unripe seeds harden and blacken as the pod dries and browns, completing all their changes in the closed pod, though the dark hue usually becomes paler

The blackening of the seeds of *Mucuna urens*.

and of a blackish grey when the seeds assume the final resting state. The changes in the seed are preceded by the shrinking of the fleshy cord or funicle and by the blackening of the raphe and scar, the rest of the seed's surface remaining for a time a pure white. These seeds do not mottle; but it is significant that though there is every appearance of a connection between the drying of the pod and the blackening of the seeds, the soft white seeds when detached blacken much more rapidly when wetted than when allowed to dry. Here, it seems, drying retards the process. It may be added that the subsequent blackening of the shrinking seed is apparently not connected with the previous blackening of the raphe and scar when the cord withers. The same thing happens with some white seeds (like those of *Canavalia ensiformis*) when the cord dries up, the black scar remaining a permanent feature of the white matured seed.

The indications of the seeds of *Dioclea reflexa*.

From these indications of the seeds of *Mucuna urens* we turn to those supplied by the seeds of the kindred plant, *Dioclea reflexa*. These seeds are also white when immature in the green pod, and when the pod darkens, as it begins to dry up, the seeds commence to shrink, harden, and blacken. But there is this difference. The blackening process is usually incomplete, and mottled seeds result. They also follow the general rule that the seed acquires its fixed characters as a resting seed, whether in colour or in other respects, in the closed pod. As in *Vicia sativa* and *Vicia sepium*, three kinds of seeds as regards their colour can be distinguished, the black or brownish black, the reddish brown, and the mottled seed showing black patches on a reddish-brown ground. As in *Vicia* also, the mottled seeds are most typical of the plant, and the mottling may be regarded as the failure of the blackening process. But in *Vicia* the black seed represents the end of the colouring process, whilst in *Dioclea* it represents the beginning. When the blackening of a *Dioclea* seed fails altogether the seed is reddish brown; but when the process is only partly checked there are formed black patches on a reddish-brown

Three kinds of seeds distinguished by their coloration.

ground. This blackening process accompanies the early shrinking and hardening of the soft, white pre-resting seed, and is most active after the seed has lost 20 per cent. of its weight ; but although often associated with the drying of the pod, there is good reason for holding that these changes in the colour, size, and consistence of the seed may occur, as in the berry, under very moist conditions.

Whilst observing the habits of the plants of *Dioclea reflexa* in their home in the forests of the Grand Etang in Grenada, I was able to notice the conditions under which the seed-coloration took place. Whilst the reddish-brown and the mottled seeds represented those that had undergone the greatest amount of drying in the pod on the plant, the black seeds were invariably those obtained from pods lying on the ground in the most humid parts of the forest, where the seeds failed to dry properly, and, as remarked in another page, sometimes dispensed with the resting stage and germinated in the pod. Such black seeds, when not germinating, possessed coats insufficiently hardened and still somewhat flexible.

Another indication that the blackening of the seeds of *Dioclea reflexa* is most complete under moist conditions was afforded by the circumstance that when the soft, white unripe seeds were detached and allowed to dry in a room they always began to colour and to mottle on the under surface, and were always much darker below than above. After three or four days the under surface was usually uniformly black, whilst the upper surface was only mottled. Such seeds when examined proved to be sensibly softer and considerably moister on the lower than on the upper side. Hence it was evident that a moist surface favoured the blackening process, whilst a rapidly drying surface retarded it.

Very instructive is the behaviour of the mottled seeds of *Phaseolus multiflorus* (Scarlet-runner). That the source of the colouring is in the coats alone and is not connected with the coloration of the embryo is apparently indicated in the fact that the embryo is pale green in the unripe or pre-resting

The conditions of seed-coloration as ascertained by observation and experiment.

The mottling of the seeds of *Phaseolus multiflorus* (Scarlet-runner).

seeds of both varieties of the plant, the variety with mottled black and pink or red resting seeds and that with pure white resting seeds. The seeds of the last named are also white when very small and undeveloped ; but they need not occupy further attention here.

The stages in the coloration of the variety with mottled seeds are as follows. In their immature state, when very small and soft, the seeds are pale green, with a pinkish or reddish tinge, the embryo being darker green. As the seeds increase in size they become uniformly pink or reddish, the embryo becoming paler in hue. When the seed approaches maturity as a pre-resting seed the pink colour of the coats deepens, and dark mottling begins when the soft full-grown seed commences to harden its coverings. (It may be noticed in passing that the soft, pink pre-resting seed parts with most of its colour when placed in water. This helps to explain the partial blanching which the half-sized pink seeds sometimes experience in the green pod, a change which has a bearing on the deprivation of colour in the white seeds of the other variety.)

The conditions under which coloration takes place.

During these observations and experiments on the seeds of *Phaseolus multiflorus* some indications pointed to the probability that the black mottling and hardening of the coverings were independent of the drying of the pod, though usually associated with it. Other signs seemed to show that the mottling only became at all evident after the pod had begun to dry. However, the point whether the preliminary drying of the pod was really necessary, or was merely an accidental association, was unexpectedly decided by an experiment begun with quite another object. Some fresh green pods containing only the large, soft, pink seeds, showing scarcely any black mottling, were kept in wet moss in a closed tin for nine days with the purpose of inducing the seeds to germinate without entering the shrinking stage. However, although no seeds were germinating, all of them, when the tin was opened, had hardened normally mottled coats. The pods themselves were com-

mencing to rot, but the general conditions under which the seeds underwent these changes must have been those of extreme moistness. Without intending it, I had induced these seeds to colour, harden, and probably shrink a little as well, under conditions as moist as that of a berry. The bearing of the results of this experiment has been dealt with elsewhere. Here we will merely accept their indication that the black mottling and induration of the coats of the seeds of *Phaseolus multiflorus* have but little to do with the drying of the pod with which they are so generally associated.

The results for the seeds of the four leguminous genera of plants above discussed are below tabulated. Though it is not easy at first sight to pick up the thread of the tangled data, one inference seems to shape itself out of all the observations and experiments, namely, that the black mottling and dark coloration of the seeds is not determined by the drying of the pod. From its close association with these processes in the seed-coverings, the drying of the pod has certainly all the appearance of having much to do with them. But we have seen that in berries, as well as in many capsules, seed-coloration can have little to do with the drying of the fruit.

This inference, though here drawn with regard to the black coloration of leguminous seeds, applies also to the brown coloration of seeds of this and other families, as will be brought out below, and probably to seed-coloration in general. In the berry and closed capsule, the soft pre-resting seed colours, hardens, and shrinks under conditions exceptionally moist. But the same capacity of colouring and hardening their coats under moist conditions is exhibited by the seeds of legumes, though in nature disguised by its association with the drying of the pod. We cannot also doubt that the early shrinking which accompanies the coloration and the hardening of leguminous seeds is at the same time an independent process, and is similarly not connected with the drying up of the fruit-case.

The black coloration of leguminous seeds is not determined by the drying of the pod,

but may occur under conditions as moist as those of the berry.

TABLE ILLUSTRATING THE STAGES IN THE BLACKENING AND BLACK MOTTLING OF LEGUMINOUS SEEDS.

	Colour of the Coats.					Colour of embryo.	
	Pre-resting seed of green pod.			Resting seed of dry pod.		Pre-resting seed of green pod.	Resting seed of dry pod.
	Full-grown.	Whilst shrinking detached from pod.	Whilst shrinking normally in pod.	Prematurely shrunken.	Normally shrunken.		
<i>Mucuna urens</i>	White	Blackening	Blackening	Blackish	Dark grey	...	White
<i>Dioclea reflexa</i>	White	Blackening	Mottling	Blackish	Black mottling on reddish brown ground	...	White
<i>Vicia sativa</i> <i>Vicia sepium</i>	Green	Dull green or grey; no mottling	Mottling	Dull green or grey; no mottling	Black mottling on a grey ground	Green	Yellowish
<i>Phaseolus multiflorus</i> — (a) mottled black seeds							
(b) white seeds	White	...	White	White	White	Pale yellowish green	White

The brown colour of seeds

On account of its predominance as the colour of seeds, brown deserves especial attention. As in the case of black, the indications by no means lend themselves to an easy interpretation. The brown coloration of resting seeds, which may vary in shade from a pale hue, as in Mahogany seeds, to a blackish brown, as in old seeds of *Entada scandens*, seems to be usually developed in seeds that were white in the soft, moist, unripe condition. That the browning process, whether in the leguminous pod or in the capsule or in the berry, is usually completed before the seeds are exposed to the air has been already established in this and in previous chapters. In all cases it is

associated with a shrinking and hardening of the soft, unripe, and pre-resting seed. But the brown coloration, with its associated processes, is to be noticed alike under moist conditions, as in baccate fruits, or under dry conditions, as in drying capsules and leguminous pods, a subject dealt with in preceding chapters.

Although seeds acquire their brown colour in the closed capsule and pod, their coloration, early shrinking, and hardening are so conspicuously associated with the early drying of the fruit that it is not a matter for surprise that there should seem to be some causal connection between them. However, experiment showed that these changes in the seed may take place where no drying of the fruit has occurred. Perhaps the most conclusive piece of evidence in this direction is afforded by the aborted seeds of the Horse-chestnut (*Æsculus Hippocastanum*). In full-grown moist capsules showing no signs either of dehiscence or of drying, and containing full-sized white moist seeds, it is not uncommon to find two or three aborted seeds only 2 to 4 millimetres across, but typically brown and hard-coated. The behaviour of the white moist seeds in a full-grown green capsule that has been placed in wet moss in a closed tin is also very significant. Though the capsule at the end of the experiment shows no signs of drying, since the air in the tin would be quite saturated with moisture, the seeds in a few days become normally brown, and experience a slight shrinking in size and a hardening of the coats. In spite, therefore, of their moist conditions, the Horse-chestnut seeds in this experiment experience the same changes that they exhibit in the drying capsule, thus behaving like the seeds of a berry.

We can therefore no longer suppose that the drying of the capsule is needed for the preliminary shrinking, hardening, and coloration of the seeds within. In the case of brown or black seed-coloration the inference is the same. In the pod, as shown in the case of *Phaseolus multiflorus*, and in the capsule, as illustrated by *Æsculus Hippocastanum*, the régime involved in the coloration, early shrinking, and preliminary hardening

not connected with the drying of the fruit.

Horse-chestnut.

The régime of the berry is reproduced in the colouring seeds of the pod and the capsule.

of the seed and its coats is that which is displayed by the colouring, shrinking, and hardening seed in the moist berry.

Whatever the nature of the connection may be, there is no doubt that the browning process of soft unripe seeds is associated in capsules and in leguminous pods with shrinking and hardening of the seed-coats. It has already been shown in the case of the soft, moist white seeds of the Horse-chestnut (*Æsculus Hippocastanum*) that they suffer a loss of 17 per cent. of their weight during the browning that accompanies the preliminary drying in the closed capsule (see Chapter XI). In the instance of *Entada scandens*, where the soft white seeds on removal from the green pod were allowed to dry on a table, the seeds did not attain their normal dark reddish-brown hue until they had lost about half of their weight. Passing through a preliminary yellowish stage, they lost in five or six days about 20 per cent. of their weight and became a light mahogany brown. After between two and three weeks, when they had lost about 55 per cent., they assumed the typical colour of the resting seed, the drying process being prolonged until the loss amounted to 60 per cent. The white soft seeds of *Entada polystachya* turn brown in a similar way; and here the two varieties, the large pale brown seed containing 10 per cent. of water, and the small dark brown seed with only 6 per cent., clearly show that the colour deepens as the seed becomes drier (see Chapter V). The white flabby seeds of the closed woody capsule of the Mahogany tree (*Swietenia Mahogani*) harden and turn light brown in four or five days after their removal. As a final example, the seeds of *Iris Pseudacorus* may be taken, which, when first exposed by the opening capsule in the early stage of browning, have already lost about 20 per cent. of their original weight as soft white seeds. It should, however, be observed that with fruits ripening late in the season, as, for instance, in October instead of the latter part of August and in September, the seeds may be drier and farther advanced in the browning process before dehiscence occurs. Such fruits, however, are backward in maturing, and may even fail to dehisce altogether.

The browning of unripe seeds in capsules and pods is associated with shrinking and hardening of the coats.

A curious distinction between capsules and legumes unfolded itself as I collated my notes on fruits and seeds. As shown in the subjoined comparison of the results given in the following tables, the so-called immature or pre-resting seeds of capsules are usually white, whilst those of leguminous pods are usually green. The proportion of green seeds would have been still greater for the pods, if herbaceous leguminous plants had been as well represented as a strictly natural comparison would have required. The green immature seed is typical of the dehiscent legume, as is shown in the general table. Nearly all the pods with green seeds are thus characterised. On the other hand, the pods with white unripe seeds are generally indehiscent, as in *Mucuna*, or break up into closed joints, as in *Entada*.

Indication that unripe seeds are usually white in capsules and green in leguminous pods.

SUMMARY OF THE TABLES GIVEN BELOW, SHOWING THE COLOURS OF UNRIPE OR PRE-RESTING SEEDS IN DIFFERENT KINDS OF FRUITS.

	Number of genera experimented on.			
	Total.	With green seeds.	With white seeds.	With seeds of other colours.
Legumes . . .	35	24	8	3
Capsules . . .	31	5	26	...
Berries . . .	7	3	4	...

With the exception of *Canavalia* the genera behave uniformly.

As frequently happens in such cases, a number of points have arisen during the development of this distinction, which it is now too late for me to elucidate. Though in the habit of noting the colour of immature seeds, I did not discover its significance as a distinction between types of fruits until I came to elaborate my notes on seed-coloration. I will not enlarge on this distinction here; but some of the characters associated with it will be noticed when I deal a page or two later with white and green immature seeds and with the colour of the embryo. Below are appended the tables to which the summary of results above given refers.

THE COLOURS OF IMMATURE AND MATURE SEEDS IN LEGUMES,
CAPSULES, AND BERRIES.

I. LEGUMES.

	Colours of seeds.		Special characters of legume.
	Immature (pre-resting).	Mature (resting).	
<i>Abrus precatorius</i> . . .	Pink	Scarlet	...
<i>Acacia</i> (near <i>arabica</i>) . . .	Pale green	Dark brown	...
„ <i>Farnesiana</i> . . .	White, then pale green	„	Indehiscent, pulpy
<i>Adenanthera pavonina</i> . . .	Green, then yellow, then pink	Scarlet	...
<i>Bauhinia</i> (species of) . . .	Green	Black	...
<i>Cæsalpinia Sappan</i> . . .	„	Light brown	...
„ <i>sepiaria</i> . . .	(A) Green	Mottled black and brown	...
<i>Cajanus indicus</i> . . .	(B) White	„	...
	Green	Pale brown with slight black mottling	...
<i>Canavalia ensiformis</i> . . .	White	White	...
„ <i>gladiata</i> . . .	Pink	Dull red	...
„ <i>obtusifolia</i> . . .	White	Mottled brown	...
<i>Cassia bicapsularis</i> . . .	Green	Dark brown	...
„ <i>fistula</i> . . .	„	Light brown	...
<i>Cytisus Laburnum</i> . . .	„	Deep brown	...
<i>Dioclea reflexa</i> . . .	White	Mottled black and brown	Indehiscent
<i>Entada polystachya</i> . . .	„	Brown	} Breaks up into closed joints
„ <i>scandens</i> . . .	„	Reddish or blackish brown	
<i>Faba vulgaris</i> (Broad Bean) . . .	Yellowish white	Brownish green	...
<i>Genista</i> (species of) . . .	Green	Chocolate brown	...
<i>Guilandina bonducella</i> . . .	Yellowish green, then olive	Lead grey	...
<i>Lathyrus pratensis</i> . . .	Green	Mottled black on light ground	...
<i>Leucæna glauca</i> . . .	„	Dark brown	...
<i>Lotus corniculatus</i> . . .	„	Mottled black and brown	...
<i>Mucuna urens</i> . . .	White	Blackish	Usually inde- hiscent
<i>Phaseolus multiflorus</i> (A) . . .	Pink	Mottled black on pink or red ground	...
„ (B) . . .	White	White	...
<i>Pisum sativum</i> (wrinkled) . . .	Green	Green	...
„ (unwrinkled) . . .	„	Yellowish white	...
<i>Poinciana regia</i> . . .	Pale green	Mottled black on light grey ground	Tardily dehis- cent
<i>Sophora tomentosa</i> . . .	Yellowish green	Pale brown	...
<i>Spartium</i> (species of) . . .	Green	Dark brown	...

I. LEGUMES—*continued.*

	Colours of seeds.		Special characters of legume.
	Immature (pre-resting).	Mature (resting).	
<i>Ulex europæus</i>	Green, then yellow	Chocolate brown	...
<i>Vicia Cracca</i>	Green	Dark mottled	...
„ <i>sativa</i>	„	„	...
„ <i>sepium</i>	„	„	...
<i>Vigna luteola</i>	„	Dark brown	...

II. CAPSULAR FRUITS.

	Colours of seeds.		Special characters of fruit.
	Immature (pre-resting).	Mature (resting).	
<i>Æsculus Hippocastanum</i> (Horse-chestnut)	White	Dark brown	...
<i>Allium ursinum</i>	„	Blackish	...
<i>Aquilegia</i> (species of)	Green	Black	Follicular
<i>Arenaria peploides</i>	White	Dark brown	...
<i>Argemone mexicana</i>	„	Black	...
<i>Bignonia</i> (species of)	„	Light brown	Siliquiform
<i>Canna indica</i>	„	Black	...
<i>Cardiospermum grandiflorum</i>	Green	„	...
<i>Convolvulus Batatas</i>	White	„	...
<i>Datura Stramonium</i>	„	„	...
<i>Digitalis purpurea</i>	Pale green	Reddish brown	...
<i>Dodonæa viscosa</i>	„	Black	...
<i>Gossypium barbadense</i>	White	„	...
<i>Hypericum Androsæmum</i>	„	„	...
<i>Ipomœa pes-capræ</i>	„	Brown	...
„ <i>tuba</i>	„	„	...
„ <i>tuberosa</i>	„	Black	...
<i>Iris foetidissima</i>	„	Scarlet	...
„ <i>Pseudacorus</i>	„	Light brown	...
<i>Lychnis diurna</i>	„	Blackish	...
„ <i>vespertina</i>	„	Brown	...
<i>Papaver Rhœas</i>	„	Blackish	...
<i>Portulaca oleracea</i>	„	Black	...
<i>Primula veris</i>	Green	Brown	...
<i>Ricinus communis</i>	White	Mottled black on grey ground.	Tri-coccous
<i>Scilla nutans</i>	„	Black	...
<i>Sesuvium portulacastrum</i>	„	„	...
<i>Stellaria Holostea</i>	„	Red	...
<i>Swietenia Mahogani</i>	„	Light brown	Ligneous
<i>Thespesia populnea</i>	„	Brown	Baccate
<i>Veronica</i>	„	„	...

III. BACCATE FRUITS.

	Colours of seeds.		Special characters of fruit.
	Immature (pre-resting).	Mature (resting).	
<i>Arum maculatum</i> . . .	White	Reddish	...
<i>Berberis</i> (species of) . . .	Green	Brown	...
<i>Chrysophyllum Cainito</i> (Star Apple)	White	"	...
<i>Momordica Charantia</i> . . .	"	Yellowish brown	Baccate capsule
<i>Passiflora pectinata</i> . . .	Green	Purplish	...
<i>Pyrus Malus</i> (Apple) . . .	White	Brown	...
<i>Tamus communis</i> . . .	Greenish yellow	"	...

The green hue of the unripe seed has but little influence on the colour of the resting seed with leguminous plants.

As seen in the previous table, green pre-resting seeds are frequent with Leguminosæ. A few of the plants there named are albuminous, having large foliaceous embryos of almost the length and breadth of the seed, and enclosed between two slabs of albumen, namely, *Bauhinia*, *Cassia fistula*, and *Poinciana regia*. Speaking of leguminous seeds in general, there seems usually to be little or no connection between the green coloration of the unripe or pre-resting seed and the ultimate hue of the resting seed. Thus with the seeds of *Adenanthera pavonina*, the successive stages of coloration in the pod are green, yellow, pink, and, finally, scarlet. It seems rarely to happen that the green hue of the unripe seed is retained in the resting seed. This, however, occurs with the wrinkled varieties of Peas, *Pisum sativum*. In smooth Peas the green is replaced by yellowish white. Then, again, the green colour of the immature seed may be exchanged in the resting seed for black, as in *Bauhinia*; for different shades of grey, as in *Guilandina bonducella*; for light brown, as in *Cassia fistula*; for dark brown, as in *Leucæna glauca*; for chocolate brown, as in *Ulex europæus*; and for a black mottling on a light ground, as in *Vicia*, *Poinciana regia*, *Cesalpinia sepiaria*, and *Cajanus indicus*.

Nor can we look for an explanation of this variation in colour of the resting seed to the colour of the embryo in the pre-resting or unripe seed. Thus exalbuminous seeds like those of *Pisum sativum* (unwrinkled variety), *Cæsalpinia Sappan*, *Ulex europæus*, *Vicia sativa*, *Cytisus Laburnum*, etc., which display great differences in coloration in the resting seed, all have green embryos as well as green coverings in the soft unripe condition; and the same remark applies to the albuminous seeds of *Bauhinia*, *Cassia fistula*, and *Poinciana regia*.

If we expect to find a clue in the colour of the leguminous embryo in the resting state, we shall be also disappointed. There is a uniformity of colouring in the embryo of the resting exalbuminous seed which stands in no sort of relation with the varied colouring of the coats of such seeds. As the green embryo enters the resting state, its assumption of a pale yellow or brownish-yellow hue indicates the destruction of the chlorophyll. That green embryos thus change their colour when the immature soft seed contracts and hardens in the shrinking stage seems to be a general rule. This is brought out by the table below in my discussion of green embryos of leguminous seeds; but more examples might be given, where, although I have no note of the colour of the embryo in the immature seed, its green colour is indicated by its yellowish coloration in the resting seed, as, for instance, in *Albizzia Lebbek*.

In making further reference to the green embryos so commonly found in unripe or pre-resting leguminous seeds, one must notice that when the embryo is green the seed-coat is generally green, but of a markedly paler shade. However, it is not difficult to find exceptions to the rule amongst exalbuminous seeds. Thus with *Entada polystachya* the coats of the soft unripe seed are white, but the enclosed embryo is bright green; whilst with the Broad Bean (*Faba vulgaris*) the embryo is bright green and the coats are white, tinged faintly with greenish yellow. Nevertheless, as indicated in the samples given in the table below, it is evidently the rule for

The colour of the embryo in the pre-resting and resting seeds has no influence on the final colour of the leguminous seed.

In unripe leguminous seeds green embryos and green coats usually go together.

TABLE SHOWING THE COLOURS OF THE SEED-COATS AND OF THE EMBRYO IN SOFT IMMATURE, AND HARD MATURED OR RESTING LEGUMINOUS SEEDS.

	Albuminous or exalbuminous indicated by A. and E.	Seed-coats.		Embryo.	
		Immature (pre-resting).	Matured (resting).	Immature (pre-resting).	Matured (resting).
<i>Acacia Farnesiana</i> .	E.	Green	Brown	Green	Pale yellow
<i>Bauhinia</i> (species) .	A.	"	Black	"	"
<i>Cæsalpinia Sappan</i> .	E.	"	Light brown	Yellowish green	"
<i>Cassia bicapsularis</i> .	A.	"	Dark brown	Green	"
" <i>fistula</i> .	A.	"	Light brown	"	"
<i>Cytisus Laburnum</i> .	E.	"	Dark brown	"	"
<i>Entada polystachya</i> .	E.	White	Brown	"	"
<i>Faba vulgaris</i> (Broad Bean)	E.	Yellowish white	Brownish green	"	"
<i>Genista</i> (species) .	E.	Green	Dark brown	"	"
<i>Guilandina bonducella</i>	E.	"	Grey	White	"
<i>Lathyrus pratensis</i> .	E.	"	Mottled black on light brown ground	Green	"
<i>Leucæna glauca</i> .	E.	"	Dark brown	"	"
<i>Phaseolus multiflorus</i>	E.	Pink	Mottled black on pink ground	Pale green	White
<i>Phaseolus multiflorus</i>	E.	White	White	"	"
<i>Pisum sativum</i> (wrinkled)	E.	Green	Green	Green	Green
<i>Pisum sativum</i> (unwrinkled)	E.	"	Yellowish white	"	Pale yellow
<i>Poinciana regia</i> .	A.	"	Dark mottled	"	"
<i>Sophora tomentosa</i>	E.	Yellowish green	Light brown	Pale green	"
<i>Spartium</i> (species) .	E.	Green	Dark brown	Green	"
<i>Ulex europæus</i> .	E.	"	Chocolate brown	"	"
<i>Vicia Cracca</i> . .	E.	"	Dark mottled	"	"
" <i>sativa</i> . .	E.	"	"	"	"
" <i>sepium</i> . .	E.	"	"	"	"

SUPPLEMENTARY RESULTS FOR SEEDS OF OTHER ORDERS.

<i>Thespesia populnea</i>	A.	White	Brown	Whitish	Whitish
<i>Gossypium barbadense</i>	A.	"	Black	Pale greenish yellow	Dirty white
<i>Dodonæa viscosa</i>	E.	Pale green	"	Pale green	Pale yellow
<i>Convolvulus Batatas</i>	A.	White	"	Dark green	"
<i>Ipomœa tuba</i> .	A.	"	Brown	"	"

this family, both for albuminous and exalbuminous seeds, that in the pre-resting or so-called immature state green embryos and green seed-coats go together.

In this connection I come now to refer especially to the behaviour of the embryos of albuminous seeds. The changes in colour which the green embryos of full-sized unripe seeds undergo when entering the resting stage, and subsequently when germination begins, are well illustrated for leguminous plants by *Poinciana regia*, *Cassia fistula*, and *Bauhinia*. These seeds are similar in the general sense that the embryos, which have large foliaceous cotyledons, are nearly as long and as broad as the seed, and are placed between two slab-like masses of albumen. When these seeds are here characterised as unripe or immature, reference is made only to those seeds that have reached the maximum size in the soft condition in the green pod. In such seeds the embryos, being fully formed, are, as shown in Chapter XIX, quite able to dispense with the resting stage altogether, and to proceed with their growth, or to germinate, as we term it. But on account of the cutting off of the fluid supplies and the drying of the pod, a resting period is imposed upon them. It is this break in the continuity of its life that is strikingly shown in the changes of the coloration of the embryo.

In this respect my remarks will be mainly confined to the behaviour of the embryo of *Poinciana regia*, and I will make but a brief reference to those of the other two plants, since they behave in a similar manner. In a green semi-ligneous pod of full size the seeds of *Poinciana regia* are pale green, and possess soft, flexible coverings. The albumen is white or colourless, and remains so during the subsequent stages. The embryo has dark green cotyledons and a white caulicle or stem; whilst the pale green plumular bud, which is partly expanded and stands 3 millimetres high, is far more suggestive of a continuously growing plantlet than of an embryo that is shortly to be compelled by the stress of circumstances to enter the rest-period. When the pod begins to dry and to

The colour-changes of the embryos of albuminous seeds,

as illustrated in the seeds of *Poinciana regia*.

turn brown, the seeds respond ; and as they shrink become much paler, almost white, except in the centre, which becomes darker. The embryo is also paler. When the pod has become dry and the seeds have acquired their normal resting characters, the signs of active life are gone. The entire embryo has now a yellowish hue, and the plumular bud, that was beginning to expand before the influences resulting in the suspension of the life of the embryo prevailed, has now closed up again, its tiny leaves being closely appressed. But the impress of the rest-period remains after the seed has begun to germinate. The signs of waking vitality in the embryo in the early stage of germination are only displayed in the lengthening of the axis or stem by the growth of the radicle. The cotyledons maintain their yellowish, lifeless hue ; whilst the plumule bleaches and becomes quite colourless, making little or no effort to unfold its leaves again, until the protruding radicle exceeds three-fifths of an inch in length. The bleaching of the green plumule of the pre-resting seed as the resting stage is reached probably occurs also with cucurbitaceous plants. It seems to happen with the Walnut (*Juglans*). Lord Avebury speaks of the plumule bearing five or six rudimentary leaves "often just tipped with green" (*Contribution to our Knowledge of Seedlings*, i. 8).

The lethargy displayed in the waking up of the dormant embryo of *Poinciana regia* came quite as a revelation to me. For some time after the radicle has struck into the soil the plantlet's existence is mainly hypocotylar and scarcely cotyledonary or plumular. The plumular bud is very slow to unfold its tiny leaves, so long closed up during the rest-period ; but gradually it assumes a pale greenish-yellow colour. So also the cotyledons retain their yellowish, lifeless hue during all the germinating process.* But notwithstanding, they considerably increase in size by absorbing the albumen ; and by the time they have extricated themselves from the seed-case there is but little of the reserve food left. They soon then acquire a more active green, and the plumule

similarly responding to the young plant's needs, vigorous growth begins.

The lesson of the embryo of *Poinciana regia* will be dealt with in Chapter XIX, where the general subject of the rest-period of seeds is discussed. Brief reference will now be made to the other two leguminous plants possessing the same seed-structure, namely, *Cassia fistula* and *Bauhinia*. They behave in a similar fashion as regards the coloration of the embryo, which in the immature seed is bright green in the first-named and pale green in the last-named plant; but in both cases it assumes a pale yellowish hue when the seed enters upon the resting stage.

*Cassia
fistula and
Bauhinia.*

The alteration in the colour of the embryo in seeds of the foregoing type, where the embryo with large foliaceous cotyledons lies between two slabs of albumen, sometimes amounts to complete decoloration as the seed proceeds with its development. Thus, in *Hura crepitans* (Euphorbiacæ) the embryo is coloured green only in the earlier stage of the growth of the seed. When the seed has attained its full size in the ripening fruit, and before the drying process has begun, the embryo is already white, and that state it retains. It would seem that the embryo in seeds of this type, whether it be white or yellowish in the resting seed, has usually functioning green cotyledons in the unripe or pre-resting seed. This seems to be true also of the seeds of *Ricinus communis*, in which, although (as I found) the embryo of the resting seed is always colourless, the cotyledons may be green in the pre-resting stage (see Pfeffer's *Physiology of Plants*, i. 596). It may be inferred again in the case of *Colubrina asiatica* (Rhamnaceæ), where resting seeds of the same structural type have pale yellow embryos.

*Non-legu-
minous
seeds, such
as Hura
crepitans and
Colubrina
asiatica.*

Since in the leguminous embryo the hypocotyl is relatively insignificant, the cotyledons making up its mass, I have usually spoken of green embryos rather than of embryos with green cotyledons. It would seem, however, that in this family when the cotyledons are green the caulicle or hypocotyl may be

*The colour
of the hypo-
cotyl when
the coty-
ledons are
green.*

either white or green. But this point has only arisen during the preparation of these pages; and I append a few results of observations respecting it in the case of plants ready at my hand.

OBSERVATIONS ON THE COLOUR OF THE HYPOCOTYL OR CAULICLE IN EMBRYOS OF SOFT, FULL-GROWN, UNRIPE SEEDS WHEN THE COTYLEDONS ARE GREEN.

(With the exception of the two last in the first column all are leguminous.)

Entire embryo green.	Cotyledons green, hypocotyl white.
Cytisus Laburnum.	Vicia sepium.
Acacia (species).	„ sativa.
Lathyrus pratensis.	„ Cracca.
Leucæna glauca.	Poinciana regia.
Genista (species of).	Faba vulgaris.
Cassia bicipularis.	
Ulex europæus.	
Pisum sativum.	
Sophora tomentosa.	
Spartium (species of).	
Euonymus.	
Acer Pseudo-platanus.	

Note.—When the entire embryo is green, and the colour is dark, the hypocotyl is often paler than the cotyledons.

The frequency of green embryos in resting seeds.

With the exception of wrinkled Peas (*Pisum sativum*), green embryos have not often come under my notice in the typical resting seed. That they are not infrequent, however, is shown in the statement made in *The Natural History of Plants* (i. 622) of Kerner and Oliver that in Firs and Pines, Maples, and some Crucifera, in *Loranthus*, Mistletoe, and the Japanese *Sophora*, the cotyledons are green whilst enclosed in the seed, their epidermis being provided with stomata. In this connection it may be noted that fruits of the Sycamore Maple (*Acer Pseudo-platanus*), which I have been keeping for nearly two years, have embryos dark green in hue. It should be remarked that in the green fruit of this tree the green embryo is enclosed in whitish seed-coverings. Here also reference may be made to the dark green embryo of the seed of *Montrichardia arborescens*, an arborescent aroid that came under my observation

in Tobago and Grenada. The seed is exalbuminous, and has a thin covering or skin, which, if I remember rightly, is brownish in colour. As I write I have by my side the exalbuminous seeds of *Monstera pertusa*, a climbing aroid, gathered in Grenada over a year ago. In this case also the embryo is dark green. Further details on this subject will be found in Note 18 of the Appendix.

Before leaving the subject of the colour of embryos, a few more remarks may be made on the relation in exalbuminous seeds of the Leguminosæ between white embryos and the colour of the seed. If we can judge from the behaviour of the genera *Canavalia* and *Phaseolus*, where white embryos seem characteristic, there is no connection between the two. The four species of *Canavalia* with which I am acquainted, *C. ensiformis*, *C. gladiata*, *C. obtusifolia*, and a Tobago species, of which the specific name is unknown to me, all have white embryos. In the first the seed is white, in the second dull red, in the third banded brown, and in the last pale brown. The same indication is afforded by four kinds of *Phaseolus*, all of which have white kernels or embryos, namely, *P. vulgaris* (French Bean), with reddish-brown seeds; *P. multiflorus* (Scarlet-runner), having two varieties, one with seeds showing black mottling on a reddish ground, the other with white seeds; and a West Indian species with white seeds. From these data it would seem that, as already pointed out in the case of leguminous exalbuminous seeds where the embryo is green in the unripe and yellowish in the resting seed, there is no connection between the colour of the embryo and the coloration of the seed-coats.

The hard red seeds of different species of tropical leguminous plants, such as *Abrus precatorius*, *Adenanthera pavonina*, different species of *Erythrina*, etc., invite attention for many reasons. As presented to view in the opening pods, they must often attract the notice of birds; but with the exception of *Erythrina* and *Adenanthera* I have not come upon many references to birds selecting them for food. In my

The connection in exalbuminous leguminous resting seeds between white embryos and the colour of the seed.

The red seeds of leguminous plants.

book on the Solomon Islands (p. 293) allusion is made to my finding cracked seeds of *Adenantha pavonina* in the gizzard of a Nicobar pigeon, and it is evident that they also serve as food for Indian parrots (Mr J. Scott in *More Letters of Charles Darwin*, ii. 349). Then, again, the Layards observed in New Caledonia that a small crow and different species of parrots fed on the seeds of *Erythrina* (*Ibis*, vi. 1882). But this is all that I know of the matter. Mr P. H. Gosse in his book on *The Birds of Jamaica* names a number of seeds that are eaten by them, but no mention is made of any of the hard red seeds above noticed.

The conditions in which the red colour is produced and the changes caused during germination.

I will here confine my attention to the conditions under which such seeds acquire their red colour and to the changes they experience in this respect when absorbing water for germination, as illustrated by those of *Abrus precatorius*, *Adenantha pavonina*, and *Canavalia gladiata*. All three have these features in common. They go through the shrinking and colouring processes in the closed pod; in all of them the soft unripe seed is rose-pink in hue, the change from pink to red representing the last stage in the coloration; and, lastly, the colouring matter is readily dissolved out in water, when the coats are pierced or the cuticle is not intact.

Canavalia gladiata.

In the case of *Canavalia gladiata* the soft, unripe, rose-pink seed belongs to the green pod. As the pod dries, the shrinking and hardening seed assumes a bright red hue, and by the time the pod is well dried and on the point of dehiscence the seed is fully contracted and dull red. Whilst drying, the pod does not discolour or darken, as seems to be the rule with legumes having dark-coloured seeds; but it becomes gradually paler, and finally has a light brown, parchment-like appearance. When absorbing water and swelling for germination, the seed first resumes its original pink hue and then becomes a chestnut-brown. As shown below under *Abrus precatorius*, where the same thing occurs, this return of the germinating seed to the colour of immaturity is really due to the hydration of the coverings, the colouring matter being to some extent washed

out, so that the coats have the sodden, wrinkled appearance of a washerwoman's fingers.

With *Abrus precatorius*, as with *Canavalia gladiata*, the characters of the resting seed are all acquired in the closed pod. Here again the pink colour of the soft immature seed in the green pod gives place to a scarlet red in the hard matured seed of a pod about to open ; and here also, when the seed swells for germination, it resumes the original pink hue of immaturity. With both these plants there is but little difference either in colour, size, or consistence between an immature seed taken from a green pod and a resting seed that has swollen for germination. That this change from red to pink in the germinating seed is due to the hydration of the coverings is indicated by the behaviour of the seed when allowed to soak in water after being filed. The colouring matter dissolves out and the red seed becomes almost blanched.

*Abrus pre-
catorius.*

In the case also of the seeds of *Adenanthera pavonina* all the colour-changes take place in the closed pod. As observed for me by Mrs H. B. Warde in Jamaica, the soft immature seeds in the green pod are first green and then yellow ; and as the pod begins to brown and dry the seeds turn pink, and when the shrinking and hardening processes approach completion the permanent bright red hue is assumed. It is not necessary for the development of the last two stages in the coloration that the pod should remain connected with the plant. If the green pods are allowed to dry after picking, bright red seeds will be found in closed pods after a few weeks. Though I had not the opportunity of observing the actual stages in coloration on the tree, specimens of all of them were kept for me. When the seeds are absorbing water and swelling for germination, they do not, as with those of *Abrus precatorius* and *Canavalia gladiata*, regain the pink hue of immaturity. The outer red skin is thrown off by the swelling of the under layer, and the seed assumes the yellowish colour of the second stage of coloration in the green pod, a stage earlier in immaturity.

*Adenanthera
pavonina.*

The long duration of the red colour depends on the impermeability of the seed.

The red seeds of these three plants are more or less impermeable to liquid water. With *Adenanthera pavonina* all the seeds are typically impermeable, with *Abrus precatorius* the great majority are, and with *Canavalia gladiata* the minority perhaps are impermeable. The impermeable seeds are of necessity non-hygroscopic, whilst the permeable seeds behave hygroscopically. A seed that responded in its changes of weight to the varying degrees of humidity of the atmosphere could scarcely be expected to retain its bright red hue for a long period. Where the impermeable cuticle remains intact the colour ought to withstand the test of centuries. This would probably be true of the seeds of *Adenanthera pavonina*. Except when kept in unusually dry conditions, I should not expect the seeds of *Abrus precatorius* to preserve untarnished for many years their original scarlet hue, since the scar is their point of weakness. As an indication in this direction I may refer to 35 seeds of *Abrus precatorius*, now beside me, which I gathered from the plant in Fiji twelve years ago. Only 25, or 71 per cent., retain their original bright colour, the rest being brownish or even blackish in hue. This is a point in the history of red seeds that seems to be worthy of further investigation—I mean the permanence of the colour. Abundant data would be at hand in our own museums and in tropical countries.

Red seeds do not stain water red.

I may here refer to a curious fact that must be well known to students of vegetable chemistry. Although the red seeds of *Abrus precatorius*, *Adenanthera pavonina*, and *Canavalia gladiata* stain water freely when the water is allowed to penetrate their coats, the solution has not the colour of the seeds. The seeds of *Adenanthera* impart a beautiful amber hue to the water, which deepens after the seeds have been removed and becomes like brown sherry. On the other hand, the seeds of *Abrus* and *Canavalia* stain the water a dark green, which deepens after the seeds have been taken out, becoming steely or almost inky.

The colour of the kernel or embryo in the case of these three red seeds in the resting state varies somewhat. In *Adenanthera pavonina* it is yellowish, which indicates that the embryo was green in the unripe seed. In *Canavalia gladiata* it is white. In *Abrus precatorius* it is tinged yellow outside, but is white on section.

The colour of the kernels in red seeds of Leguminosæ.

Before quitting the subject of red seeds I will briefly refer to the stages of coloration of the orange or scarlet seeds of *Iris fetidissima*, as observed by me during two seasons in a wood at Salcombe. All the stages took place in the moist closed capsule long before the fruit dehisced or showed any signs of drying up. Up to the middle of August, when the fruits were dark green and averaged from 100 to 110 grains in weight, the seeds were white and soft, with jelly-like contents and no recognisable embryo. After this, as the capsules continued to increase in size the seeds became pale yellow; but their contents remained unchanged until the end of the month, when they began to solidify. September was principally occupied with the maturation of the seeds and with the growth of the fruit, the seeds assuming a deeper yellow hue. By the middle of October, when the capsules averaged 160 to 170 grains in weight, the seeds were solid, of full size, and of the typical orange or scarlet colour. There was not much alteration either in seed or fruit after this date, and in the beginning of November the most advanced capsules commenced to dehisce, and the remainder followed during the course of the month.

The stages in the coloration of the seeds of *Iris fetidissima*.

It is worth noting that seeds may acquire much of the coloration which they possess as resting seeds whilst their contents are still fluid and before the embryo is formed. This would seem to take place chiefly with monocotyledonous albuminous seeds of the type below exemplified. Thus, the white soft seeds of *Allium ursinum*, when they begin to ripen in the closed capsule, become dark red, though little more than bags of water. In the same way, the white soft seeds of the green capsules of *Iris fetidissima* colour yellow as the fruit

The coloration of seeds whilst their contents are still fluid.

ripens, though the embryo is not yet recognisable and the albumen is a mere mass of jelly. I should imagine also with *Scilla nutans* that seed-coloration precedes the formation of the embryo, the pearl-white immature seeds being merely sacs of fluid. Reference has already been made in the early part of this chapter to the red hue of the seed of *Barringtonia speciosa* when its contents are quite fluid.

SUMMARY

(1) The inquiry is mainly directed to the conditions of seed-coloration, to the How rather than to the Why (p. 368).

(2) Questions relating to the specially adaptive nature of the colours of seeds are summarily dismissed on the ground that we are not justified in selecting one character that happens to be conspicuous to our senses, whilst ignoring the great number of other characters that can make no such appeal to us (p. 368).

(3) After referring to the wealth of seed-colour displayed in a typical native garden in Jamaica, the author cites cases of the development and disappearance of seed-colours before the fruit is ripe or before the seeds are exposed to view (p. 369).

(4) After it has been shown that as a general rule seeds colour in the closed fruit, as illustrated in the case of berries, capsules, and legumes, inquiry is made as to the stage in the history of the fruit in which the coloration takes place, whether in the green, the ripe, or the drying stage, or in all three of them. Though it is established that coloration frequently takes place in the moist green and ripe capsule, the subject is acknowledged to be a very difficult one, especially as concerns the legume (p. 370).

(5) In this connection reference is made first to the experiment of Lubimenko, in which the seeds of young leguminous pods were exposed to the outer air by removing portions of the pods, and to the conclusion drawn that for the normal development of the seed a confined atmosphere of stable composition is needed (p. 373).

(6) The author then gives the results of his similar experiments in the case of green capsules of *Scilla nutans* on the plant, the upshot being that immature seeds exposed to the outer air by windows cut in the fruit-walls developed normally, with the exception of their failure to acquire the black colour of the resting seed. It thus became evident that the seeds acquire their shining black hue only in the confined atmosphere of the moist green capsule (p. 374).

(7) The conditions under which seeds colour in leguminous pods and in capsules are discussed in detail, and the black and brown forms of coloration, including black mottling, are especially dealt with. After observing that the coloration, early shrinking, and hardening of the seed and its coats are so conspicuously associated with the early drying of the fruit, that the presumption in favour of there being a causal connection is very strong (more especially in the case of legumes), it is shown that this view is untenable. The results of experiment demonstrate that these changes in the seed can take place under conditions so humid that the drying of the fruit is precluded. In a word, the régime involved in the coloration, early shrinking, and hardening of the seed and its coats, both in the legume and in the capsule, is that which is displayed by the colouring, shrinking, and hardening seed in the moist berry. The seed colours normally in moist fruits and continues the process notwithstanding the drying of the fruit. In some cases, however, as in black mottling, the complete coloration of the seed is interfered with by the fruit's drying (p. 375).

(8) The colours of unripe and mature seeds, that is, of pre-resting and resting seeds, are then compared in legumes, capsules, and berries, and the inference is drawn that unripe or pre-resting seeds are usually white in capsules and green in legumes (p. 385).

(9) It is pointed out that the colour of the coats of the resting seed in leguminous plants has but little connection either with the colour of the coats of the pre-resting or unripe seed, or with the colour of the embryo in the pre-resting and resting states; but it is indicated that with unripe leguminous seeds green embryos and green coats usually go together (p. 389).

(10) The changes in colour which the green embryos undergo when entering the resting stage and subsequently when germination begins are then discussed in the cases of seeds of *Poinciana*, *Cassia*, and *Bauhinia*. They all assume a pale yellow lifeless hue in the resting seed, and, as illustrated by the seeds of *Poinciana regia*, display considerable lethargy in the waking up of the dormant embryo during the germinating process. In some non-leguminous seeds, as with those of *Hura crepitans*, the green embryo becomes decolorised and blanched when entering the resting state (p. 391).

(11) The colour of the hypocotyl in leguminous embryos, as with green cotyledons, is shown to be sometimes white and sometimes green (p. 393).

(12) It is observed that whilst the embryos of leguminous resting seeds are usually pale yellow, green embryos are not uncommon in the resting seeds of other orders (p. 394).

(13) With regard to white embryos in leguminous resting seeds, it is remarked that since in genera like *Phaseolus* and *Canavalia*, where

they occur, the coloration of the seed-coats varies greatly, there is no connection between the two characters (p. 395).

(14) The red seeds of leguminous plants are then discussed, especially with reference to the conditions in which the red colour is produced and to the changes caused during germination. Those of *Abrus precatorius*, *Adenanthera pavonina*, and *Canavalia gladiata* are taken as examples (p. 395).

(15) It is shown that the long duration of the red colour of the above seeds depends on the impermeability of their coats and on the non-hygroscopic behaviour of the seeds (p. 398).

(16) The stages in the coloration of the seeds of *Iris fœtidissima* are described (p. 399).

(17) The coloration of immature seeds whilst their contents are still fluid and before the embryo is recognisable is remarked in the cases of some monocotyledons (p. 399).

CHAPTER XVIII

THE WEIGHT OF THE EMBRYO

ANY discussion of the proportional weight of the embryo in albuminous resting seeds must be surrounded by a host of difficulties. The first question to present itself is concerned with the utility of such a discussion, since, if we cannot bring the subject into some sort of relation with other matters affecting the seed, it would not be worth while following it up. But if this seems feasible, we are at once confronted with other difficult questions. Although not directly concerned with exalbuminous seeds, we cannot ignore their close connection with albuminous seeds. We must at the outset select some standpoint for viewing this relationship, and much depends on our answer to the query—Which is the older of the two?

A difficult subject.

I suppose that on biological grounds there can be no doubt that the albuminous is the primal state ; but one has only to watch a germinating seed bravely endeavouring to strike into the soil, whilst its cotyledons still within the seed-case are appropriating the albumen, to decide that the albuminous state is the older condition. We here perceive the transition from an albuminous to an exalbuminous state in actual operation, the chief point of difference being that whilst the change, as generally understood, occurs in the seed before it enters the resting condition, here it takes place in the germinating seed after the resting-state stage is passed. Our plantlet is now doing what is often effected within the seed at an earlier stage

The albuminous and the exalbuminous seed.

before the resting state is imposed. All exalbuminous seeds have in a sense been once albuminous, and the distinction which we draw between exalbuminous and albuminous seeds mainly depends on whether the transition occurs before or after the rest-period. The after-ripening of seeds must be often concerned with the change from the albuminous to the exalbuminous condition. That which happens in the Jasmine, where the albumen is at first copious in the seed and disappears when the seed is ripe for germination, occurs with many other plants. It would be quite possible, for instance, in the case of the Ivy (*Hedera*), as described in Chapter XIX, to describe the seed as albuminous in its first stage and as exalbuminous when about to germinate. The interposition of the rest-period in the early portion of a plant's existence is responsible for many false distinctions and many incorrect comparisons.

Other difficult points.

Another difficult point has been already indicated. In the resting albuminous seed, as is well known, the embryo may exist in all stages, from that in which it is imperfectly differentiated to that in which the plumular leaves are developed and we have a perfect plantlet within the seed. Between these two extremes all gradations occur. Then, again, we have often genera with exalbuminous seeds and genera with albuminous seeds in the same order. Thus with Sapotaceæ, at first sight the seeds seem very similar in structure. Yet the proportion of albumen may vary in different genera, from that found in *Achras*, where it amounts to about 84 per cent. of the kernel's weight, to its condition in *Chrysophyllum*, where it may range between 20 and 40 per cent. in different species, whilst in *Lucuma* there is none at all. Of the 222 families of angiosperms described in the *System of Botany* of Le Maout and Decaisne, about 18 per cent. possess both albuminous and exalbuminous seeds.

Dr Goebel in his *Organography of Plants* (English edition, ii. 262) lays stress on the far-reaching nature of the changes in the form of the embryo arising from the different modes of

disposition of the food-reserve ; and one has only to refer to Lord Avebury's volume on seedlings in the International Scientific Series to become apprised of this fact. For example, we have its disposition in the cotyledons, as in many leguminous seeds ; its disposition in the hypocotyl, as in the *Barringtonia* and with some Guttiferæ, and its disposition outside the embryo altogether, as occurs with many plants. The embryo in different resting seeds varies so much in its stage of development and so much in its relation to the reserve supply of food that one hesitates to consider the matter of its relative weight at all.

However, one has only to observe that whilst over 100,000 *Juncus* embryos are required to make up the weight of a single embryo of the Coco-nut palm, they are in relation to the kernel more than 200 times as heavy, in order to perceive that a study of the secondary relations involved in such measurements may lead to some interesting conclusions. Whilst the Coco-nut embryo is in an absolute sense one of the very largest and heaviest amongst embryos of its kind, it is in a relative sense, as compared with the kernel, one of the very smallest and lightest. The subject from this standpoint seems to lend itself for inquiry, and here again the principal instrument of investigation is the balance, weight as a general rule connoting size.

The estimation of the weight of the embryo in very small seeds, as in those of the Common Rush (*Juncus*), is easier than it might at first seem to be. It soon became apparent to me that I could begin by ascertaining the proportional bulk and the proportional weight of the embryo as part of the kernel in a seed that could be easily examined, and that by a comparison of the two results a constant error might be found which could be applied in those numerous cases where, owing to the use of the balance being impracticable, one is compelled to rely on the proportional size of the embryo for the clue to its weight.

Method of measuring the weight of minute embryos.

As suiting my purpose the light brown seeds of dehiscing

fruits of *Iris Pseudacorus* were chosen. A hundred embryos were found to make up the weight of a single kernel; and since the kernel weighed 1·3 grain, this gave 0·013 grain as the weight of the embryo. It was then ascertained that in point of bulk about 85 embryos went to a kernel, which, interpreted as weight, gave the weight of the embryo as 0·015 grain, which is 16 per cent. greater than the actual weight determined by the balance. It was then assumed that weight calculated from relative size displayed an error of this amount, but, taking into consideration the fact that the method is at its best crude, and remembering that only approximate results could be looked for, I decided to ignore it altogether and to accept bulk as roughly indicative of weight.

As it was evident that in very small seeds one would have to rely mainly on the bulk-data, the question arose as to the method of obtaining them. My choice lay between making my own seed-sections and utilising the materials offered by the illustrations in *The System of Botany* of Le Maout and Decaisne (English edition, 1873); and the last method was selected. From the sections of seeds there figured I could procure the requisite measurements, obtaining for myself, when needed, the data for the relative thickness of the seed. But in the first place I tested the method by comparing the results obtained by estimations from the figures in the above-named work with those supplied by actual measurements of the seed. They came fairly close together in the case of the seeds of *Iris Pseudacorus*, 85 embryos going to make up a kernel by my own measurements of the seeds, and 75 according to the data offered by the illustration of an *Iris* seed of the same type in the general work. The seeds of the Elder (*Sambucus nigra*), weighing only 0·05 grain, were then employed. Actual measurements of a seed indicated that the embryo formed about a tenth of the bulk of the kernel, whilst the data supplied by the figure of the same seed gave the proportion as one-twelfth.

Still smaller seeds, those of *Aquilegia* weighing only 0·03

grain, gave similar proportions for the two methods, the size of the embryo, whether obtained from the actual seed or from the illustration, being about $\frac{1}{200}$ of that of the kernel. In this case the proportional weight of the seed-coats was taken as one-third of the total weight of the seed, which left $\cdot 02$ grain as the weight of the kernel. I was therefore dealing with an embryo which weighed not more than $\frac{1}{10,000}$ part of a grain. From the case of the *Aquilegia* seed to that of the minute seed of a rush (*Juncus*) the step was not a very difficult one. Having found that about 5500 seeds of *Juncus communis* went to make a grain, I had to allow for the weight of the seed-coats, which, judging from the figures and from my own examination of the seed, was relatively much less than with a seed of *Aquilegia*, so I placed it at about one-fifth of the seed's weight. The weight of the embryo was then calculated to be about one-tenth of that of the kernel, and from these data the following results were obtained :—

<i>Juncus communis</i>	{	Entire seed	$\frac{1}{5500}$	grain or	$\cdot 00001118$	gramme.
		Kernel	$\frac{1}{6875}$	”	$\cdot 0000094$	”
		Embryo	$\frac{1}{68750}$	”	$\cdot 0000009$	”

In this manner, therefore, the minutest of embryos are shown to be within reach of the balance. Whilst nearly 70,000 of the embryos of *Juncus communis* are required to make a grain, nearly 200 of them placed in line will make an inch, and nearly 8 will make a millimetre, the length of the embryo being one-third that of the seed, which, according to my measurement, is $0\cdot 4$ millimetre long.

With these preliminary remarks I will now give in tabular form the results of my observations on the weights of the embryos of albuminous resting seeds in the case of more than fifty plants. They are arranged in the order of the embryo's relative weight as a portion of the kernel. The indications supplied by such an arrangement are full of suggestiveness, and are especially discussed in the remarks that follow the table, as well as in the last paragraph of the chapter.

THE WEIGHTS OF EMBRYOS IN ALBUMINOUS RESTING SEEDS.

(Palms are indicated by P. When a figure of the seed has been utilised, as in the case of small seeds, L. is placed after the name, the *System of Botany* of Le Maout and Decaisne being usually employed. See text before and after table for further explanation.)

	Weight of the Embryo.		Remarks. (S. entire seed ; C. coats ; K. kernel. Weights in grains.)
	Actual weight.		
	Grains.	Grammes.	
P. <i>Cocos nucifera</i>	2	'129600	$\frac{1}{1888}$ A ripe fruit of average weight with mature kernel.
P. <i>Bactris</i>	$\frac{1}{30}$	'002160	$\frac{1}{1800}$ A dry fruit.
P. <i>Cocos</i> (<i>schizophylla</i> ?)	$\frac{1}{2}$	'012960	$\frac{1}{1800}$ " "
P. <i>Tamus communis</i> , L.	$\frac{1}{4000}$	'000015	$\frac{1}{1000}$ S. '27 ; C. '02 ; K. '25.
P. <i>Acrocomia lasiospatha</i>	$\frac{1}{20}$	'003240	$\frac{1}{800}$ A dry fruit.
P. <i>Licuala grandis</i>	$\frac{1}{80}$	'000810	$\frac{1}{800}$ " "
<i>Mercurialis</i> , L.	$\frac{1}{2000}$	'000013	$\frac{1}{200}$ S. '125 ; C. '025 ; K. '1.
P. <i>Prestœa montana</i>	$\frac{1}{40}$	'001620	$\frac{1}{400}$ A dry fruit.
P. <i>Anona Cherimolia</i>	$\frac{1}{100}$	'000648	$\frac{1}{400}$ S. 8'0 ; C. 3'4 ; K. 4'6.
P. <i>Areca Catechu</i>	$\frac{1}{8}$	'012960	$\frac{1}{200}$ A moist ripe fruit.
P. <i>Elæis guineensis</i>	$\frac{1}{20}$	'003240	$\frac{1}{200}$ A dry fruit.
P. <i>Sabal umbraculifera</i>	$\frac{1}{100}$	'000648	$\frac{1}{300}$ S. 4'0 ; C. 1'0 ; K. 3'0.
P. <i>Hyophorbe Verschafftii</i>	$\frac{1}{20}$	'001296	$\frac{1}{200}$ A fresh fruit.
P. <i>Mauritia setigera</i>	$1\frac{1}{2}$	'097200	$\frac{1}{200}$ A fruit beginning to dry.
P. <i>Sabal umbraculifera</i>	$\frac{1}{20}$	'001296	$\frac{1}{200}$ A dry fruit.
P. <i>Manicaria saccifera</i>	1	'064800	$\frac{1}{200}$ " "
P. <i>Oreodoxa oleracea</i>	$\frac{1}{20}$	'001080	$\frac{1}{200}$ " "
P. <i>Livistonia</i>	$\frac{1}{14}$	'004630	$\frac{1}{200}$ " "
P. <i>Caryota</i>	$\frac{1}{7}$	'009260	$\frac{1}{200}$ A fruit beginning to dry.
<i>Aquilegia</i> , L.	$\frac{1}{10000}$	'000006	$\frac{1}{200}$ S. '03 ; C. '01 ; K. '02.
<i>Anona palustris</i>	$\frac{1}{70}$	'000926	$\frac{1}{100}$ S. 3'9 ; C. 1'2 ; K. 2'7.
P. <i>Oreodoxa regia</i>	$\frac{1}{40}$	'001620	$\frac{1}{100}$ A dry fruit.
<i>Dracena Draco</i>	$\frac{1}{20}$	'003240	$\frac{1}{100}$ S. 6'0 ; C. 0'2 ; K. 5'8.
<i>Carex</i> , L.	$\frac{1}{2500}$	'000026	$\frac{1}{100}$ S. '05 ; C. '01 ; K. '04 ; an average.
P. <i>Cocos plumosa</i>	$\frac{1}{20}$	'003240	$\frac{1}{100}$ Fruit partly dry.
<i>Iris Pseudacorus</i>	$\frac{1}{80}$	'000810	$\frac{1}{100}$ Seeds partly dry ; S. 2'0 ; C. 0'7 ; K. 1'3.
<i>Luzula</i> , L.	$\frac{1}{3750}$	'000017	$\frac{1}{70}$ S. '03 ; C. '01 ; K. '02.
<i>Hedera Helix</i>	$\frac{1}{70}$	'000926	$\frac{1}{50}$ S. '8 ; C. '07 ; K. '73. (See Chap. XIX.)
<i>Veronica</i> , L.	$\frac{1}{13000}$	'000019	$\frac{1}{30}$ S. '013 ; C. '003 ; K. '01.
<i>Ricinus communis</i>	$\frac{1}{10}$	'006480	$\frac{1}{20}$ S. 2'7 ; C. '7 ; K. 2'0.
<i>Papaver</i> , L.	$\frac{1}{10000}$	'000006	$\frac{1}{20}$ S. '0025 ; C. '0005 ; K. '0020.
<i>Canna indica</i>	$\frac{1}{10}$	'006480	$\frac{1}{20}$ S. 2'6 ; C. '6 ; K. 2'0.
<i>Jatropha Curcas</i>	$\frac{1}{2}$	'025920	$\frac{1}{10}$ S. 12'0 ; C. 4'4 ; K. 7'6.
<i>Ravenala madagascariensis</i>	$\frac{1}{10}$	'012960	$\frac{1}{10}$ S. 5'5 ; C. 2'5 ; K. 3'0.
<i>Sambucus nigra</i> , L.	$\frac{1}{300}$	'000196	$\frac{1}{10}$ S. '05 ; C. '02 ; K. '03.
<i>Rumex</i> , L.	$\frac{1}{250}$	'000260	$\frac{1}{10}$ S. '054 ; C. '014 ; K. '04.

THE WEIGHTS OF EMBRYOS IN ALBUMINOUS RESTING SEEDS—*continued.*

	Weight of the Embryo.			Remarks. (S. entire seed ; C. coats ; K. kernel. Weights in grains.)
	Actual weight.		As a part of the kernel.	
	Grains.	Grammes.		
Scrophularia, L.	$\frac{7}{8888}$	'000010	$\frac{1}{10}$	S. '002 ; C. '0005 ; K. '0015.
Berberis, L.	$\frac{1}{100}$	'000648	$\frac{1}{10}$	S. '14 ; C. '04 ; K. '1.
Anagallis, L.	$\frac{1}{2800}$	'000026	$\frac{1}{10}$	S. '006 ; C. '002 ; K. '004.
Sparganium ramosum	$\frac{1}{100}$	'000648	$\frac{1}{10}$	S. '11 ; C. '01 ; K. '1 (fresh).
Saccoglottis amazonica	$\frac{7}{10}$	'045360	$\frac{1}{10}$	S. 8'3 ; C. 1'3 ; K. 7'0.
Juncus, L.	$\frac{1}{88780}$	'000001	$\frac{1}{10}$	See p. 407.
Hura crepitans	$\frac{1}{2}$	'113400	$\frac{1}{3}$	S. 20 ; C. 6 ; K. 14.
Glaux maritima *	$\frac{1}{10000}$	'000040	$\frac{1}{10}$	S. '007 ; C. '002 ; K. '005
Viola tricolor, L.	$\frac{1}{800}$	'000108	$\frac{1}{8}$	S. '016 ; C. '003 ; K. '013.
Achras Sapota	$\frac{7}{10}$	'045360	$\frac{1}{10}$	S. 9'0 ; C. 4'8 ; K. 4'2.
Cassia †	1	'064800	$\frac{1}{10}$	S. 8 ; C. 2 ; K. 6.
Ipomoea pes-capræ	$\frac{1}{2}$	'032400	$\frac{1}{4}$	S. 3'7 ; C. 1'7 ; K. 2'0.
„ tuberosa	6	'388800	$\frac{1}{3}$	S. 22'5 ; C. 4'5 ; K. 18'0.
Plantago, L.	$\frac{1}{310}$	'000216	$\frac{1}{10}$	S. '02 ; C. '01 ; K. '01.
Poinciana regia	2	'129600	$\frac{1}{10}$	S. 9'3 ; C. 4'3 ; K. 5'0.
Colubrina asiatica	$\frac{1}{8}$	'010800	$\frac{1}{10}$	S. '60 ; C. '31 ; K. '29.
Chrysothylum Cainito	5 $\frac{1}{2}$	'362880	$\frac{1}{10}$	S. 12 ; C. 5 ; K. 7.
Exalbuminous seeds	$\frac{1}{10}$...

* Proportions of the embryo of *Glaux maritima* from figure in *Das Pflanzenreich*, iv. 237.

† This represents a mean result for three species of *Cassia* (*fistula*, *grandis*, *marginata*).

Here we have the weights of the embryos for about fifty-three species and generic types of albuminous seeds, of which almost a third belong to palms. For reasons before implied, the relative weight of the embryo in proportion to the kernel is alone given. This is the only ratio that is generally applicable, it being apparent that the inclusion of the seed-coats in the discussion would have but little significance in a series comprising the seeds of palms, whilst the proportional weight of the embryo with regard to the fruit would possess but little value, if only for the reason of there being many-seeded as well as single-seeded fruits.

If required, the proportional weight of the embryo with reference to the entire seed (kernel and coats) can be

Remarks on the preceding table.

determined for any ordinary seed by making use of the data given in the last column of the table. Thus, in the instance of *Canna indica*, the embryo is given as $\frac{1}{20}$ of the weight of the kernel; but by employing the data given for the entire seed we obtain a proportional weight of $\frac{1}{26}$. Then, again, if further particulars relating to the palm-embryos are needed, the weight of the kernel can be readily calculated from the results given in these columns, and by referring to Chapter XIV the weight of the entire fruit can in most cases be found. For instance, in the case of ripe coco-nuts, where the kernel makes up about one-fourth of the weight of the fruit, the total weight for the fruit illustrated in the table would be about 17,500 grains, and the relative weight of the embryo would be therefore about $\frac{1}{8750}$. Coco-nuts vary so much in weight both in their several stages and in their different varieties that the same result can be scarcely looked for. So again with the dry fruit of *Licuala grandis*, since the embryo weighing $\frac{1}{80}$ grain is equal to $\frac{1}{500}$ of the weight of the kernel, we obtain 6.2 grains as the kernel's weight. In a table in Chapter XIV the average weight of the entire fruit is stated to be 10 grains, from which the relative weight of the embryo may be placed at $\frac{1}{800}$ of the fruit's weight.

Another important point is that we are here dealing with the embryos of resting seeds. In most cases this is a seed that has dried spontaneously on the plant; but with palms several other considerations arise, and it is often more than probable that a palm seed which has completed the normal drying process has lost its capacity for reproducing the plant. In some palm seeds it is likely, as in the case of that of the coco-nut, that during the ripening of the kernel the oil increases as the water diminishes.

With nearly all the palm seeds experimented upon the embryos belonged to dry fruits and were more or less shrunken. In a few instances, as with *Cocos nucifera*, *Mauritia setigera*, and *Areca Catechu*, the fruits were ripe and still moist, the kernel reaching maturity after the husk had commenced to

The embryos
of palms.

dry. According as we take the ripe moist fruit or the fruit that has completed its drying process, the proportional weight of the embryo as concerns the kernel varies greatly. This is due to the fact that whilst the albumen of such a ripe fruit usually loses when dried about a third of its weight, the embryo loses about two-thirds. The effect of this, as shown in the results given below, is to halve the relative weight of the embryo as compared with the kernel in the spontaneously dried fruit. Thus with *Cocos nucifera* the embryo is $\frac{1}{2186}$ of the weight of the kernel in the ripe fruit and $\frac{1}{4165}$ in the dry fruit many months old, though it is more than doubtful whether the shrunken embryo in the last case would retain its vitality.

TABLE SHOWING THE LOSS OF WEIGHT, WHEN DRYING SPONTANEOUSLY, OF THE ALBUMEN AND EMBRYO OF THE RIPE SEEDS OF PALMS, AND ITS EFFECT ON THE PROPORTIONAL WEIGHT OF THE EMBRYO.

	Loss of weight.		Proportional weight of the embryo as a part of the kernel.	
	Albumen.	Embryo.	Ripe seed.	Dry seed.
<i>Cocos nucifera</i>	33 per cent.	66 per cent.	$\frac{1}{2186}$	$\frac{1}{4165}$
<i>Acrocomia lasiospatha</i>	40 "
<i>Mauritia setigera</i>	30 "	66 per cent.	$\frac{1}{300}$	$\frac{1}{330}$
<i>Areca Catechu</i>	28 "	66 "	$\frac{1}{320}$	$\frac{1}{337}$
<i>Oreodoxa oleracea</i>	$\frac{1}{100}$	$\frac{1}{100}$
<i>Prestoea montana</i>	70 per cent.
<i>Licuala grandis</i>	60 "

It is thus seen that the discussion of this subject as concerns the palm embryo presents serious difficulties. Every type of palm seed would probably have its own régime, and we are for ever thwarted by the interposition of the rest-period and its results. An important contrast is brought out by observing the behaviour of different embryos when placed in water. In the ripe coco-nut the embryo fills its cavity and is more or less in a state of saturation as regards its water-contents, since on being placed in water its weight

The embryo of *Cocos nucifera*.

remains unchanged or is increased only 2 or 3 per cent. As the fruit proceeds with its drying the albumen and the embryo lose weight together during the first few months. The weight of the embryo, originally about 2 grains, is reduced to 1.8 grain after three months and to 1.5 after six months, the embryo still almost filling its cavity and showing only a slight collapse at the sides, whilst its weight is only increased by 14 or 15 per cent. when placed in water. There is but little marked shrinkage in the form of the embryo, a result that is certainly due to the increase in its oily constituents; and we have already seen in Chapter XIV that as the kernel ripens the oil increases in amount. It is only with very old lifeless coco-nuts that we would expect to notice great shrinkage of the embryo.

Thus the behaviour of the embryo of the coco-nut is evidently peculiar. When comparable with those of other palms in the early mature state of the fruit it is, as shown in the table above, full of water, losing two-thirds of its weight when drying spontaneously in the detached condition, and returning to its original weight when resting on water. But in the later stages of maturation, when the oil in the kernel increases in quantity and the fruit is drying, the embryo becomes more oily, and loses but little water when detached and allowed to dry, and only increases its weight slightly when placed on water. This peculiarity is also brought out in the next table.

The embryos
of other
palms.

Now, the embryos of most of the other palms examined behaved very differently, as shown in the results below tabulated. Whilst with the fresh ripe fruits the embryo usually fills its cavity and is more or less in a state of saturation, it shrinks considerably as the fruit dries, so that in the course of two or three months it usually presents itself as a more or less shrivelled object but partly filling the cavity. Such shrunken embryos, when placed in water, double their weight in a couple of hours and regain their original form. The shrinking of the embryo may even be evident in ripe

fruits that have been gathered only two or three weeks. This happens with the embryos of *Mauritia* and *Cocos plumosa*.

TABLE SHOWING THE CONDITION OF PALM-EMBRYOS IN FRUITS SOME TIME AFTER GATHERING, AND THEIR BEHAVIOUR WHEN ALLOWED TO REST ON THE SURFACE OF WATER.

	Period since gathered.	Condition of the embryo.	Increase of weight when placed on water.
<i>Oreodoxa regia</i>	7 weeks	Rather shrunk	40 per cent.
„ <i>oleracea</i>	8 months	Much shrunk	130 „
<i>Sabal umbraculifera</i>	16 „	Shrunk	160 „
<i>Acrocomia lasiospatha</i>	12 „	Somewhat shrunk	100 „
<i>Bactris</i>	2 „	A little shrunk	...
<i>Cocos nucifera</i>	6 „	Slightly shrunken	15 per cent.
„ <i>plumosa</i>	2 weeks	Much shrunk	100 „
„ <i>schizophylla</i>	2 years	Very much shrunk	200 „
<i>Areca Catechu</i>	5 weeks	Greatly shrunken	200 „
<i>Licuala grandis</i>	18 months	Much shrunk	100 „
<i>Prestœa montana</i>	4 „	Greatly shrunk	250 „
<i>Hyophorbe</i>	2 „	Shrunk	...
<i>Elæis guineensis</i>	2 „	Rather shrunk	90 per cent.
<i>Livistonia</i>	2 years	Much shrunk	...
<i>Caryota</i>	2 months	Rather shrunk	...

Although in four cases the behaviour of the shrunken embryo in water was not tested, it is evident that the same effect would be produced.

The gain of the shrunken embryo in water represents the original loss in the drying process, the embryo acquiring its full outlines and approximately its original size and weight in the moist ripe fruit. It should be allowed to rest on the surface of the water for a couple of hours, when it usually ceases to gain weight. The albumen of the seed containing the shrunken embryo takes up much less water. Thus, to take the behaviour of a *Sabal* seed sixteen months old, whilst the albumen, when placed in water, added only 33 per cent. to its weight, the embryo increased its weight by 160 per cent. This is consistent with the principle before stated that when a ripe palm fruit dries spontaneously the albumen loses about one-third of its weight and the embryo about two-thirds.

That palm seeds retain their vitality but a short time would seem to be the rule. Mr Hart, late Superintendent

of the Botanic Gardens at Trinidad, tells me that the limit for *Acrocomia*, *Oreodoxa*, *Sabal*, *Thrinax*, etc., when the fruits are protected from the sun and rain, would be from three to six months, whilst for *Mauritia*, he says, the limit would be only a week or two. Unless the embryo increases its oil during its loss of water in the drying process its longevity would seem to be but slight. The reciprocal relation between oil and water in the embryo is a matter of importance for certain palms. Thus I would assume that the oily embryo of *Elæis guineensis* would possess a greater staying capacity than the watery embryo of *Areca Catechu*, though in both cases marked shrinkage might take place in the case of the embryo removed from the fresh ripe fruit. Let the fruits remain on the palm and the difference in the behaviour would assert itself; but if both fruits are allowed to dry in the detached condition, their embryos will probably be similarly shrunken. One would only look for the contrast in the condition of the embryos in the case of fruits that have dried on the tree. Speaking generally, I would consider that palm seeds where the albumen is ruminant, as with *Areca*, *Caryota*, and *Thrinax*, would preserve their vitality for a much shorter period than where it is homogeneous, as in the majority of palms, the more rapid drying of the ruminant albumen being promoted by its peculiar structure.

One may mention in passing a fact which, though familiar to the students of palm fruits, may be new to some of my readers. The water filling the cavity of the fruit is not peculiar to *Cocos nucifera* (Coco-nut), but occurs with other palms of the same tribe of the family, at least in the immature condition of the fruit, and in fruits so small that 300 or 400 of them are needed to make up the weight of a single coco-nut. Thus in *Bactris* the hard black shell or endocarp of the ripe fruit is soft and white in the immature fruit. The cavity within the shell of the young fruit is lined by jelly-like albumen and is quite full of water. As maturation proceeds the albumen solidifies and increases so as ultimately to fill

The water of
the coco-nut.

the cavity, leaving only traces of the original central hollow. The narrow fissure-like central cavity found in the albumen of moist ripe fruits of other genera of the same tribe of palms, such as *Acrocomia* and *Elæis*, gives an indication of a similar history of the young fruit. I may remark that even the large cavity of the coco-nut may be sometimes nearly obliterated. The kernel is so thick in a variety growing in the Moluccas that there is scarcely any central space (*Tropical Agriculturist* for 1833).

It would be possible to greatly lengthen this chapter, but I have approached the subject mainly as a preliminary to the discussion of the rest-period in the next chapter. Measurements of weight may have but little meaning in themselves, but they acquire a significance when we arrange them in order, as in the general table before given. The indications of the separate seeds are full of suggestiveness. Here we have a series of resting seeds, beginning with those where the embryo constitutes only $\frac{1}{2000}$ of the weight of the kernel (the other 1999 parts belonging to the albumen) and ending with seeds where the embryo has appropriated all the reserve-food, storing it either in its cotyledons or in other parts of its substance. The series speaks eloquently of the true relation between an albuminous and an exalbuminous seed. But it is as concerns the rest-period of seeds that the story of these figures has its most important lesson for us, nature having imposed it on the young plant at all stages of its early development. It is around the mystery of the resting seed that the discussion in the following chapter will chiefly centre.

The rest-period of seeds.

SUMMARY

(1) Any discussion of the weight and size of the embryos of resting albuminous seeds must be beset with difficulties. Foremost comes that concerned with the relation between the albuminous and exalbuminous state, and it is assumed that the first is the primal condition. Then there are the disturbing facts that not infrequently

the same order possesses plants with both albuminous and exalbuminous seeds, and that the rest-period has been imposed on the embryo in very different stages of its development (p. 403).

(2) The method of measuring the weight of minute embryos is then discussed, and it is shown that even those of *Juncus communis*, of which nearly 70,000 go to a grain, are not beyond the reach of the balance (p. 405).

(3) The author then gives his results for the weight of embryos in the case of more than fifty kinds of plants, of which nearly a third belong to palms. The only weight-ratio of the embryo that is given is its proportional weight as a part of the kernel, though in the case of ordinary seeds data for estimating other ratios are added. It is considered that the embryo-kernel ratio is the only one that is generally applicable; and in the table the results are arranged in order, beginning with those seeds where the embryo forms a very small proportion of the albumen and terminating with the exalbuminous seed, where the albumen has all been appropriated by the embryo (p. 408).

(4) The embryos of palms are specially dealt with, and though the subject has many difficulties, some broad results follow from the author's observations. In the first case it is shown that as a rule the embryo shrinks in the drying fruit about twice as much as the albumen, and that in consequence its proportional weight with regard to the kernel is much less in the dry than in the moist fruit (p. 410).

(5) Then stress is laid on the fact that this great shrinkage of the embryo in the drying fruit usually occurs in the first few weeks or months, and that for this reason the seeds of palms could scarcely be expected to retain their vitality for a long period. Facts are given which show that although the period may be as little as two or three weeks, it does not generally exceed six months. On account of rapid drying being favoured by their peculiar structure, it is considered that ruminant seeds of palms would possess the least staying power (p. 412).

(6) Allusion is made in passing to the fact that the coco-nut is not peculiar in possessing in the unripe condition a large cavity filled with water, the fruits of other genera of the same tribe of palms being thus characterised, even in cases where they are only an inch in size when full-grown (p. 414).

(7) The author concludes with the remark that he has approached the subject of the weight and size of embryos mainly as preliminary to the discussion of the rest-period in the next chapter.

CHAPTER XIX

THE REST-PERIOD OF SEEDS

If everything comes from the egg, it is certain all lines of biological investigation lead back to it, and thus it is that in the resting seed our interests converge towards that point in a plant's life. Many botanists of eminence have dealt with this matter, and the salient facts must be familiar to my readers. There are, however, certain aspects of the subject which have come more particularly under my notice; and ever since I studied the vivipary of Mangroves, like *Rhizophora* and *Bruguiera*, in the Pacific, twelve to fifteen years ago, the matter of the rest-period of seeds has been frequently before my mind.

The rest-period represents a break in the continuity of the young plant's existence. As Goebel well puts it, the seed here submits to an interruption in its development; and so it is that the real mystery of the seed lies not so much in the resumption of active vitality implied in germination as in the suspension of its vitality. That singular phase in a seed's life, the entering into the rest-period when it is quite able to proceed continuously with its growth and to go on to germination, is the true mystery. The potential vivipary of plants I hope to establish later, meaning thereby the inherent ability of the embryo to proceed with its growth.

But in the first place it is necessary to acquire a correct notion of the prevalence of the resting habit in seeds, since we are apt to invest this character of seeds with a universality that it does not actually possess and with a persistence that it can

A break in the continuity of a young plant's life.

The degree of prevalence of the resting habit in seeds.

scarcely claim. Since much of the substance of the two following pages will be found in the text-books, it will be sufficient to refer to the works consulted at the end of the chapter.

Goebel points out that whilst with Ferns, *Lycopods*, and *Equisetums* there is no rest-period, in Seed Plants with few exceptions the embryo experiences sooner or later an interruption of its development which is resumed in germination. In reality, though the pronounced exceptions are few, there are many in degree, as is indicated by the transient nature of the rest-period in a large number of plants and by the prevalence of after-ripening, a term applied to the growth of the embryo in the resting seed before and after detachment from the parent plant. As regards the shortness of the period, let us take our own forest trees. The seeds of the Oak, Beech, Elm, Poplar, Horse-chestnut, Maple, Fir, etc., have, as is well known, a very transient germinative capacity, as a rule only preserving this power until the next spring, and even then usually requiring to be planted soon after gathering. Probably not a few of them, when their seeds germinate during a mild autumn, supplement the short rest-period within the seed by a period of repose outside the seed, remaining stationary during the winter under the protection of the fallen leaves, and doing little more than protrude their radicle an inch or two. This capacity in the case of acorns is alluded to later on in this chapter.

Many other seeds are known to behave similarly. Thus, those of *Oxalis* and *Salix* fail usually after a few weeks or months. Professor Ewart strikes the true note when he remarks that in very many cases seeds are very intolerant of even ordinary air-drying. According to De Candolle, the seeds of most Rubiaceæ, Myrtaceæ, and Lauraceæ lose their germinative capacity soon after detachment from the mother plant. The seeds of the Palmaceæ also often retain this capacity but a few months. In reply to a letter, Mr Hart, late Superintendent of the Botanic Gardens in Trinidad, tells me that those of *Oreodoxa*, *Sabal*, *Thrinax*, *Acrocomia*, *Attalea*,

etc., will, if kept in a protected position, maintain their vitality for from three to six months. If, however, there is an excess of atmospheric moisture on the one hand, or drought on the other, the time is much shortened. Some seeds of palms, he adds, like those of *Mauritia*, will not keep more than a week or two. Tropical seeds in general, according to Mr Hart, are as a rule possessed of a very fugitive vitality. To keep seeds in stock is, he says, an absurdity, and the only practical rule is to clean partially and sow at once for the best success.

It is thus evident that the rest-period must be often a transient feature with the seeds of many plants. Not only is this the case, but there are many plants, as already indicated, where the seeds experience after-ripening, the immature embryo of the resting seed continuing to grow up to the time of germination. Such seeds, as Ewart observes, have apparently no rest-period. Amongst examples given by Goebel and others are those of *Anemone*, *Corydalis*, *Crinum*, *Ranunculus Ficaria*, *Eranthis hiemalis*, *Gnetum gnemon*, *Utricularia*, etc. ; but the same may be inferred of numbers of other plants where the embryo is immature or but slightly differentiated, such as *Cuscuta*, *Orobanche*, *Monotropa*, *Balanophorææ*, etc., named by Kerner, and *Styloidium*, *Gagea*, and *Erythronium*, suggested by Ewart.

The after-ripening of seeds.

But in this matter we can make a much wider cast with our net. After-ripening must often be counted upon by the agriculturist and the gardener. They know that certain seeds cannot be forced. It is the experience of the gardener, says Kerner, that many seeds have to mellow or ripen before germination ; and he reminds us that in many cases seeds germinate in the spring under apparently much less favourable conditions of temperature and moisture than they enjoyed in the late summer and autumn of the previous year, when they were first detached from the plant.

There is another familiar feature in connection with resting seeds which has been already implied, namely, the great variation in the degree of development attained by the embryo when entering the resting stage. In some the embryo is in

The varying degree of development of the embryo in the resting seed.

different stages of incompleteness. In others it is ready to germinate. No one has stated the matter more clearly than Goebel, and to no one are we indebted for a more authoritative discussion of the subject. It is indeed quite a commonplace feature in seed-life, and I hesitate to add the results of my own observations on a matter long recognised. The data supplied by Goebel in his *Organography of Plants* (ii. 248-254) supply a most important lead for the investigator. Differences of this kind we are wont to associate with a genus or a family, but here we learn that, as in *Anemone* and *Utricularia*, they may be found within the limits of a species and even in the same individual.

We are told that we can only conjecture about the causes of this behaviour ; but the problem restricted to such narrow limits presents an inviting field for the investigator. As will be subsequently pointed out in other plants, the differences in the degree of development of the embryo in these cases is probably associated with the displacement of the period of fruit-maturation as regards the seed. Thus, I would suppose that when the embryo in the resting seed is able to produce its cotyledons and even its first leaves, the fruit is much later in maturing than when the embryo is merely an "unsegmented acotyledonous body." We should then have to inquire into the causes of the postponement or acceleration of the maturation of the fruit with reference to the seed and its embryo.

But before discussing this view of the matter I will adduce further evidence in support of the contention that embryos, whatever may be their stage of development in the resting seed, are inherently able to continue the growth suspended through the intervention of the rest-period. This is of course implied for many plants in the after-ripening of their seeds and in the occasional premature germination of seeds on the plant during exceptionally humid weather ; but I desire now to show that all seeds, or rather their embryos, possess an inherent capacity of dispensing with the rest-period. That the embryo of an albuminous seed is able to continue its growth

The
embryo's
inherent
capacity of
dispensing
with the rest-
period.

after removal from the seed was long ago established by Van Tieghem in the cases of Maize and *Mirabilis* (Nobbe, pp. 310, 311). Here, however, the resting seed was concerned; and it is more to the point to establish it for the embryo removed from the seed before drying and shrinkage begin.

I found that embryos of *Iris Pseudacorus*, removed from their bed of albumen in the moist, uncontracted pre-resting seed and then placed in water, increased their length in a few days from 4 to 7 millimetres and displayed the plumular knob. The progressive growth of the embryo as the fruit grows and matures is in this plant very evident. Whilst the seed maintained much the same dimensions (7 millimetres), I obtained the following results for the growth of the embryo in different stages of the fruit's development:—

Detached embryos of *Iris Pseudacorus*.

Immature fruit . . .	embryo	1.5 mm. long
Ripe fruit before dehiscence . . .	„	2-2.5 „
Fruit beginning to dehisce . . .	„	3-4 „

With the object of inhibiting the rest-period and inducing pre-resting seeds to proceed at once with germination, I placed at different times a number of seeds of *Iris Pseudacorus*, *Vicia sepium*, *Arenaria peploides*, and *Quercus Robur* under favouring conditions in the moist, uncontracted state and obtained successful results. Thus, after keeping some of the freshly gathered, ripe, non-dehiscing fruits of the *Iris* in wet moss under warm conditions (60°-70° F.) between ten and fourteen days, I found that the drying of the fruits and seeds had been prevented and that some of the seeds were germinating. The full-grown, soft, uncontracted seeds taken from the green legumes of *Vicia sepium* behaved in the same way under the same conditions of experiment. In four or five days they commenced to germinate, and in five days the seedlings were half an inch long. The white, soft seeds from the green capsules of *Arenaria peploides* responded to my experiments precisely in the same fashion. So also with *Quercus Robur*, it is not difficult to procure the rapid germination of ripe acorns in September and October.

Experiments inhibiting the rest-period.

If fresh green acorns of full size and still vitally connected with the cupule are placed in wet moss under warm conditions, some of them will be found germinating within a week.

Nature's hint
to the
gardener.

The germinative capacity of so-called unripe seeds does not seem to have been fully appreciated by foresters, gardeners, and horticulturists, the advantages to be derived from dispensing with the rest-period being obvious. As subsequently shown, nature offers us some valuable suggestions in this direction in the case of the Oak. Many plants must afford similar indications. Thus Pfeffer points out (ii. 205) that the seeds of *Senecio vulgaris* and *Stellaria media* can germinate as soon as they are ripe. Take again the soft, scantily protected seeds of *Pithecolobium flicifolium*, the Bastard Tamarind of Jamaica. They germinate a few days after falling from the tree, or else lose their vitality altogether.

The causa-
tion of the
rest-period.

The causes of the phenomena displayed in the resting of seeds must be sought far back in the plant's life-history, not in the seed alone, but in the seed as it depends on the fruit, and in the fruit as it depends on the parent plant, and in the parent plant as it responds to its conditions of existence. Therefore, in dealing with the causation of the rest-period, we should proceed in this order of investigation: the seed, the fruit, the mother plant, and, lastly, the conditions. Yet it is at first requisite to distinguish between the general causes that determine the suspension of growth and the special influences that determine the stage of development of the embryo at which the rest-period is imposed. Any discussion of the general causes must necessarily begin with an inquiry into the influence of the fruit, and be then extended to the influence of the parent, and then back to the conditions. Being unprepared to venture into such a wide field of investigation, I will confine my remarks to the influence of the fruit, and that only in an illustrative fashion.

The influence
of the fruit.

The biological disconnection of the seed indicated by the shrivelling of the funicle is proximately determined by the limit of the fruit's vitality. The fruit dries, the funicle shrivels up,

and the rest-period begins. In other words, the fruit dies and the seed lives, or rather it retains the potentialities of life. In Chapter XIII I have dealt with the different behaviours of the legume and the capsule as regards dehiscence, the first dehiscing after drying is nearly or quite complete, the second before drying commences or in its earliest stage. As the result of these changes, the seeds shrink and harden rapidly when exposed in the drying, dehiscing capsule, and less rapidly, but not less effectually, in the drying but still closed pod.

If it were not for the drying of the fruit there would be no reason why the soft seeds in the moist living fruit should not proceed continuously with their development and dispense with the rest-period altogether. In theory this should be brought about by preventing the drying of the fruit. In practice actual experiment has shown that this can be arranged, as I have done with different fruits of *Vicia*, *Arenaria*, *Quercus*, and *Iris*, by placing the fruit in moist, warm conditions when in the full-grown living state. Under such circumstances the capsular valves separate, whilst the legume decays rather than dehisces, and the seeds will be found germinating in a week or two without having experienced any pronounced check in the development of the embryo.

But these are not the conditions usually presented in nature. The capsule dehisces and dries, whilst the legume dries and dehisces; and the further development of the embryo is arrested by the resulting shrinking and hardening of the seed. On the assumption that the continuous growth of the embryo-plant is the primal normal condition, there is an obvious lack of co-operation or co-ordination here, since experiment is able to arrange for the working together of the conditions so as to ensure the uninterrupted growth of the embryo. There is a lack of co-ordination in the capsule, because the seeds are exposed in the moist fruit before the embryos can lead an independent existence. There is a lack of co-operation in the legume, because the pod begins to dry before the seeds can sprout.

The rest-period results from the failure of co-ordination of the fruit and the seed.

The rest-period therefore represents the failure of co-operation between the parent, the fruit, and the seed. Over both seed and fruit hangs the fate of ultimate detachment from the parent, and according as there is concurrence or not we get a viviparous or a resting seed. Successful co-operation ensures not only that before the fruit begins to dry the seeds are ready to germinate, but also that the germinating seed should quickly find suitable conditions for further growth, either by the timely fall of the fruit or by the liberation of the germinating seed. But even here in the great majority of cases germination on the plant takes place in a dying or decaying fruit. Nature is seen at her best in the co-ordination of the growth forces of the fruit and the seed in those plants, like the Mangroves (*Rhizophora* and *Bruguiera*), where the fruit still lives and the seed still grows, until at length the seedling drops from the mother plant. This is the truest form of vivipary.

But to return to the question of the lack of co-operation between the seed and the fruit in the legume and capsule, there is not much significance in the mere statement that dehiscence occurs early in the capsule and late in the legume. But there is a good deal of meaning when, viewing the possibilities of vivipary, we state that dehiscence takes place too early in the capsule and too late in the legume. If vivipary took place in the capsule or in a legume, it would be under the moist conditions illustrated in my experiments, where soft, uncontracted pre-resting seeds were induced to germinate without entering the resting stage. But in the capsule nature defeats such an end by bringing about the early dehiscence of the living fruit and the rapid drying of the exposed seeds. In the legume nature would usually render such an event impossible by bringing about the failure in the living but still closed pod of the connection between the parent and the fruit. The pod dries, the funicle shrivels, the seed shrinks and enters the resting stage, and last of all the fruit dehisces. Regarded from the possibility of vivipary, this therefore is the significance

of the early dehiscence of many capsules and the late dehiscence of the legume. For the continuous growth of the embryo, which we assume to be nature's primal condition, the opening of the fruit is wrongly timed in both cases, too early in the one, too late in the other.

Let us take a conspicuous example of the ushering in of the rest-period in the case of the seeds of a ligneous legume like that of *Poinciana regia*. In the chapter on seed-coloration, I have already described the remarkable changes which the embryo of these seeds undergo when entering the resting stage and when resuming active life and growth in the germinating process. The embryo of the large, soft pre-resting seed in the green and living pod is a plantlet full of vitality with green cotyledons and green, partially unfolded plumular leaves. When the fruit begins to dry the green hue of the embryo disappears. The plumule folds up its tiny leaves, and the rest-period commences.

The case of
Poinciana
regia.

The closing in and the cutting off from the external world of the soft green respiring seeds of *Poinciana regia* seem almost tragical, and one marvels at the fine adjustment which allows these unresistant seeds to hold their own when everything is hardening into tough wood around them. Let one of the seeds fail in its early stage and the ligneous tissue invades its area and occupies its place. What concerns us here is that when the embryo loses its green hue, as the tissues harden around the seed, it ceases to respire, and with its vitality completely suspended it becomes buried in a hard woody fruit that dehisces but tardily. In one's ignorance one almost doubts the wisdom of such a suspension of active life in the warm genial climate which this tree enjoys, since the embryo has already advanced considerably in its growth and is well able to proceed with its development.

Coming to the special influences that determine the stage of development of the embryo when the rest-period begins, one may observe that the great variation displayed by the embryo in this respect ought to be associated with correspond-

The special
influences
determining
the stage of
the rest-
period.

ing variations in the period of the fruits' maturation relatively to the seed. If the fruit matures early and dries quickly the embryo will not have reached the same stage of development when the rest-period begins as when the fruit matures and dries late. Where the fruit reaches the limit of its growth far in advance of the seed, we might expect the embryo to be small and but partially differentiated. Where the fruit is not so advanced in growth, the embryo would be much more developed when the suspension of vitality sets in. Where matters are reversed and the embryo grows quicker than the fruit-case, as in *Avicennia*, the plant is viviparous. Here, however, germination is associated with the rupture and death of the fruit-envelopes. The truest form of vivipary, as already observed, is seen in *Rhizophora*, where the fruit still lives and the seed still grows, the young plant remaining for a long time attached to the parent.

It lies with the future inquirer to ascertain how the mother plant through the fruit determines the stage at which the rest-period is to be imposed on the embryo in the seed. Over both seed and fruit, as previously remarked, hangs the fate of ultimate detachment from the parent; but this fate may be avoided if the two co-operate so that when the fruit is ripe the seeds have already begun to germinate. The seed depends on the fruit and the fruit on the parent plant; and since the parent has its part to play in determining the relation of growth between the seed and its fruit, it follows that it has the first word to say in shifting the plane of the rest-period. I may perhaps be allowed to suggest to some investigator that he should inquire into

- (a) The relation between the stage of development acquired by the embryo in the resting seed and the time of maturation of the fruit;
- (b) The relation between the early and late maturation of the fruit (relatively to the seed) and the conditions influencing the mother plant.

The problem, however, is an extremely complex one. A method of approaching it is indicated in Chapter XIV, where it is shown that two types of fruits can be differentiated when we deal with the proportions of parts for the successive stages of the fruit, as tabulated on p. 303. But this ignores the transition from the albuminous to the exalbuminous state of seeds, which involves a factor of paramount importance, and one that carries us back to a very early state of the seed's development. The whole subject will acquire a very complicated character when we introduce this consideration into the discussion.

A chance observation in May 1908 led me to suspect that the embryo of the seed of the Ivy (*Hedera Helix*) grew continuously through the winter and that germination occurred without any rest-period in the spring. My suspicion was to some extent confirmed when I found early in June that many of the embryos had nearly doubled their length since the last observation, and that some seeds were germinating within the fruit on the plant. However, the actual growth of the embryo in the winter had yet to be established. To this end my sister, Mrs H. Mortimer, made periodical collections of the berries at Redland, Bristol, during the winter 1908-9; and on my return to England from the West Indies in the spring I made use of these materials, the principal data obtained from them being incorporated in the table subjoined. The behaviour of the embryo in the spring was observed by me during the four years, 1908-11.

It will be seen from the results tabulated on p. 428 and from the accompanying figures that the berries increased gradually in size from the beginning of November 1908 to the latter part of January 1909, the green colour giving place to a blackish hue and the maximum growth corresponding to the complete blackening of the fruit. The increase during this period of the solid constituents of the growing fruit as the water-percentage diminished is especially noteworthy. Up to January also the seeds grew with the fruit, their increase in

The winter growth of the embryo of the Ivy seed on the plant.

The growth of the embryo of the Ivy up to March.

OBSERVATIONS ON THE GROWTH DURING THE WINTER AND SPRING OF THE FRUITS, SEEDS, AND EMBRYO OF THE IVY (*HEDERA HELIX*).

(Weights in grains and lengths in millimetres.)

	Moist fruit.		Air-dried seed.		Embryo of moist seed.			Loss of weight of the air-dried fruits.	Remarks.
	Colour.	Weight.	Weight.	Length after soaking.	Length.	Proportion of bulk of moist seed.	Colour.		
1908.									
Nov. 9	Green	1'69 grs.	'06 gr.	4'5 mm.	0'7 mm.	1%	White	79%	
" 18	"	2'86 "	'12 "	5'0 "	1'5 "	1'5%	"	79%	
Dec. 3	"	4'02 "	'20 "	5'5 "	1'6 "	1'5%	"	76%	
" 17	Blackening	4'96 "	'24 "	6'0 "	2'0 "	2'5%	"	71%	
1909.									
Jan. 9	Black	5'44 "	'34 "	6'0 "	2'2 "	3'0%	"	65%	
" 24	"	5'50 "	'35 "	7'0 "	2'7 "	4'0%	"	63%	
Feb. 21	"	4'10 "	'36 "	6'7 "	2'5 "	3'5%	"	60%	
Mar. 19	"	4'02 "	'34 "	6'3 "	2'3 "	3'5%	"	61%	
1909.									
Apr. 20	4'5 "	10%	Green	(57%)	Some seeds germinating on the plant on May 6.
May 6	6'0 "	20%	"	...	
1910.									
Mar. 11	2'0 "	...	White	...	On May 22 some seeds germinating on the plant.
Apr. 2	2'5 "	...	"	...	
" 8	3'0 "	...	"	...	
May 3	4'0 "	...	"	...	
" 22	5'0 "	...	Green	...	

Explanation.—The observations of November 1908 to March 1909 were made from collections obtained from the same plant by Mrs Mortimer at Redland, Bristol. Each sample, consisting of from forty to sixty berries, was weighed at once, and subsequently weighed and examined by me when the drying was complete some months after. The other observations were made by me from fruits gathered at Salcombe in South Devon.

In the case of the Bristol fruits the data for the embryos were obtained after soaking the seeds in water for a day.

The water-contents indicated by the loss of weight of the berries when air-dried are taken from the table at the end of Chapter XII. The entry for April 20, 1909, relates to an observation made on fruits in the same stage in the following year.

The diminution in the weight of the fruit in February and March is due to most of the larger fruits having fallen.

FIGURES ILLUSTRATING THE GROWTH ON THE PLANT OF THE SEED AND EMBRYO OF THE IVY (*HEDERA HELIX*) FROM NOVEMBER 1908 TO JUNE 1909.

November 9.



Seed, 4.5 mm.
Embryo, 0.7 ,,

December 3.



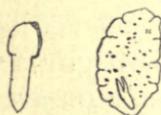
Seed, 5.5 mm.
Embryo, 1.6 ,,

January 9



Seed, 6 mm.
Embryo, 2.2 mm.

January 24.



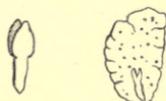
Seed, 7 mm.
Embryo, 2.75 mm.

February 21.



Seed, 6.7 mm.
Embryo, 2.5 ,,

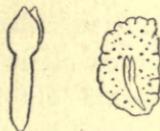
March 19.



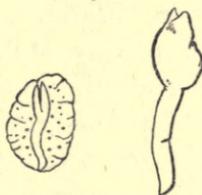
Seed, 6.3 mm.
Embryo, 2.3 ,,

May 16.

April 20.

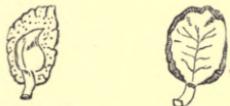


Seed, 6.3 mm.
Embryo, 4 mm.



Seed, 6 mm.
Embryo, 6 ,,

Early in June.



Germinating seeds.

All enlarged; in the case of the seeds twice the natural length, and in the case of the separate embryos four times, but the germinating seeds are drawn about one and a half times the normal length.

With the exception of the germinating seeds, therefore, all the seeds are drawn to one scale, and since the separate embryos are also drawn to one scale, it follows that the changes in size are respectively in true proportion.

These figures are intended to illustrate the results given in the preceding table.

size being principally due to the growth of the endosperm. The small embryos also added to their bulk, but at a rate not much faster than the seed. They displayed but little evidence of having grown at the expense of the food-reserve, and remained white, with their cotyledons appressed. From the end of January up to the middle of March there was a suspension of the growth of the fruit, seed, and embryo; and here the observations for that season ended, the embryo remaining in the same colourless, inert condition. The winter was severe, and I think it very probable that under milder conditions there would not have been this check.

The latter part of the history of the growth of the embryo in the seed on the plant is supplied by my own observations during four successive springs. Since their general results agree, I have only given in the table those for 1909 and 1910. It is there indicated that after March the embryo grows with fair rapidity. Taking all the data of the four years, the average growth in the spring would be as follows:—By the end of March or the beginning of April the embryo would be about 3 millimetres long, or just half the length of the kernel, but remaining white and showing no enlargement of the cotyledons. During the latter part of April and the early part of May most of the berries fall to the ground, their detachment being hastened by wind and rain. The seeds of those that remain usually display embryos 4 or 5 millimetres long, increasing perceptibly at the expense of the albumen and with enlarged green cotyledons. As May advances the embryos attain the length of the kernel (6 to 7 millimetres), some of them becoming even longer, so that they are compelled to accommodate themselves to the kernel's length by bending, as shown in the figure for May 16. A few seeds will be found germinating within the fruit, which has already begun to shrivel and soon drops off. Whilst the berry is attached to the plant the radicle pierces the seed-coats, but not the pericarp, the hypocotyl becoming bent over the seed inside the fruit. In these germinating seeds the albumen has largely disappeared.

The growth
after March.

In different years, when the season is unusually mild, all the stages above referred to the month of May will be found in April. The seeds will not generally be found all germinating in the same berry, but all will show embryos advanced in growth. Nature only offers a small number of fruits to illustrate the germination of the seeds on the plant, since the final stage is usually anticipated by the early shrivelling and detachment of the berry when the embryo is 3 or 4 millimetres long, the result of late frosts, wind, and rain. However, of the surviving berries the proportion with germinating seeds in May will vary from 10 to 50 per cent. By the beginning of June all the fruits have fallen. I have here been describing the behaviour of Ivy berries in the mild climate of South Devon. The growth of the embryo in the spring is a good deal influenced by the situation of the plant. Thus in sunny places sheltered from the cold winds it will be much in advance of that found in plants growing in bleak, exposed localities.

The nature of the growth of the embryo of the Ivy during the winter is well brought out in the table. The seed grows with the berry and the embryo grows with the seed, the increase in its proportional bulk being but slight. There is little or no growth at the expense of the endosperm, the embryo remaining white and the cotyledons retaining their small dimensions. But with spring in progress the berry and the seed no longer add to their size. The embryo, now 4 or 5 millimetres long, grows independently. Its cotyledons enlarge and its whole surface becomes green, this independent growth being associated with a gradual diminution of the food-reserve, so that when the seed is found germinating in the berry on the plant, the albumen has mostly disappeared. The two kinds of growth of the embryo, first during the winter with the seed and the fruit, and then in the spring at the expense of the albumen, are the conspicuous features in the vivipary of the seeds of the Ivy. We can thus distinguish two stages in the after-ripening of these seeds.

Two modes
of growth of
the embryo
of the Ivy in
the seed on
the plant.

The connection between the late flowering and the viviparous tendency of the Ivy.

There are therefore two singular features that must be closely linked together in the life-history of the Ivy—the autumnal flowering and the ripening of the seeds on the plant during the winter, followed by germination in the spring, without the intervention of a rest-period of more than a few weeks' duration. Much depends on the causal connection between them. If the plant is viviparous because it flowers in the autumn, then the vivipary appears to be adaptive; but if it flowers late because it is viviparous, then the autumnal flowering would be an adaptation. It may be that the cause of the late flowering is to be found in the absence of any proper rest-period for the seed. For if the plant flowered in the spring, it would mature its fruit at the close of the summer, and the seedlings would be cut off by the winter's cold. The retention of the viviparous habit would lead to extinction, unless flowering occurred in the autumn. It is likely that a difference in the mode of ripening of the seeds may explain why *Hedera Helix* (as stated by Kerner) grows in Central Europe without any protection from the winter's cold, whilst the Ivy of Southern Europe (*Hedera poetarum*), which is very similar in characters, can only survive the winters of Central Europe under a protecting roof.

The tendency to vivipary displayed by acorns.

I come now to my observations on the normal tendency to vivipary displayed by the seeds of acorns (*Quercus Robur*). This is not only exhibited in the occasional germination of these fruits on the tree, but in the actual stages of growth of the seed within its shell before maturity is reached. The steady growth of the seed on the tree long after the pericarp or shell has begun to dry has been discussed at length in Chapter XIV. It was then said that the tendency of a seed to continue its growth on the plant after the pericarp or fruit-case has commenced to dry and lose weight, finds its final expression in the germination of the seed on the plant, or, in other words, in vivipary. Such was the tendency displayed by the oaks near Salcombe, in South Devon, during the successive autumns of 1908 to 1911; and doubtless it is characteristic of this tree in other localities.

It can be easily demonstrated that ripe moist acorns are able to proceed at once with germination if placed under conditions inhibiting the drying of the fruit. Thus on September 17, 1908, I collected some ripe acorns and placed them at once in damp moss in a warm cupboard. They were still biologically connected with the cupules, and their shells, though beginning to brown, were still thick and moist. Within eight days I found some of them germinating normally, and one of them when planted grew healthily under protection during the winter. (Whilst preparing this chapter (September 1911) I repeated this experiment with green ripe acorns showing no signs of drying, and possessing, as in the first case, entire shells. In five days half of them were splitting their shells, and several of these were protruding the radicle.)

Every autumn I noticed a small but variable number of ripe acorns showing signs of germination on the trees in the splitting of their shells and in the slight protrusion of the radicle. The growing seed had burst the fruit-case, and in many cases it was evident that the seed was larger than its shell. This was recorded at the end of September 1908, in the first half of October 1909, in the middle of October 1910, and in the second week of September 1911. A number of the split nuts placed at once in wet moss in two different autumns were found in four or five days well advanced in the germinating process. When the acorn begins to split at its sides it is full-sized, moist, and green, and is still vitally connected with the cupule. Usually the protrusion of the radicle is not great on the tree; but I can recall a case where its growth was considerable, and where the inner surfaces of the cotyledons were turning green whilst the fruit was still attached.

This attempt at germination on the tree soon brings about the fall of the nut. The shell browns rapidly as it dries, and the fruit is soon vitally disconnected from the cupule. Generally the fallen acorn dies; but it must frequently happen in moist mild weather that it continues the growth commenced on the

The fate of the acorns that germinate on the tree.

tree ; and if it is subsequently protected by the fallen leaves, there is no reason why it should not survive an ordinary winter's weather and be ready for active growth in the spring.

Here is an experience that bears directly on this point. Some acorns which had germinated a few days after being picked from the tree in October were left covered up in the basin of wet moss in my greenhouse and forgotten. Early in March I was surprised to find that several of the acorns were still alive, with radicles protruding about an inch, the moss being still damp. The winter growth had been very slight, the germinating seeds having undergone a period of almost complete repose. Healthy seedlings were raised from them. During the months of January and February there had been no artificial heat in the greenhouse, and the contents were at times frost-bound, the lowest reading of the thermometer inside the house having been 23° F.

The proportion of acorns exhibiting the early stage of germination on the tree in the autumn varied in different years. Thus in the season of 1909 I placed it at 2 per cent. In 1911, after the abnormally long and dry summer, extending into the fall of the year, the proportion in the fourth week of September was as high as 10 per cent. The exceptionally dry season had not affected the foliage of the trees, whilst the fruits were much larger and much more abundant than in the previous years. Whilst in 1908 the average weight of an acorn was from 60 to 70 grains, and in 1910 from 50 to 60, in 1911 it was about 100 grains. The fruits ripened nearly a month earlier than usual, being mature in the middle of September instead of early in October.

I had a remarkable experience with ripe acorns during three successive Octobers. After being gathered from the tree in the green moist stage, before any loss of weight by drying had occurred, I placed them on each occasion in a dry saucer in a room which was rather damp, as there was no artificial heat. The nuts were quite entire and showed no signs of splitting their shells. On the first occasion

The proportion of acorns that begin to germinate on the tree.

The germination of detached acorns during the drying process.

eleven out of fifty-five nuts were found in the typical germinating state about seventeen days after. The fruits had germinated whilst actually drying ; and I estimated their loss of weight when germination began at from 10 to 20 per cent., the total loss of weight of a mature fruit when completely air-dried being from 50 to 60 per cent. The same thing happened under the same circumstances in the two following Octobers. In an experiment carried out whilst writing this chapter, I placed thirteen ripe acorns in a dry cup. In nine days one was protruding its radicle and two were splitting their shells, the aggregate loss of weight since the seeds were gathered in the moist entire condition from the tree being just 10 per cent.

We are not concerned here with after-ripening, such as frequently occurs with detached albuminous seeds, since in the mature acorn on the tree the embryo is fully formed and develops a plumule which may be turning green. The interest lies in the fact that germination took place in the case of a mature exalbuminous seed in a drying fruit. It is evident that with the acorn the ripe moist seed is not necessarily prevented from proceeding continuously with its growth by drying in air for a week or two. But the drying process must be slow. In most cases the loss of water is too rapid and the tendency to proceed at once to germinate is suppressed. Evidently the detached ripe acorn, provided that the drying is checked, can make good use of the water it holds, which is more than is actually needed for the continued growth and germination of its seed. Anything that impedes the air-drying process of the freshly detached acorn will assist the seed in its endeavour to dispense with the rest-period altogether.

In this way we may explain Uloth's observation of acorns germinating in ice. The explanation given in Nobbe's book (p. 104) is, that the requisite water would be supplied by the melting of the surrounding ice through the natural warmth of the seed. However, we learn from my observations above

Uloth's
observation
of acorns
germinating
in ice.

given that the detached fresh acorn does not need any water from outside in order to proceed at once with the germinating process. In fact, we have seen that such acorns will germinate without a rest-period after losing a good proportion of their weight by drying. Any check to the drying process of the fresh detached nut would directly aid the seed in proceeding continuously with its growth and in dispensing with the usual period of repose. This check would be found in the inclusion of acorns in ice. Drying would thus be inhibited, and the acorn would have sufficient free water within its own substance for the uninterrupted growth of the seed.

For important particulars relating to the stages of growth of the acorn the reader is referred to two tables given on pp. 303, 311.

Vivipary in
Artocarpus
incisa.

Germination within the fruit on the tree may take place in the case of the seeded variety of the Bread Fruit (*Artocarpus incisa*). This came under my notice in Grenada and Tobago. Mr Anstead, the Superintendent of the Botanic Gardens in Grenada, assured me that this habit was well known in the island. In the case of a fruit that had just fallen I found a third of the seeds (about sixty in all) germinating or "showing eyes," as the coloured people call it. In another fruit that had fallen the day before three-fourths of the seeds were germinating. It was evident that germination began on the tree in the ripe fruit ready to fall. With the ordinary seedless variety suckers burst through the ground all around the tree. They are absent altogether with the seeded kind.

Crinum.

I made some observations on the viviparous habit of detached *Crinum* seeds. This habit is well known, so that I will refer the reader to Note 29 of the Appendix for my remarks on the subject. Here, in the case of seeds packed away in my collections, germination took place in seeds that had lost more than half of their weight, the embryo increasing its size ten- or fifteen-fold within the seed during the drying process.

Some of the works quoted in this chapter are—Goebel's *Organography of Plants*; Kerner's *Natural History of Plants*; Ewart's "Longevity of Seeds" (*Proc. Roy. Soc. Victoria*, 1908); Ewart in *Trans. Biol. Soc. Liverpool*, 1896; Nobbe's *Handbuch der Samenkunde*; Schröder in *Untersuch aus dem Botan. Inst. zu Tübingen*, Band ii., 1886.

SUMMARY

(1) The rest-period represents a break in the continuity of the young plant's life, and is the effect of external conditions acting through the parent and the fruit on the seed. The author's main object in this chapter is to establish the inherent capacity of all embryos to proceed uninterruptedly with their growth, whatever their stage of development when the resting state is imposed.

(2) In dealing with this subject he discusses the prevalence of the resting state in seeds, and the well-known circumstance just implied that the rest-period has been imposed on seeds in all stages of development of the embryo.

(3) In the first case, he shows that this state of repose is often very transient with a large number of plants, and that when we reflect that many plants experience "after-ripening" in their seeds, when the embryo continues to grow after the seed has entered the resting state, the rest-period is deprived of some of its prominence as a feature in plant-life (p. 418).

(4) As concerning the second point, he directs attention to the great importance of Goebel's observations on *Anemone* and *Utricularia*, from which we learn that all the stages, from that of the unsegmented acotyledonous embryo to that of the embryo producing its cotyledons and even its first leaves, may be found not only in the resting seeds of different individuals of the same species, but even in the same individual. It is suggested that the problem thus confined within such narrow limits presents an inviting field for further inquiry (p. 420).

(5) The author points out that the inherent ability of the embryo to continue its growth without the interruption of the rest-period is itself implied in its existence in such varied stages of development in the resting seed. The familiar after-ripening of seeds, above noticed, and the well-known occasional germination on the plant of seeds accustomed to submit to a normal rest-period, are also facts indicative of this inherent capacity (p. 420).

(6) Experimental proof is adduced to show that in the case of any plant taken at random, such as *Arenaria*, *Iris*, *Vicia*, *Quercus*, etc., it is

possible, by placing under suitable conditions the soft uncontracted seed of the moist living fruit, to induce it to proceed continuously with its growth and to germinate without any resting stage (p. 421).

(7) Coming to the question of causation, it is urged that we must distinguish between the general causes of the rest-period and the special influences that determine the stage of development of the embryo at which the period of suspended growth is imposed (p. 422).

(8) In references to the general causes it is shown that although in some ways certain climatic influences may be recognised, as those concerned with excessive humidity, yet the subject is really far more complicated than such an explanation would suggest. Indeed, the causes must be sought far back in the plant's life history, not in the seed alone, but in the seed as it depends on the fruit, and in the fruit in its dependence on the mother plant, and in the mother plant in its responses to its conditions of existence (p. 422).

(9) Being unprepared to undertake such a profound inquiry, the author here limits himself to the influence of the fruit, and that only in an illustrative way. He shows that the suspension of the active growth of the seed presents itself as the result of failure in the co-ordination or co-operation of the growth of the seed and the fruit. Only in the truly viviparous plant, as in *Rhizophora*, is there complete co-ordination. Over both seed and fruit hangs the fate of ultimate detachment from the parent; but this fate may be avoided if the two co-operate, so that when the fruit is ripe the seed has already begun to germinate (p. 423).

(10) Taking the capsule and the legume, it is remarked that there is a lack of co-ordination in the first because the seeds are exposed in the moist fruit before the embryos can lead an independent existence; and there is a lack of co-operation in the legume because the pod begins to dry before the seeds can sprout. There is not much significance in the mere statement that dehiscence takes place early in the capsule and late in the legume. But there is a good deal of meaning when, regarding the possibilities of vivipary, we state that dehiscence occurs too early in the capsule and too late in the legume. Nature has wrongly timed the opening of the fruit in both cases (p. 423).

(11) As showing the way in which the rest-period may be imposed, and how the life of a young plant well able to proceed with its growth may be abruptly suspended, the case of the seeds in the woody legume of *Poinciana regia* is taken (p. 425).

(12) With regard to the special influences that determine the stage of development of the embryo at which the rest-period is imposed, the author looks for them in the different stages of growth of the fruit and the seed. Since, however, the rest-period is directly determined by the limit of the fruit's growth, and since the limit of the fruit's growth is determined by the mother plant, it follows that the mother plant has

the first word to say in shifting the plane of the rest-period. But restricting his remarks to the special influences of the fruit, the author points out that the more the fruit's growth is in advance of that of the embryo, the earlier should be the onset of the rest-period, and that only when the two are co-ordinated does true vivipary occur (p. 425).

(13) Then follow the results of the writer's observations on the viviparous tendency displayed by the seeds of the Ivy (*Hedera Helix*), and of the Oak (*Quercus Robur*). In the case of the Ivy it was ascertained that the ripening of the seed on the plant during the winter is followed by germination in the spring without the intervention of a rest-period of any long duration. The ripening in the winter months is characterised by the associated growth of berry, seed, and embryo, the embryo growing as the endosperm increases. The ripening in the spring is confined only to the embryo, which grows at the expense of the endosperm. The result is germination on the plant in the case of the seeds of berries that remain long attached to the parent (p. 427).

(14) In the case of the Oak it is established not only that the freshly detached moist acorns can be readily induced to pass on to germination, but that there is a decided tendency for the ripe acorn on the tree to dispense with the rest-period. This viviparous habit has been already regarded as the final expression of the tendency of a seed to continue its growth on the plant after the fruit-case has commenced to dry, a capacity that was established for the seed of the acorn in Chapter XIV. As a result the seed not infrequently becomes too large for the fruit-case and splits the shell, the radicle protruding when the acorn remains some time longer on the tree. The proportion of acorns beginning to germinate on the tree varied between 2 and 10 per cent. (p. 432).

(15) The chapter is concluded with some notes on the germination of the seeds of *Artocarpus incisa* (seeded variety of the Bread-fruit tree) in the fruit on the tree, and on the continuous growth of the embryo of *Crinum* during the drying of the seed (p. 436).

CHAPTER XX

THE COSMIC ADAPTATION OF THE SEED

THE physics of seeds ought to be a subject of deep interest, if only from the circumstance that whilst the seeds, generally speaking, can live or retain their vitality in any climate, the parent plant is as a rule rigidly restricted in this respect. The fact that the seed is less specialised for terrestrial conditions than the parent plant is one of the first suggestions that nature offers to us when we approach the consideration of seeds from the cosmic standpoint. It is one of the purposes of this chapter to extend this distinction by showing that seeds might live on a planet where conditions destructive for the parent plant prevail. Where the discussion appears disconnected and inconsistent, the defect is usually due to the circumstance that I have here strung together notes and ideas jotted down generally during botanical rambles in the last four years. To endeavour to adjust some of them would be to displace others, so I have preferred to let them stand, feeling assured that in the opening up of new ground of this sort the reader will be to my faults a little blind.

It was the behaviour of the seed of *Guilandina bonducella* in the oven and in the balance that first led me into these speculations. The spectacle of a plant-embryo living its own life in its hermetically sealed case and irresponsive to outside conditions seemed to offer a near approach to an unconditioned existence on this planet. Though crude and only partly true, this notion proved to be very suggestive ; and I came to see

Intro-
ductory.

The seed is
less special-
ised and less
conditioned
than the
plant.

that the transition from the seed to the full-grown plant is a transition from the less conditioned to the more conditioned state of plant-life. The seed often appears to be largely independent of its conditions on the earth's surface ; but this could only be true in a relative sense as compared with the plant. The plant is conditioned only for terrestrial existence, the seed for existence in the cosmos. This it is that makes the seed so often seem to be out of touch with terrestrial conditions. Whilst there is so much about the seed and its fate that appears to be haphazard and to be determined by accidents when regarded from the standpoint of our planet, it may be, as before observed, that regarded from the broader standpoint of the cosmos such a lack of harmony does not exist.

The seed in the universe or cosmos may be like a great traveller on the earth adapted to all climes and acquainted with all peoples. He is cosmopolitan in his habits, and as such seems fitted for all conditions. Yet if we were to ask the peoples of the different countries amongst whom he had lived, we should find that they judged him merely from the restricted standpoint of their experience, and that only in proportion as he acquired proficiency in their special way of living would he be regarded as a profitable member of their society. His general fitness would not be appreciated by a North American Indian if he could not follow a trail, or by a Pacific islander if, when stranded on a coco-nut islet, he could not climb the tree. Though in a general sense fitted to live everywhere, in a special sense he would be suited for nowhere. Yet the judgment of the savage would be the pity born of ignorance.

So it is with ourselves and the seed. We only notice its want of special fitness for its terrestrial life. Whether it will reach a suitable soil or whether it will ever germinate at all seem to be matters of chance. Yet we are apt to forget that its great capacity for preserving its vitality presents us with a range of conditions that extends beyond the earth. A seed that could withstand the intense cold of space, or is able to ger-

Its potentialities present us with a range of life-conditions that extends beyond the earth.

minate after prolonged immersion in an atmosphere of nitrogen or chlorine or in alcohol, would lack those special adaptations to terrestrial life which give the appearance of fitness to the typical organism. The variations of climate on our planet merely concern the purely terrestrial characters of plants. The seed often ignores them. Theoretically a seed should live for ever ; but unceasingly subjected on the earth to the strain of special conditions, its tenacious hold on life in any circumstances is apt to be lessened, so that with us it evinces only the tendency to immortality. It cannot be doubted, indeed, if this point of view be correct, that seeds have in varying degree undergone adaptations on the earth, and that a greater fitness for the special terrestrial conditions has often become a source of weakness in an organism generally adapted for existence in the cosmos.

Offers a clue to the conditions of existence in other worlds.

In spite, however, of the disposition to yield to the adaptive influences of terrestrial conditions, the seed still offers us the only instance of a terrestrial organism that is non-terrestrial in many of its potentialities. It seems to be the only clue presented to us on our planet to the conditions of existence in another world, a world such as the moon appears to be, where the requisite conditions for plant-development beyond the seed-stage, such as we know them, do not probably exist. If we study the ways of the seed we may be able to learn something of the nature of existence possible on the lunar surface ; and it is quite feasible that vegetable organisms in what we term the seed-stage of their existence may be living on the arid surface of that satellite, propagating themselves perhaps by some means unknown to us.

Although most of what is written above may be mere fancy, it is a fancy that might stimulate investigation ; and it should be remembered in this connection that the transference of germs from one world to another is on this view far from preposterous. De Maillet, when he promulgated this notion about two centuries ago, made a wild guess ; but modern investigators have independently advanced the same idea. In

concluding these introductory remarks to this chapter, I would point out that we on this planet, with our limited experience of conditions of existence, are not in a position to judge of "misfits" in nature. Beyond us lies the cosmos, of which the earth forms a part, and that an insignificant one; and we should surely be more liberal in judging nature when lack of harmony occurs if we were to regard it in this light only as connected with our planet. What is a disharmony on earth may be in tune with the life of the cosmos. For the naturalist the "great beyond" is an unexplored region. Yet it may prove to be full of suggestiveness in matters terrestrial. The life of one world may be the complement of another; and both worlds may be largely unintelligible when viewed alone. Let us hope that in time enlightenment will come.

In this chapter I propose, therefore, to avail myself of the privilege of giving freer play to the fancy than a strict adherence to the ordinary canons of scientific research usually allows. This licence I venture to claim as a recompense for the tedious labour involved in the elaboration of the abundant "facts and figures" in the preceding chapters. When dealing with the rest-period, one of the most mysterious features in the history of the seed, I treated the subject on orthodox lines. Here it is my intention to break through the bounds that there held me in check.

In pursuing such speculations as those concerned with the significance of the seed, one finds oneself in difficulties at the outset, not only on account of the number of roads approaching the subject, but also because it is by no means easy to appreciate their relative value. Those starting-points that present us with the largest view of the matter will probably be the safest for a first selection; and, this being granted, we have to choose whether we will deal with the conditions of plant-life in which the seed-stage is involved or with the general biological phenomena of the seeds themselves.

One consideration has determined my choice, and it is

The significance of the seed.

this. We get a tangible clue at the very start when we reflect that in its habits the seed is in a cosmic sense more cosmic than the fully developed plant. The plant needs an atmosphere, whilst the seed does not. While the plant appears to be specially adapted for terrestrial conditions, the seed might conceivably retain its vitality where no atmosphere of the terrestrial type exists. Admittedly it can withstand the cold of space, and it might survive even the extreme conditions of the lunar surface. Thus, whilst the seed is adapted as such for existence "in other worlds than ours," the full-grown plant seems to be fitted for terrestrial life only. The question of "cosmic adaptation" as a general principle is discussed in a later page of this chapter. Here, then, I take the position that whilst the seed is cosmically adaptive, the plant as far as we can know at present is only terrestrial in its adaptation. It will probably prove, however, as will subsequently be shown, that every stage in the development of the plant-organism has its cosmic side, but that the cosmic element diminishes as the organism develops, being greatest in the seed and least in the full-grown plant.

Adaptation of the seed for existence in other worlds and of the plant for terrestrial life only.

The difference between the cosmic conditions and those specially terrestrial.

The cosmic conditions would be those common to all the planetary worlds; whilst the terrestrial conditions would be those peculiar to our planet. Now, the nature of the difference between the cosmic conditions common to all inhabited worlds and the special conditions of any particular planet is the first question that presents itself. How should we characterise it? It would be fallacious to assert that the continued existence of a seed during a voyage in space or on the surface of a planet without an atmosphere like that of the earth would imply existence under a negation of conditions. It would not even involve a complete negation of terrestrial conditions, since the terrestrial conditions would comprise a residuum which our planet possesses in common with all the planetary worlds. These residual conditions are common to the cosmos, and we may here include space itself. They are the cosmic conditions to which the seed is adapted.

Now what is the nature of the difference between the cosmic conditions and the specially terrestrial conditions? On our planet we can recognise by their effects two kinds of influences—those which result merely in the increase or in the diminution in the size of the plant-organism, and those which bring about changes in the characters of its type. As examples of the first effect we may associate the gigantic *Sequoias* of California with the dwarfed pines of Japan; whilst to illustrate the second we may cite the ordinary variation of plants under different environments. In the first we see the effect of expansion and contraction of the life-conditions. In the second we have the result of their diversification. When nature diversifies the conditions, only a part of the organism responds to each change in the environment. When nature relaxes their pressure or increases their rigour the whole organism responds; and it is evidently to this order of things that we must refer the differences in effect between the cosmic and the special planetary conditions.

Take the indications afforded in the culture of dwarf trees, where man so successfully imitates the repressive side of nature. In an article on "The Dwarf Tree Culture of Japan" by Mr Percy Collins that was published in the *Windsor Magazine* for October 1907, we find the method thus pithily described: "Everything is done to concentrate the life of the tree within the narrowest possible limits. And at last, after years of unremitting labour, the tree begins to respond to the touch of its master. It loses its tendency to shoot forth lusty and far-reaching twigs. Its leaves become tiny and proportioned to its dwarfed branches. It surrenders in the fight for liberty and becomes quiet and tractable." Many kinds of forest trees ultimately yield to this repressive treatment, a period of at least half a century being required for the production of a good saleable dwarf tree. Of course with herbaceous plants much less time is needed. The writer of this book about twenty years ago conducted a series of experiments on the effects of very dry conditions on the growth of *Bidens cernua*

Appeal to the different influences of conditions on our planet.

The dwarfing of trees, etc., in illustration of the repressive side of nature.

and *Bidens tripartita*, two species that grow in wet stations by the sides of ditches, ponds, and rivers. After three generations the height of the plants was reduced from 17 or 18 inches to 5 or 6 inches, the fleshy stems becoming dry, woody, and wiry, the length of the achenes being reduced by half. The details of this experiment are given in Note 13 of the Appendix.

What man effects after years of tedious labour in the dwarfing of trees, nature accomplishes in the course of ages through the rigid pressure of the life-conditions. It is even conceivable that in time, by a still more severe treatment of repression, man could accomplish what nature seems to have aimed at in the case of the West African *Welwitschia*. In other words, he would be able to confine the growth of the plant to its cotyledonary stage. It is arguable, indeed, that he could carry this treatment so far as to destroy the possibility of a special terrestrial existence, or, to put it in ordinary language, he would restrict the life of the plant to the seed-stage. The seed would be by no means devitalised; but the conditions on which the maintenance of its vitality depended would be only those which the earth possesses in common with the cosmos.

For the experimenter the seed would merely be a plant-organism that could not proceed with its development on account of the repressive influence of the conditions. Substitute nature for the experimenter, and we should regard the seed as representing the organism's response to the iron-bound cosmic conditions, whilst the subsequent stages of growth would depend on the relaxation of the pressure of these conditions on the earth's surface. The seed would thus represent the cosmic life of the plant-organism, whilst the fully developed plant would be regarded as its special terrestrial form; and we might almost hold that the flowering and seeding stage represents the plant's effort to return to its general cosmic habit, the vegetative mode of reproduction being viewed as based on purely terrestrial necessities. Under conditions where the pressure of the life-conditions is much less than prevails on our planet it is conceivable that the whole plant would be "proliferous."

In this way it is conceivable that the growth of a plant could be confined to the cotyledonary stage illustrated by *Welwitschia* and even to the stage of the resting seed.

The seed would thus represent the cosmic life of the plant and the full-grown organism its special terrestrial form.

We have above been concerned with the effects of the repressive influence of the life-conditions. I will now illustrate the results of their relaxation or expansion. Here the conditions press gently on the organism, and we see the results in the giants amongst our trees, as represented by the *Sequoias* of the elevated plateaus and flat-topped mountain-spurs of the Sierra Nevada in California and by the gigantic Eucalyptus trees of the deep valleys and gorges of the mountains of South-eastern Australia.

The *Sequoias* illustrate the expansive side of nature.

Those who have read Clarence King's *Mountaineering in the Sierra Nevada* and can recall his graphic description of the environment of the *Sequoias* will remember that it was the peculiarity in the climatic conditions that appealed to the imagination of this gifted writer. Life's conditions press lightly on the trees of this ancient race. "Possessing hardly any roots, and resting on the ground with a few short pedestal-like feet penetrating the earth for a little way," they grow under "a sky which at this elevation of 6000 feet is deep, pure blue, and often cloudless." . . . "It is, then, the vast respiring power, the atmosphere, the bland regular climate, which give such long life, and not any richness or abundance of food received from the soil." So it may be premised that in a kindred fashion nature makes existence easy for the giant Eucalyptus trees that attain heights of 400 feet and over in the shelter of the deep valleys and gorges of the mountains of Victoria, as described by Thomas Ward in his *Rambles of an Australian Naturalist* (1907).

From the point of view, therefore, of plant-life which postulates a flora of the cosmos, the stage of development attained depends on the pressure of the conditions, being least advanced where the conditions are the most rigid and unyielding, as in the state where only the stage of plant-life represented by the seed is possible, and most advanced where the conditions are light and easy, allowing the relatively unhampered growth of trunk, branch, and foliage. From such a standpoint also the flowering and seeding stage would present

Postulating a flora of the cosmos, the stage of development of the same type in different worlds depends on the degree of pressure of the conditions.

itself as the result of an increase in the repressive influence of the conditions, or, in other words, as above suggested, it would indicate a tendency to return to the primitive cosmic state as presented in the seed. There is a profound significance in the notion of the gardener that if he gives a plant "a bad time" it is more likely to flower and mature its seed. From plants which have received exceptionally favourable treatment, or, in other words, plants with their existence specially favoured at his hands, he would look for "size," an increased tendency to vegetative reproduction, and but little seed. (See Note 30 of the Appendix.)

It will thus be seen that we are here concerned with the expansion of the life-conditions and not with their diversification. The seed on this view may represent the minimum of life's possibilities under extremely contracted conditions of existence; whilst the fully developed plant, as we know it, points in the direction of the maximum growth of the organism. The seed indicates the cosmic side of the conditions of plant-life in all the planets; and it would follow that the same seed exposed to expanding life-conditions very different in their character would develop in very different fashions. It is probable that under conditions far more expanded than those familiar to ourselves plant development would follow lines strange and inconceivable to us, conditions capable of extension in a multitude of ways, and favouring the production of plant-forms utterly different from any with which we are acquainted, though recognisable for us in the seeds.

Cosmically
viewed, the
laws of
inheritance
may lose
their validity.

I am inclined to consider that the laws of heredity as we formulate them on this planet may become very shadowy when applied to the life of the cosmos, and that with a knowledge of the life of other worlds we would attach far more importance to the determining influence of conditions. What we call the working of the laws of heredity here may be the only response that the organism could possibly make to terrestrial conditions. This response, as viewed from the broad field of the cosmos, we would regard as determined by the conditions of existence;

whilst, considered from the contracted standpoint of a single planet, we interpret it as the result of heredity. The laws of heredity as we frame them on our planet may be real enough for us, yet they may eventually present themselves as part of a much wider principle extending over the cosmos. The fact that an organism must be true to its conditions may indicate a principle that involves our laws of heredity and very much more. With this digression I will return to my main argument.

We are not directly concerned here with any evolutionary process, but simply with the effect of different degrees of rigidity of the conditions of existence on the development of the several stages of a plant's life, from that of the seed to that of the full-grown organism. Under severe repression a pine could be forced back into the cotyledonary state in which it exists in the seed. Under conditions less severe or less repressive it would develop into the ordinary pine tree; and where the conditions pressed lightly on the organism it might acquire the size of the *Sequoias*. But we have here neither the beginning nor the end of the scale of the stages of a plant-organism, though, as will presently be shown, it is sufficiently extended to be of some value to us in affording indications of the line of possible extensions at either the beginning or the end of the scale in other worlds. Between the two extremes of indefinite contraction and indefinite expansion seem to lie the average conditions of our terrestrial plants.

But there is sufficient variation of conditions on our planet to enable us to perceive as through dimmed glasses the possible influence of extreme conditions in other worlds. For instance, let us suppose that in very gradual fashion the earth dries up, losing its water and its atmosphere and presenting conditions such as now seem to prevail on the lunar surface. During such changes the plants would be gradually driven back to the seed-stage, until, when the earth approached the lunar condition, all surviving vegetable life would be reduced to that state. There are seeds, like those of *Guilandina bondu-*

Extreme conditions on the earth may illustrate normal conditions in other worlds.

cella, that seem fitted to withstand the conditions prevailing on the surface of the moon. Even now in some of our desert plants we can recognise a stage intermediate between the seed and the full-grown plant, such, for instance, as in those plants where, as in the West African *Welwitschia*, the cotyledonary leaves are the only leaves produced by the plant. Cases like this suggest the penultimate stage of a plant's life in a planet attaining the last stage of desiccation. They would also represent the first stage in plant-development, when in a desiccated world inhabited only by plants in the seed-condition an atmosphere began to form. As the expansion of the conditions of existence proceeded we should obtain a state of things similar to that in our own world, and plants would acquire the vegetative habit familiar to us on the earth. From this point of view, therefore, the development of the stem and foliage would be regarded as the plant's response to the production of an atmosphere. The return to the cotyledonary stage would be its response to the gradual disappearance of an atmosphere, until at length it would be forced back to the seed-stage.

Yet not in this way only could such changes be brought about. The extension of the possibilities of growth involved in the expansion of life-conditions may be in other directions. That indicated by the *Sequoias* is in one direction, whilst that illustrated by the gigantic *Equisetums* and *Lycopods* of the Coal Age would be in another. We have already referred to the case of the *Sequoias*, where existence is favoured by a bland regular climate on a mountain-plateau and beneath a cloudless sky. During the coal epoch the moisture-laden atmosphere and an ever-clouded sky offered favouring conditions of quite another type. It was the expansion of the life-conditions in this direction that gave rise to the huge *Calamariæ*, *Sigillariæ*, and *Lepidodendra* of the Coal Age. It is the contraction of the life-conditions in the opposite direction that has resulted in the production of our modern Horsetails (*Equisetums*) and Club-mosses (*Lycopods*). If our *Equisetums* have any story to

tell, it is certainly this. Similarly, it is the contraction of the life-conditions, the waterless, sandy soil, the intense insolation, etc., that has reduced *Welwitschia* to little more than a gigantic embryo. There are seeds, like those of *Poinciana regia*, as described in Chapter XIX, where, before the rest-period is imposed, the embryo, as far as the production of plumular leaves is concerned, attains a more advanced stage of development than we find in the adult *Welwitschias*.

Although plant-types, for all we know, may be eternal, the seed represents the only immutable, or, to put it less forcibly, the most persistent part of a plant. Excluding its coverings and appendages, it remains unaltered either under diversified conditions or in the lapse of the ages. Plants are often thus connected which have seemingly little else in common. Take, for instance, the *Tillandsias*, which vary so greatly in form that if it were not for the flower and the seed we should probably never connect them. It is the cosmic characters, the seed with the preparatory flower, that tend to link plants together. It is in its cosmic characters that the plant is most persistent and least mutable.

The plant is least mutable on its cosmic side, as in its seed.

We possess in our plant-world a scale of possibilities ranging from the seeming suspension of life in the resting seed to the full development of vegetative life in the tall forest trees, where, in extreme cases, as in those of *Sequoia*, the evenly preserved balance of growth and decay gives promise almost of eternity. There may be but little difference between the apparent suspension of life in the seed embryo and the calm repose of the life forces in *Sequoia*, where the organisms seem to be so nicely adjusted to its conditions. The vital processes, subdued though they be in the tall *Sequoia*, may be only proportionately less active than what actually takes place in the embryo shut up in its hard coverings. Recent discoveries in physical science would justify us in regarding the possibility of other means of communication between the embryo and the outer world than those concerned merely with respiration, transpiration, and the ordinary nutritive processes

The terrestrial scale of possibilities of plant-life.

of a plant-organism. However this may be, there is a promise almost of eternity in the life both of the seed-embryo and of the tall *Sequoia*, though both are ever liable to the accidents of their surroundings, the seed after its repose of a hundred years, and the tall conifer after an existence of centuries.

Although we possess a scale of plant-development beginning with the seed and ending with the fully-grown plant, yet it by no means follows that our terrestrial scale presents us with the beginning and the end of the possibilities of the plant's development, or that we have in the seed the absolute minimum or in the tall forest tree the absolute maximum. Yet, looking just beyond the terrestrial scale at either of its limits, we obtain indications of plant-development in other worlds. Thus, if at the maximum end of the scale we emphasise or intensify the life-conditions of the *Sequoias* on the Sierra Nevada, so vividly portrayed by Clarence King, we may be reproducing the conditions under which plants exist in another planet. Let us similarly extend the terrestrial scale a little at the minimum end, and it will not be difficult to imagine a world where vegetable life is only represented by plant-organisms in the seed-stage or by plants that do not pass beyond the cotyledonary stage of the West African *Welwitschia*.

Its indications of life in other worlds.

There is no necessity to suppose that other worlds possess forms of plant-life altogether outside the terrestrial scale. All possibilities should be indicated on our sphere. We get there indications of the possible forms of plant-organisms on a planet presenting the surface conditions of the moon, where the conditions for plant-life, as we know it, are reduced to a minimum for which the seed-stage appears to be alone suitable. We can also thus obtain indications of the possible forms of plant-life on planets where the present terrestrial conditions are greatly extended as regards the denseness of the cloud-envelope, humidity, and high temperature, where plants like the huge *Calamites* of the Coal Age may flourish and where the rest-period is unknown. Or, again, these conditions of

existence may be expanded in another direction, and we have then a calm reposeful world with a relatively light atmosphere but little disturbed by air currents, where the equilibrium between the organism and its environment is preserved for almost an eternity and vegetation of the *Sequoia* type prevails.

We are thus not called upon to suppose that the plant-life in other worlds is necessarily quite beyond the range of our terrestrial experience. There are doubtless worlds where the very conditions of life are on quite another plane, and for such the indications supplied by the earth would have no value. But there must be many for which the terrestrial scale would be ample enough in its scope; and as our knowledge of these matters increases it will be along the lines there indicated that progress will be made. There is, however, much that is not conceivable in the possibilities of other forms of life under other conditions; but the point urged here is that we have not yet exhausted the conceivable, as suggested by the variety of the forms of life and of the life-conditions presented on the surface of the earth.

Before quitting this part of my subject for the discussion of "cosmic adaptation," let me remind my readers that nothing in the nature of evolution has been here implied. I have regarded plant-life from this particular standpoint as if the doctrine of evolution had never been propounded. Evolutionary phraseology has become so established that it is not easy to state any problem or to indicate any new standpoint without doing so in terms of that theory. This seems to be unfortunate in some respects. In the previous pages I have been concerned with the development of the several stages of the same plant-type in response to the varying pressure of the conditions, the seed-stage and that of the fully developed forest trees representing respectively the effects of the maximum and minimum repressive influence as indicated in our terrestrial scale. (Some further remarks on this matter will be found in Note 19 of the Appendix.)

Not the evolution of a type but the development of different stages of the same plant-type is here implied.

All terrestrial organisms are generally adapted to the earth's

Cosmic
adaptation.

conditions, and specially adapted to their particular environment on the planet. Now, we may fairly argue that in their turn terrestrial organisms possess in common with those of other worlds an adaptation to the general cosmic conditions prevailing in those worlds. This cosmic adaptation must be postulated for all forms of terrestrial life. Though the primal cosmic habit belongs to all, it is apparent that it may be concealed or disguised or even lost through changes due to the special conditions of a particular planet. Thus, regarding the capacity of a seed for resisting desiccation as a part of its primal habit, the loss of this capacity in the case of the seeds of certain plants might be viewed as arising from adaptation to the special terrestrial conditions. Strip an organism of its specially terrestrial adaptations and the residuum is the link that joins it to the life of other worlds. The moment we introduce the life of the cosmos into our speculations concerning adaptation, we are compelled to make this assumption, since every special adaptation implies a more general habit of existence. We cannot doubt that the biological problems of the future will in the main centre round the disentanglement of this cosmic adaptation, or rather with its disinterment from beneath the terrestrial adaptations that lie heaped upon it.

Its results
represented
by the
characters
common to
types of
organisms in
different
worlds.

From this point of view an organism is to be regarded as specially adapted to the earth as a separate world and as generally adapted to the earth as a part of the cosmos. The points in common between the types of organisms in different worlds would thus present themselves as the result of cosmic adaptation, whilst the points of difference would appear as due to special adaptations to particular planets. On these grounds we should expect to find in this world characters that are not suggestive of any direct relation with the conditions of existence, or are even out of harmony with them. Many difficulties that seem insuperable for us, such as those concerned with reproduction and the distinction between plants and animals, may ultimately be overcome when regarded from

the standpoint of cosmic adaptation. If the supposition that the primal cleavage between plants and animals may be cosmic and not terrestrial goes to account for its inexplicability to us, may we not imagine that similar difficulties may find their solution in a like manner? Even the flowering and seeding of plants, as before suggested, may be an assertion of the tendency to resume the cosmic habit. Then, again, man's endeavours to throw off the chains of adaptation that bind him to the earth or to rise above his conditions may be virtually the assertion of the cosmic side of his nature. Terrestrially he may be man, but cosmically he may be of such stuff as dreams are made of. It is only on the cosmic side that man could be immortal. In such cases it is likely enough that our ideas of them are warped and narrowed through regarding them solely from the contracted standpoint of our planet, and that we have often failed to grasp the true significance of the problem before us.

Or we may put it in another way. Our senses enable us to follow the later part of the process, which is purely terrestrial, namely, the differentiation and adaptation of types; but the earlier portion connected with their origin comes abruptly into our experience as a completed result affording us no clue as to the beginning. Stated in a more reverent fashion, the Creator has permitted us to see the differentiation of a type, but He has hidden its origin from our view. Of the working of the larger plan that links the life of this planet to that of the cosmos we can, as terrestrial beings, have no direct cognisance. Only the operations of its adaptation to life on the earth are evident to our senses. Viewing our planet as incomplete in itself, since it is but a fragment of the cosmos, it follows that in no event can our investigations be ever complete. There will always be the unfinished border, the side that fits with nothing in our experience or system. There will belong to all inquiries a cosmic side and a terrestrial side, the one incomplete and indicative of a barrier that sooner or later brings all investigations to a halt, the other

The cosmic and terrestrial sides of all inquiries.

The unfinished border of all investigations.

neatly rounded off and offering in its adaptive appearance an easy road for the inquirer.

The principle of cosmic adaptation is implied in all schemes that postulate a common evolutionary development of organisms in the cosmos, or what we may term cosmic evolution, such a scheme, in fact, as Haeckel outlines in *The Riddle of the Universe* (English trans., chap. xx.).

Cosmic evolution.

Now, with reference to such schemes of cosmic evolution, meaning thereby the progressive development of higher from lower forms, it should be at once remarked that although all organisms would possess the cosmic impress to a greater or less degree, its extent would vary according to a well-known principle that is embraced by the evolution theory. Thus, on our planet the rule prevails that the lower the organism the wider is its distribution. It would be illogical if we did not assume that in cosmic evolution the same principle would prevail. The lowliest organisms, being most widely distributed in the cosmos, would possess the cosmic impress to a far greater degree than the higher organisms more or less specialised in individual planets.

Its control by the principle that the lowest organisms possess the widest range.

That an evolutionary scheme of the cosmos would be expected to proceed on similar but much broader lines than in the case of that limited to our planet is indeed suggested in Haeckel's book above quoted; and as the passage bears directly on this matter, I give it here partly *verbatim* and partly in my own words:—"We are justified in supposing that thousands of the planets are in a similar stage of development to that of our earth." But although "it is very probable that a similar biogenetic process to that of our own earth is taking place on some of the other planets of our system, as on Mars and Venus, and on many planets of other solar systems," by which the lower plants and animals have been evolved, such as we have on earth, yet "it is very questionable whether the different stems of the higher plants and animals run through the same course on other planets as on our earth. In particular, it is wholly uncertain whether there are verte-

Haeckel on cosmic evolution.

brates on other planets or whether mammals culminating in man are formed there as on the earth. It is much more probable that other planets have produced other types of the higher plants and animals unknown on earth. Perhaps from some higher stem, superior to the vertebrate, higher beings far transcending man in intelligence have been formed."

Thus in *The Riddle of the Universe* do we find the scheme of cosmic evolution roughly outlined. It involves the principle established for this planet that the lowest types of organisms have the widest distribution, from which it follows that the planets would resemble each other more in the lower forms and would differ most in the higher forms of life. Further than this it would be unsafe to go. The How and the Why of evolution remain still very much in the clouds of disputation. But, speaking for myself, I do not hold that we have yet even a glimpse either of its real significance or of the forces working behind it. The investigations into the nature and origin of species do not, as I think, aid us at all in the matter. They may help us to understand the differentiation of a type, but not its origin, and still less the progressive steps from lower to higher types. May we not believe that we see the evolutionary scheme of life only in part on this planet, that there is an evolution of the cosmos in which the earth with myriads of other worlds shares, and that much that seems inexplicable on the earth will find its explanation in other worlds?

We know how much light is thrown on one group of organisms by studying those related to it, and how much at sea we are with an isolated group that is akin to none. May we not extend the principle and consider that many of our difficulties here on the earth will disappear by the extension of our knowledge to worlds outside? However, from the point of view here adopted any scheme of evolution limited to the earth must in the nature of things be incomplete. It may even be that evolution has been misinterpreted by us, and that the true evolutionist is he who, regarding all types as eternal,

The consequent incompleteness of any scheme of evolution restricted to a single planet.

holds that the gamut of change has been run through unceasingly in endless worlds and that there is nothing ever new, nothing ever old, all being eternal.

SUMMARY

(1) The author in this chapter gives freer play to the imagination than is usual with orthodox scientific investigation. In some introductory remarks he first points out that the seed is less specialised and less conditioned than the plant, presenting us in its potentialities of existence with a range of life-conditions that extends beyond the earth.

(2) Discussing first the significance of the seed, he takes the position that whilst the seed can live in other worlds, that is to say, it is cosmically adaptive, the full-grown plant is purely terrestrial in its adaptation.

(3) Then follows a consideration of the nature of the difference between the cosmic conditions common to all inhabited worlds and the special conditions of any particular planet.

(4) To elucidate this difference appeal is then made to the different influences of conditions on our planet, those where the whole plant responds without alteration of its type, and those where only part of the plant responds and we get a variation of type.

(5) The changes in the whole plant without alteration of the type are regarded as illustrated by the behaviour of the gigantic *Sequoias* of the Californian Sierra Nevada and of the dwarfed trees of Japan, the first exemplifying the result of the relaxation of the life-conditions, the second the result of the increase in their rigour, the one indicating the expansion of the conditions of existence, the other their contraction. It is in this direction that we have to look for the influence of the cosmic conditions.

(6) What man effects after years of tedious labour in the dwarfing of trees nature accomplishes in the course of ages through the rigid pressure of the life-conditions; and in this way it is conceivable that the growth of the plant could be ultimately confined to the cotyledonary stage exemplified by *Welwitschia*, and even to the earlier stage of the resting seed.

(7) The seed would thus represent the cosmic side of the plant, whilst the fully developed plant-organism would be regarded as its special terrestrial form, the one pointing in the direction of the minimum of life's possibilities, the other toward the freest conditions for growth.

(8) Postulating a flora of the cosmos, the stage of development of the same type in different worlds would depend on the degree

of pressure of the life-conditions, being least advanced where the conditions are most repressive (and in such cases it might even be restricted to the seed-stage), and most advanced where the conditions are light and easy, allowing the relatively unhindered growth of stem and foliage.

(9) From such a standpoint the flowering and seeding of terrestrial plants would present themselves as the result of an increase in the repressive conditions, or of a tendency to return to the cosmic state; whilst vegetative reproduction or the proliferous habit would mark the expansion of the conditions of existence and the fuller growth of the plant. This goes to explain why in horticulture seeding is most favoured by harsh treatment and vegetative reproduction and foliage by generous treatment.

(10) The terrestrial scale of possibilities of plant-life may offer in its extremes indications of the direction of plant-growth in other worlds. Under the most repressive conditions, such as prevail on the lunar surface, plants may be confined to the cotyledonary stage, as in the case of *Welwitschia*, or restricted only to the seed-stage. Where the conditions are most conducive to growth, the climatic environment may favour in one planet huge plant-organisms like those of *Calamites*, and in another planet vegetation of the *Sequoia* habit.

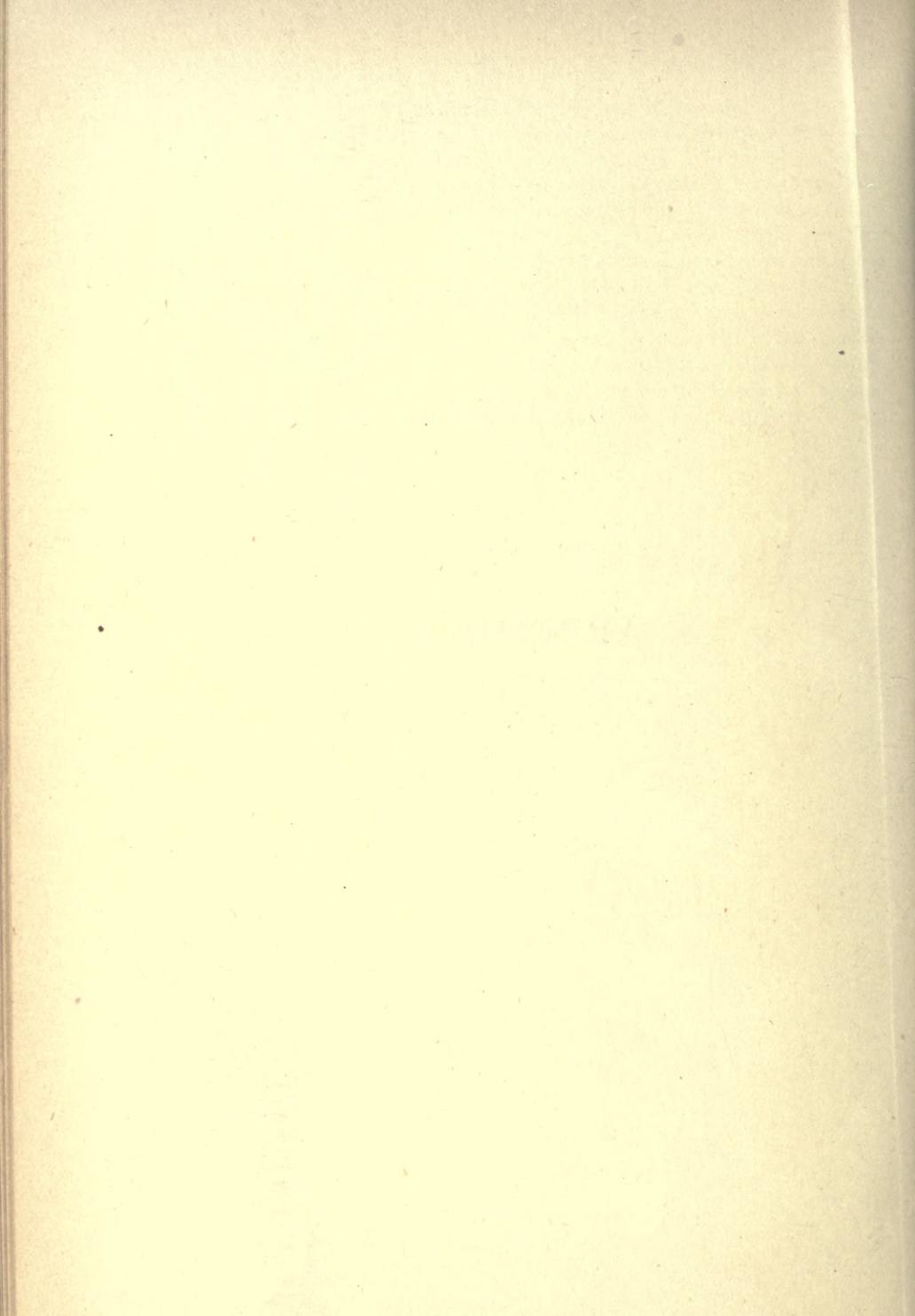
(11) It is on its cosmic side that a plant is most persistent and least mutable, namely, in the seed-stage. This explains why terrestrial plants have often little else in common than their seed-characters. It is on their cosmic side that the primal affinity of plants lies.

(12) The principle of "cosmic adaptation" above assumed is an extension of the principle adopted as concerning the earth, that all terrestrial plant-organisms are generally adapted to the earth's conditions, and specially adapted to their particular environment on that planet. So, it is argued, a plant-organism may be specially adapted to the earth as a separate world and generally adapted to the earth as a part of the cosmos. Strip an organism of its special terrestrial adaptations and the residuum will be the link connecting it with the life of other worlds. It is on its cosmic side that a terrestrial organism will usually present itself as out of harmony with the earth's conditions, and it is on the cosmic side that all investigations will present an unfinished border, a side that fits with nothing in our experience or system. The biological problems of the future will be mainly concerned with the disinterment of the cosmic adaptation from beneath the terrestrial adaptations that lie heaped upon it.

(13) Nothing in the sense of the evolutionary theory of the progressive development of types has been implied in the foregoing discussion, which is concerned only with the different stages of development of the same plant-type under the pressure of the life-conditions. But if we

accept the principle of evolution for the earth, we must necessarily extend it to the cosmos ; and it is in this connection noteworthy that the principle of cosmic adaptation must be implied in all schemes of organic evolution of the cosmos. Thus Haeckel would hold that whilst the lower forms of plants and animals have probably been evolved on similar lines on the earth, Venus, Mars, etc., it is questionable whether the higher plants and animals run through the same course on those planets. It is thus implied that the principle "the lower the type the wider its distribution" is true alike of the earth and of the whole system of which it forms a part. From this it follows that the planets would resemble each other most in the lower forms of life and would differ most in the higher forms. Any scheme of evolution applied only to a single planet must necessarily therefore be incomplete.

APPENDIX



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NOTE I (p. 28).

Swelling capacities of the seeds of Faba vulgaris, Pisum sativum, Phaseolus vulgaris, and Phaseolus multiflorus.

IN the case of the four plants below named I experimented on seeds which had also been employed by one or both of the German investigators, and the comparison of results given in the table is instructive.

COMPARISON OF RESULTS OBTAINED BY HOFFMANN, NOBBE, AND THE AUTHOR ON THE SWELLING CAPACITY OF SEEDS OF *FABA VULGARIS*, *PISUM SATIVUM*, *PHASEOLUS VULGARIS*, AND *PHASEOLUS MULTIFLORUS*.

Species.	Increase of weight stated as a percentage of the weight of the resting seed.			References to pages in Nobbe's <i>Handbuch der Samenkunde</i> .
	Hoffmann.	Nobbe.	Guppy.	
<i>Faba vulgaris</i> . . .	104	157	{ (a) 90 (b) 101 }	} 109-111, 119
<i>Pisum sativum</i> . . .	107	{ (a) 96 (b) 71 }	{ (a) 91 (b) 137 }	
<i>Phaseolus vulgaris</i>	{ (a) 117 (b) 101 }	} 84	119, 123, 124
<i>Phaseolus multiflorus</i> .	92	...	98	119 (Weisse Bohnen).

The names of the two varieties of *Faba vulgaris* and *Pisum sativum* are given below.

The botanical names are those used by Nobbe in describing his experiments, except in the case of the last named, for which he gives Hoffmann's result for "Weisse Bohnen," which is placed with other species of *Phaseolus* in the general list of results on p. 119. I have taken these to be the white-seeded variety of *Phaseolus multiflorus*, of which I experimented on the ordinary mottled seeds.

In the case of *Faba vulgaris* I experimented on the two varieties known as Long-pod Beans (a) and Green Windsor Beans (b). Whilst

my estimates come close to that of Hoffmann, the estimate of Nobbe is considerably greater, being in excess even of the ordinary weight of a saturated seed, an increase of 120 per cent. being required for saturation (see p. 44). Nobbe took as the first indication of germination the protrusion of the tip of the radicle through the coats; but it is shown in the next paragraph that in the case of Peas, when the coats are much wrinkled, excessive estimates of the swelling capacity may thus be formed.

Two varieties of Peas were used by me—the Early Sunrise Pea (*a*), a slightly wrinkled kind, and a Marrowfat Pea (*b*), with excessively wrinkled coats. The causes of the great difference in the swelling capacities of these two varieties, 91 per cent. for the slightly wrinkled and 137 per cent. for the greatly wrinkled seeds, lie in the excessive wrinkling of the coats, which not only allows an excess of water to collect between the kernel and its loosely fitting coats, but also permits a considerable growth of the radicle before the irregular rupture of the coats, so that when the seed is weighed it is well advanced in germination and in a saturated state. This therefore explains not only my excessive result for Marrowfat Peas, but probably also Nobbe's abnormal estimate for *Faba vulgaris*.

NOTE 2, A (p. 30).

Comparison of the weight of a leguminous seed dried under ordinary air-conditions after swelling for germination with its original weight in the resting state.

THERE are several disturbing causes that would come into play in drying a seed that has swelled for germination. In my own experiments only those seeds were accepted which had proved their germinative capacity by displaying evident signs of the earliest stage of the process. Owing to the slight growth of the radicle thus involved, this would slightly increase the weight of the dried seed. However, on comparing the weight of seeds just before and just after the first signs of germination, I find that the correction to be applied rarely exceeds 0.5 per cent.

This increase, however, would be counterbalanced by the slight decrease in weight during the swelling process arising from the loss of solid materials which pass into the water that dampens the surface of the swollen seed. This is evident enough when seeds are allowed to go through the whole swelling stage immersed in water, especially with highly coloured seeds, when the water is deeply stained, or where colloidal substances in the coats ooze out as mucus or slime. Easily

permeable seeds like those of the Broad Bean (*Faba vulgaris*) would experience a noticeable loss of solid material when swelling in water. Yet Nobbe (p. 111) in his carefully guarded experiments on the swelling of these particular seeds in water found that the residue left on evaporating the distilled water employed amounted only to 2.3 per cent of the weight of the resting seed. Immersion in water, it should be remarked, is not Nature's method of procuring germination; and no doubt the loss is much exaggerated in such experiments. In my own experiments, where the seed was placed in damp moss as soon as it began to increase its weight in water, such a loss would be much diminished, and with most hard-shelled seeds it would be almost *nil*. However, with some seeds it is nearly impossible to obtain a good result. Thus it is with those of *Adenanthera pavonina*, where a gelatinous material escapes from the puncture in the coats that is required to induce germination. Then, one may add, it is very difficult to prevent a slight loss in the case of seeds like those of *Poinciana regia* and of species of *Guilandina*, where the cuticle is apt to scale off. On the whole, however, I consider that the disturbing influences in such experiments tend to counterbalance each other. This remark also applies to hygroscopic variation of a seed's weight in response to atmospheric changes, if the seed is kept under observation for some days after the drying has ceased.

As regards the mode of conducting such experiments, it is obvious that much depends on the uniformity of the conditions of drying, which should be carried out in a room but little affected by artificial heat, except in the case of damp weather, when the seed may be placed at first in a warm, dry room.

Most of my results on entire seeds are included in the table subjoined. The effect of hygroscopic variation is excluded by taking the mean weight for a few days after the drying has reached its minimum. A column is added for the periods required to reach the minimum, the drying period corresponding roughly to the swelling period preceding germination, since a seed that swells quickly would also dry quickly.

Conclusions to be drawn from this table are confined here to immediate inferences that can be legitimately deduced from its inspection. Remarks on the bearings of the data here arranged will be found under the reference given at the head of the note. It is therefore sufficient to point out that although all these results indicate that a seed swollen for germination returns when air-dried to approximately its resting weight, there are regular variations both on the plus and minus side, the ultimate weight being in excess in the case of impermeable seeds, on the minus side generally with permeable seeds, and variable in seeds where the permeability is a variable character.

TABLE SHOWING THE EFFECTS OF DRYING IN ORDINARY AIR ON LEGUMINOUS SEEDS SWOLLEN FOR GERMINATION.

Species.	Weight in grains.			Period of drying.	Effect of drying stated as a percentage of resting weight.		Permeable or impermeable or variable.
	Resting seed.	Swollen for germination.	After drying.		Loss.	Gain.	
Bauhinia sp.	3'70	8'00	3'70	3 days	Variable
Entada polystachya, A	5'06	12'70	5'30	4 "	...	4'7%	Impermeable
" " B	7'15	15'90	7'25	4 "	...	1'4%	Variable
" scandens	312'50	728'00	318'70	19 "	...	2'0%	Impermeable
Erythrina indica	12'00	31'60	12'30	4 "	...	2'5%	Variable
Faba vulgaris, A	41'50	86'30	40'60	5 "	2'2%	...	Permeable
" B	28'60	53'50	27'00	4 "	5'6%	...	"
Guilandina bonducella, A	44'16	124'60	46'90	12 "	...	4'0%	Impermeable
" B	33'35	97'30	35'35	11 "	...	6'0%	"
Mucuna urens, A	88'00	176'40	92'40	13 "	...	5'0%	"
" B	87'40	174'00	89'20	12 "	...	2'1%	"
Phaseolus vulgaris	13'50	24'60	13'35	3 "	1'1%	...	Permeable
Pisum sativum	6'00	14'30	5'75	3 "	4'2%	...	"
Poinciana regia	8'70	19'50	8'70	4 "	Variable

Note.—Variable seeds are those sometimes permeable, sometimes impermeable.

NOTE 2, B (p. 29).

A further proof of the mechanical nature of the swelling process of seeds indicated by their ability to proceed with germination when dried, after absorbing most or all of the water required for germination.

(THIS proof was omitted on p. 29, and has been added since. It is illustrated in the following table by the results of my experiments on the influence of previous swelling and drying on the germinative capacity of different seeds.)

Knowing from the results of previous experiments, as given in the table on p. 24, the swelling limit indicated by the maximum weight attained before there were any external signs of germination, I was able to conduct the experiments accordingly. In the case of the seeds of *Hura crepitans* I repeated the experiment on the same seed, but the seed in the instance of two experiments rotted.

	Weight of resting seed.	Weight of the swollen seed.	Weight after being slowly air-dried.	Maximum weight after being placed in water and then in wet moss.	Result.	Total duration of experiment.
Guilandina bonducella.	30 grains	71 grains in 3 days	31 grains after drying for 32 days	91 grains after swelling for 6 days	Germinated	41 days
Abrus precatorius.	1'5 "	3 grains in 21 hours	1'4 grains after drying for 11 days	3 grains after swelling for 36 hours	Germinated	13½ "
Abrus precatorius.	1'5 "	2'7 grains in 22 hours	1'2 grains after drying for 12 days	2'85 grains after 45 hours	Germinated	14¾ "
Canavalia obtusifolia.	9'7 "	23'3 grains in 26 hours	9'7 grains after drying for 8 days	22'3 grains after 40 hours	Germinated	10¾ "
Canavalia ensiformis (average for three seeds).	20'0 "	45 grains in 24 hours	20'5 grains after drying for 18 days	46 grains after 36 to 40 hours	All germinated	20½ "
Hura crepitans.	22'0 "	41 grains in 2 days	21'5 grains after drying for 12 days	46 grains after 7 days	Germinated	21 "
Hura crepitans.	21'5 "	41 grains in 2 days	21 grains after drying for 12 days	42 grains after 9 days	Germinated	23 "

With the exception of the last-named plant, which belongs to the Euphorbiacæ and has albuminous seeds, all are leguminous and have exalbuminous seeds.

The time occupied in attaining the maximum weight was the time required for germination, as indicated in the "maximum weight" column.

These experiments should be of interest to the agriculturist. At the time they were made I was not aware that Professor Ewart had several years before experimented upon the effect of previous swellings and drying on the germinative capacity of Peas (*Pisum sativum*). The seeds were well soaked in water and then slowly air-dried. After the first soaking and drying they all germinated. After the second soaking and drying only 40 per cent. germinated when the integuments were entire, but all germinated when the integuments were broken. Seeds subjected to a third soaking and drying failed to germinate whether the coats were entire or broken (*Trans. Liverpool Biol. Soc.*, 1894, viii. 207).

NOTE 3 (p. 31).

COMPARISON OF THE RELATIVE WEIGHTS OF THE COATS, KERNEL, AND EMBRYO OF RESTING SEEDS, AND OF THE SAME SEEDS DRIED AFTER SWELLING FOR GERMINATION. THE SEED ON DRYING RETURNS APPROXIMATELY TO ITS ORIGINAL WEIGHT.

(With the exception of *Hura crepitans*, which belongs to the Euphorbiaceæ, all the seeds are leguminous.)

Name.	Albuminous or exalbuminous.	Permeable or impermeable, or variable.	Weight.	Relative weight of the separate parts, taking the entire seed as 100.		
				Parts.	Resting seed.	Dried swollen seed.
Canavalia obtusifolia .	Exalbuminous	Impermeable	12 grains	Coats	27'0	29'0
				Kernel	73'0	71'0
Entada scandens .	"	"	400 "	Coats	49'0	49'0
				Kernel	51'0	51'0
Erythrina corallodendron .	"	Variable	3 "	Coats	33'0	35'0
				Kernel	67'0	65'0
" indica .	"	"	12 "	Coats	30'5	29'0
				Kernel	69'5	71'0
Faba vulgaris .	"	Permeable	35 "	Coats	14'0	14'7
				Kernel	86'0	85'3
Guilandina bonducella .	"	Impermeable	40 "	Coats	58'0	57'0
				Kernel	42'0	43'0
Mucuna urens .	"	"	90 "	Coats	26'0	25'0
				Kernel	74'0	75'0
Phaseolus vulgaris .	"	Permeable	12 "	Coats	6'2	6'6
				Kernel	93'8	93'4
Cassia fistula .	Albuminous	Variable	4 "	Coats	15'0	20'0
				Albumen	66'0	60'0
" grandis .	"	"	9 "	Embryo	19'0	20'0
				Coats	25'0	25'0
" marginata .	"	"	10 "	Albumen	64'0	64'4
				Embryo	11'0	10'6
Poinciana regia .	"	"	10 "	Coats	29'0	28'0
				Albumen	58'0	59'0
	"	"	10 "	Embryo	13'0	13'0
				Coats	49'5	45'3
Bauhinia sp. .	"	"	4 "	Albumen	23'5	29'7
				Embryo	27'0	25'0
	"	"	4 "	Coats	23'5	23'7
				Albumen	41'5	42'3
	"	"	4 "	Embryo	35'0	34'0
				Coats	30'0	29'0
Hura crepitans .	"	Permeable	20 "	Albumen	61'5	61'6
				Embryo	8'5	9'4

Remarks on the table.—Only approximate results can be expected here, since we are not able to compare the relative weights of parts in

the seed dried after swelling for germination with those of the same individual seed in the resting state, but only with the average for a number of resting seeds. We are indeed merely comparing an average with an average. Then we have seen in Note 2, A that impermeable seeds when dried after swelling for germination are heavier, and permeable seeds lighter than in the resting condition. Still, the results given below will tend to emphasise the view that the swelling of germination is essentially a process of water-absorption. This matter is dealt with again in discussing the general mechanism of the shrinking and swelling processes in Chapter IX.

NOTE 4 (p. 43).

Experiments of Victor Jodin on the germinative minimum of Peas (Pisum sativum), from "Les Annales Agronomiques," October 1897.

THE peas were placed on a support of platinum suspended in air saturated with water-vapour. By these means the water-vapour was condensed in fine drops, and thus communicated to the peas. A similar experiment under the same conditions, but in which the peas were placed on a support of cork, gave no germination result, even after 55 days. In this last case the seeds had absorbed water in varying degrees from 22 to 42 per cent. of their weight, but they had failed to reach the germinative minimum of 67 per cent. This investigator states his results in terms of the hydration of a seed—that is to say, as a ratio of the dry and not of the wet weight; and it has been necessary to convert them into percentages of the weight of the resting seed.

NOTE 5 (p. 69).

Canavalia ensiformis, DC.

Canavalia gladiata, DC.

THE seeds chosen by me as the type of permeable seeds in Chapter IV belong to *C. ensiformis*, DC., with white seeds. In his *Flora of the British West Indian Islands*, Grisebach gives *C. gladiata*, DC., as having two forms or varieties: (a) with rufous brown, and (b) with white seeds (*C. ensiformis* proper). I experimented on both forms, the (a) form possessing seeds with varying degrees of impermeability, the (b) form with seeds typically permeable. In this work I have applied the specific name of *C. gladiata* only to the rufous-brown or red-seeded variety, reserving that of *C. ensiformis* for the plant with permeable white seeds. Professor Ewart in his paper (*Proc. Roy.*

Soc. Vict. 1908) places the seeds of *C. ensiformis* amongst his "macrobiotic" seeds with more or less impermeable coats (p. 200). But in the entry in his tables (p. 35) he says that five out of six seeds swelled without assistance. It is, however, evident that his use of the specific name *C. ensiformis* covers both varieties as well as others, and therefore includes both permeable and impermeable seeds.

NOTE 6 (pp. 71, 166).

The influence of the coverings on the drying of permeable seeds. (See also Note 12 on the time required for drying.)

THIS is by no means an easy subject, since the drying régimes of seeds vary much, and an experiment very simple in its operation may be influenced by a number of antecedent conditions. Some oily seeds, like those of *Ricinus communis*, are but slightly, if at all, affected in the freshly gathered condition by the removal of the coverings. Thus in the case of two samples of seeds, one just collected from the fruits, and the other gathered seven weeks before, the bared kernels showed no loss of weight, but merely varied about 1 per cent. in response to the changes in the atmospheric humidity.

On the other hand, the coverings may be inert in their influence on the drying process, as in the instance of seeds containing in the fresh state an abundance of water. This is the case with the seed of the Horse-chestnut (*Æsculus Hippocastanum*), which, when freshly gathered from the dehiscing capsule, contains about 48 per cent. of water, and dries, as shown in the results given below, more quickly and more completely in its coverings than when it is bared.

DRYING OF SEEDS FROM THE DEHISCING CAPSULES OF
THE HORSE-CHESTNUT.

Condition of the seed.	Original weight.	Weight after 10 days.	Weight after 5 months.	Weight after 2 years.
A. Dried as bared seed . . .	100	67	63	60.5
B. Dried in its coats, which are included in the total weight	100	62	57.5	55
C. Dried in its coats, but weight of coats not included	100	60	55	52

The weight of a moist seed varies from 200 to 240 grains. In the case of C, I have deducted the weight of the coats; 25 per cent. in the first, 27 per cent. in the second, and 28 per cent. in the third and fourth columns as obtained from other seeds.

In the Horse-chestnut seed the peculiar drying régime is connected with the closely adhering absorbent tissue of the inner coverings, which readily take up the kernel's moisture, and allow it to escape through the large unprotected scar. The soft, swollen, white unripe seed, when passing into the resting stage, mainly dries through the scar, which occupies about one-third of the surface, and is not covered by the ultimately impervious skin that protects the rest of the seed. Long after this outer skin has undergone browning and hardening during the shrinking stage, the scar remains moist and gives off water. The relative impermeability of the brown skin of the resting seed is well displayed by allowing the seed to soak in water for a day or two. On examination the inner coverings are then found to be saturated with water, which oozes out through the scar.

It would, however, seem that the peculiarity in the drying régime of the Horse-chestnut seed is in degree rather than in kind; and indeed it probably represents in an exaggerated fashion the behaviour of a typical permeable seed. It is apparent from the researches of Becquerel that the permeable integuments of peas (*Pisum*), lupines, and beans (*Faba*) after a certain amount of artificial desiccation become impervious to air, except when it is saturated with moisture. This implies a sluggishness during exceptionally dry atmospheric conditions of the coats of permeable seeds; and it may well be that such seeds in the resting state are most pervious at the hilum or scar. If also we are able to consider seeds rendered impervious to air by artificial desiccation as in process of becoming impermeable to water, one might rank permeability as a quality by default.

But to return to the subject of the influence of the seed's coverings on its drying in the resting state, it may be remarked that the seed of the Horse-chestnut, on account of the great size of the unprotected scar, is exceptional in this respect. If the coats are able to restrain the hygroscopic reaction of a permeable seed they will also check its surrender of water to the air; and the capacity first named has been established on pages 71 and 166. Not many of my experiments were made on permeable seeds as soon as they were gathered from the plant; but I append the results of those on *Citrus decumana* (Shaddock). Here we notice that the coats restrain the drying of the seed for the first three weeks, after which it assumes a stable weight affected only by the ordinary hygroscopic reaction. The subject, however, will not be pursued here, as there are many factors determining the results, of which the relative importance cannot now be estimated.

In the reference to this note on page 226 mention is made of the case of *Mammea americana*; but as the fruit is drupaceous another

DRYING OF SEEDS OF THE SHADDOCK (*CITRUS DECUMANA*)
WITH AND WITHOUT THEIR COATS.

(The first weighing was made 24 hours after removal from the same fruit.)

Conditions of Experiment.	Weight in grains.				Loss.
	Original weight.	After 4 days.	After 10 days.	After 20 days.	
A. Bared of their coats .	100	64·4	63·4	...	36·6 grains in 10 days
B. In their coats . . .	100	81·8	69·0	62·3	37·7 grains in 20 days.

The A seeds attained a stable weight in 10 days and the B seeds in 20 days, subject only to the ordinary hygroscopic variation.

In order to eliminate the influence of the coats in the B seeds the separated coats of the A seeds were also experimented on. It then appeared that in the B seeds the coats lost 2 grains and the kernels 35·7 grains.

regime is involved. However, it may be remarked that whilst the seed proper required about six months, the seed in its fibrous covering occupied nearly a year before a stable weight was reached.

NOTE 7 (pp. 86, 107).

Mould and Impermeability.

WHILST studying in Jamaica the shrinking of the unripe or pre-resting seeds of *Entada scandens*, I found that in one set the seeds went through the normal process and became typical impermeable seeds, whilst in another set some of the soft white seeds were attacked by mould, which destroyed the cuticle in places, its absence being indicated in the coats of the hardened resting seed by light-coloured spots. The results of the attack of these minute fungi were in some cases loss of impermeability, excessive shrinking, and the death of the embryo through the penetration of the mould into the kernel. Under normal conditions the full-sized unripe seed of 1000 grains in weight would weigh about 400 grains when the shrinking and hardening process is complete; but in a few weeks the mould-infested seeds were only 30 per cent. of their original weight, the kernels on being exposed proving to be soft, sour-smelling, and in various stages of decay.

But there were others of the same set of seeds of *Entada scandens*

where the mould had attacked the cuticle of the soft immature seeds so slightly that at first it was overlooked. They went through the usual shrinking process, as it seemed, normally; and it was not until after about six weeks that the exceptional loss of weight led me to examine them more carefully, when I found their surfaces dotted with a number of light-coloured small spots where the cuticle was lacking. The seeds continued to decrease in weight for eighteen months, when they were only about 25 per cent. of their original unripe weight, instead of about 40 per cent., which is the normal shrinking ratio. After this their weight became stable, varying only 1 or 1½ per cent. in response to the changes in the hygrometric state of the air. On being cut open six months later, the kernels proved to be hard and much shrunken; but there was no discoloration.

As is shown in the tabulated results below under A and C, it is the kernel of the mould-infested seed that is chiefly affected by the excessive shrinkage. In the normal resting seed the kernel makes up about 61 per cent. of the seed; whilst in the seed attacked by the fungus

TABLE SHOWING THE EFFECTS OF MOULD ON THE SOFT UNRIPE OR PRE-RESTING SEEDS OF ENTADA SCANDENS.

	Unripe or pre-resting full-sized seed.		Weight of resting seed.			Period of Shrinking.	Effect on the seed attacked by mould.
	Condition.	Weight.	Entire.	Coats.	Kernel.		
A	Not attacked by mould	1000	400	156	244	1 to 2 months	...
B	Mould conspicuous and covering much of surface	1000	300	1 month	Kernel rotting.
C	Mould not at first noticed, as it attacks limited areas	1000	250	153	97	18 months	Cuticle alone affected; impermeability lost; germinative capacity lost after the first few months.

Explanation.—This table is intended to display a continuous record for three seeds each beginning with the pre-resting state, the normal shrinkage being exhibited only by the first. A represents an average healthy seed, whilst B and C represent mould-infested seeds, the results being obtained from observations on nine diseased seeds. The unripe weight ranged from 900 to 1150 grains, but all results are calculated for a seed of 1000 grains. By comparing A and C it will be seen that the loss of weight in the diseased seed was experienced almost entirely by the kernel, which at the end of the experiment was much shrunken, hard and flexible rather than brittle, but otherwise normal in appearance.

it was reduced to 43 per cent. in seeds five months old and to 39 per cent in seeds kept two years. The ultimate death of the embryo in the instance of the C seeds was not due to their being attacked by the mould, which in these cases does not seem to extend to the kernel; but it was brought about by the great shrinkage and loss of water which the embryo or kernel sustained through the partial destruction of the impermeable cuticle by the fungus. In the case of a permeable seed such a loss is fatal to its germinative capacity, unless it is saved by the rapid intervening of conditions favouring germination in the early stage of its history as a resting seed.

NOTE 8 (p. 109).

DR GOLA'S TABULATED RESULTS OF HIS EXPERIMENTS ON THE PERMEABILITY TO WATER OF SEEDS OF DIFFERENT DEGREES OF MATURITY (*Memorie della Reale Accademia delle Scienze di Torino*, 1905).*

	Number of seeds tested.	Number swollen.	Percentage swollen.
Acacia Farnesiana; more mature .	50	4	8
„ „ less „ .	50	0	0
Cytisus Laburnum; more „ .	50	13	26
„ „ less „ .	50	3	6
„ purpureus; more mature .	50	10	20
„ „ less „ .	50	3	6
Genista scoparia; more mature .	100	4	4
„ „ less „ .	100	1	1
„ ovata; more mature .	50	2	4
„ „ less „ .	50	1 †	2
Trifolium fragiferum; more mature	50	2	4
„ „ less „ .	50	0	0
Robinia Pseudacacia; more „	100	4	8 ‡
„ „ less „ .	100	0	0

* The seeds were tested by prolonged immersion in water.

† Si è rigonfiato piu verde evidentemente affatto immaturo.

‡ A misprint in the original; but the correction deprives the *Robinia* seeds of much of their claim in support of the view that impermeability and immaturity go together.

NOTE 9 (p. 147).

Classification of the different forms of Hygroscopicity, by Léo Errera
(Recueil de l'Institut Botanique Léo Errera, Université de
Bruxelles, tome vi. 1906).

A. PHYSICAL.

- (1) Condensation by cold surfaces, as of glass, metals, etc.
- (2) Condensation by capillarity, or capillary hygroscopicity :
 - (a) where the water enters pre-existing capillary spaces, as in the case of hair, wool, silk, cotton, wood-shavings, etc., which is capillarity properly so-called ;
 - (b) where the water makes its own passage by pushing aside the molecules or particles, as with gelatine, gum-lac, powdered clay, agate, etc., an imbibition process.
- (3) Condensation by osmosis or osmotic hygroscopicity, where the substances affected are soluble in water and become coated by a very thin pellicle of water, as with common salt.

B. CHEMICAL, of which examples occur in the behaviour of concentrated sulphuric acid, absolute alcohol, quicklime, chloride of zinc, chloride of lime, etc.

NOTE 10, A (p. 266).

On the loss of weight of ripe Gooseberries (Ribes Grossularia) when dried in air at ordinary temperatures.

THE average of two experiments which corresponded very closely in their results may be thus stated :—

Weight of moist fruit taken as	100.0
„ „ air-dried fruit	15.0
„ „ air-dried fruit after soaking two days in water to remove the sugars	5.0

The sugars in the air-dried fruit therefore weigh twice as much as the combined skin, pulp, and seeds, and the relative quantities may be thus stated for the entire berry :—

Water lost by drying in air	85.0
Sugars	10.0
Skin and pulp	2.6
Seeds	2.4

100.0

NOTE 10, B (p. 266).

On the loss of weight of ripe berries of the Prickly Pear (Opuntia Tuna) when dried in air at the ordinary temperature.

Weight of moist fruit taken as	100.0
" " air-dried fruit	18.0
" " air-dried fruit after washing	12.0
Water lost by drying in air	82
Sugars	6
Skin, pulp, and seeds	12
		100

NOTE 11 (pp. 302, 318).

TABLE ILLUSTRATING THE HISTORY OF THE FRUIT OF BARRINGTONIA SPECIOSA, BEGINNING WITH THE YOUNG FRUIT AND PASSING THROUGH THE MATURATION STAGES ON TO THE AIR-DRIED DETACHED CONDITION.

(The fruit is square, husky, of the baccate type, and myrtaceous, only one seed being as a rule matured.)

	Stage of fruit.	Weight in grains.	Girth in millimetres and inches.	Condition of the seed-cavity and of the seed or seeds.	Relative weight of the pericarp and seed, the entire fruit being taken as 100.	
					Pericarp.	Seed.
A	Young	290	100 mm. ; 4 inches	4-celled ; 3 cells empty ; 1 cell with 2 whitish seeds, each about 2½ grains	98.3	1.7
B	"	550	132 mm. ; 5.2 inches	4-celled ; 2 cells empty ; 1 cell with a whitish seed, 3 grains, aborted ; 1 cell with a red seed, 7 grains	98.2	1.8
C	"	1100	178 mm. ; 7 inches	4-celled ; 3 cells empty ; 1 cell with a red seed, 13½ grains	98.8	1.2
D	"	1680	215 mm. ; 8.5 inches	As in C ; red seed, 14 grains	99.2	0.8
E	"	2950	254 mm. ; 10 inches	As in C ; red seed, 12 grains	99.6	0.4
F	"	3060	254 mm. ; 10 inches	As in C ; but seed 20 grains and no longer coloured	99.3	0.7
G	"	5250	305 mm. ; 12 inches	Still 4-celled, with 3 cells empty ; but the growing seed, 208 grains in weight, is now encroaching on the empty cells	96.0	4.0

TABLE ILLUSTRATING THE HISTORY OF THE FRUIT OF BARRINGTONIA SPECIOSA—*continued*.

	Stage of fruit.	Weight in grains.	Girth in millimetres and inches.	Condition of the seed-cavity and of the seed or seeds.	Relative weight of the pericarp and seed, the entire fruit being taken as 100.	
					Pericarp.	Seed.
H	Ripening	8750	401 mm. ; 15·8 inches	The rapidly growing seed, 744 grains in weight, now nearly fills the seed-cavity, and the cells are suppressed	91·5	8·5
I	Mature	9000	406 mm. ; 16 inches	The mature seed, weighing 1620 grains, entirely fills the seed-cavity	82	18
J	Drying on the tree	3200	356 mm. 14 inches	The seed, weighing 1760 grains, has probably increased its weight whilst the husk has been drying	45	55
K	Drying completed on ground	1350	356 mm. 14 inches	The seed, weighing 648 grains, still fills the cavity	52	48

Explanation.—All the data, with the exception of those for I and K, are from observations in Grenada on individual fruits. The results for the moist and air-dried conditions (I and K) represent the average of a number of observations on several fruits. There is, therefore, no continuous record here, but merely a description of fruits in different stages. Notwithstanding discrepancies, which were to be, indeed, expected, the general trend of the results is reliable. The apparent increase in weight of the seed during the first part of the drying of the fruit needs further inquiry, but it is quite consistent with what occurs in the Coco-nut and in the Acorn. The sudden rise in the proportion of the pericarp in the air-dried fruit is due to the fact that the seed does not share in the early part of the drying process. The small diminution in the girth of the fruit during the drying process was exemplified by fruits that had been allowed to dry after being collected in the full-grown state.

NOTE 12 (p. 226).

On the time required by seeds to complete their drying in air, or, in other words, to acquire a stable weight.

THIS involves the whole period from the time that the soft full-grown pre-resting seed first begins to shrink in the green or moist fruit, until the time when the shrinkage is complete, and a normal contracted hard-coated resting seed is produced.

In the case of impermeable seeds, reference may be made to the results of observations made in Jamaica on some typical examples.

The seeds of *Adenanthera pavonina* accomplish the whole shrinking and hardening process in a period not exceeding six weeks, after which they assume their normal permanent condition as non-hygroscopic seeds. So also with the large seeds of *Entada scandens*, which within six or seven weeks are transformed from soft flabby white seeds into hardened mahogany-brown resting seeds that display no hygroscopic reaction. The seeds of *Guilandina bonducella* occupy about a month in passing from the soft swollen condition into the typical resting state, when they respond as little as a quartz-pebble to the variations in the humidity of the atmosphere. In the case of a large number of other seeds, mostly permeable, a stable weight was reached in a few weeks, sometimes only one or two weeks, sometimes five or six weeks, the subsequent changes in weight being merely hygroscopic in character.

However, in all these cases the experiments were made on seeds detached from the parent, so that the natural process was not followed. Then, again, drying in a room would probably be accomplished in half the time required under open-air conditions. For instance, Horsechestnuts (*Æsculus*) and Acorns (*Quercus*), the last behaving like seeds, complete their drying in five or six weeks in a room, but they would probably need two or three months in the woods. In the case of drupaceous fruits with a stony endocarp quite another régime is involved, a matter discussed in the case of *Prunus* in Note 28 (p. 501). If the skin remains entire several months would be needed.

NOTE 13 (p. 446).

Effects of very dry conditions on the growth of Bidens cernua and Bidens tripartita.

THESE experiments were carried out in my greenhouse during three years, with the object of determining the effect of very dry, warm conditions on the growth of these plants. The soil was kept as dry as possible, the quantity of water supplied being reduced to a minimum. Under such conditions the seedlings in the early part of the experiments frequently lay prostrate on the parched soil, a few drops of water soon causing them to become erect again. After they were more than 2 inches high they acquired the permanently erect habit. Ordinary garden soil was employed in the first year, sandy soil mixed with fibre in the second year, and sandy soil alone in the third year. After three generations the average height of the plants was reduced from 17 or 18 inches to 5 or 6 inches. The fleshy moist-tissued stems became in the first year dry and woody, in the next year slender and wiry, and in the third year attenuated and thread-like.

After three years the length of the achene was reduced to less than half, the breadth remaining almost unchanged. The effect of dry conditions on the foliage was displayed, as shown in the following note, in the marked tendency of the leaves of *Bidens cernua* to assume the form of those of *B. tripartita*, those of the last-named species remaining for the most part unchanged. Whilst plants of *B. cernua* raised under the normal moist conditions as a rule developed only lanceolate leaves, those grown from seed under unusually dry conditions generally produced, in the case of the second, third, fourth, and fifth pairs, the broad, deeply cut leaves of *B. tripartita*. The result of these experiments are tabulated below.

EFFECTS OF VERY DRY SOIL-CONDITIONS ON THE GROWTH OF BIDENS CERNUA AND BIDENS TRIPARTITA. (Results stated in inches.)*

	Year.	Soil.	Bidens tripartita.					Bidens cernua.				
			Height in inches.	Character of stem.	Form of leaves.	Achenes.		Height in inches.	Character of stem.	Form of leaves.	Achenes.	
						Long.	Broad.				Long.	Broad.
A. Plants from a marsh	1890	...	15-20	Moist, almost fleshy	Broad, deeply cut, tripartite	'30	'10	15-20	Moist, almost fleshy.	Undivided, lanceolate	'25-'28	'08-'10
B. Grown from seeds of A.	1891	Dry garden soil	15-20	Dry, woody	Do.	'20-'22	'08-'10	15-20	Dry, woody	Usually broad, deeply cut, and tripartite, except in the latest leaves, which are lanceolate †	'15-'20	'08-'10
C. Grown from seeds of B.	1892	Dry sandy soil, with fibre.	9-11	Slender, wiry	Do.	'20-'26	'08-'11	9-10	Slender, wiry	Do.	'15-'23	'09-'11
D. Grown from seeds of C.	1893	Dry sandy soil.	5	Thread-like	Do.	...‡	...	6	Thread-like	Do.	'12	'09

* For the conditions of the experiments see above.

† For details consult the succeeding note.

‡ The plants died after flowering.

NOTE 14. (See previous note.)

Are Bidens cernua and Bidens tripartita distinct species?

It seems questionable whether the distinction between these two allied species is always maintained, a distinction depending on differences in the leaves and possibly concerned mainly with their stations, *Bidens cernua* preferring the wet borders of ponds and ditches and *B. tripartita* the river-bank, the last growing more frequently out of the water than does *B. cernua*. This preference for a drier station on the part of *B. tripartita* acquires interest from the fact brought out in the experiments discussed in Note 13, and referred to below, that plants raised from seeds of *B. cernua* in very dry conditions develop foliage like that of *B. tripartita*. Many years since, I took a great interest in these two plants; and individuals presenting characters intermediate between those of the two species came often under my notice. The two may be sometimes observed growing side by side; and occasionally in the midst of a patch of one species will be seen a single individual of the other.

It is of importance to record that when raised under unusually dry conditions, as described in Note 13, the young plants differed but slightly from each other, broad tripartite leaves being commonly produced by both species in the case of the second, third, fourth, and fifth pairs. The specific difference began to be exhibited after the fifth pair of leaves, the plants of *B. cernua* developing afterwards only undivided lanceolate leaves, whilst those of *B. tripartita* continued to produce their typical foliage until the eighth pair, when they put forth two or three pairs of lanceolate leaves under the flower-head. Occasionally plants of *B. cernua* raised under these very dry conditions produced broad leaves of the type of those of *B. tripartita*, except that they were undivided.

Plants of *B. cernua* raised in my greenhouse under normal conditions in muddy water and in wet soil developed only the characteristic lanceolate leaves, and it was only when exposed to the dry conditions of my experiments that they began to produce foliage like that of *B. tripartita*. Grown under natural conditions the young plants of both species generally put forth their typical leaves in the third pair.

NOTE 15 (p. 325).

The proportions of pericarp and seeds in the fruit of Theobroma Cacao (Cocoa).

THE following data were kindly supplied to me in 1909 by Mr R. D. Anstead, superintendent of the Botanic Gardens in Grenada.

They refer to the yield of the Waltham Estate in that island, owned by the Hon. Macaulay Browne, and managed by Mr H. Gan. The original return in pounds has been converted by me into kilograms. (The term "pericarp" is here applied to the whole fruit excluding the seeds.)

TABLE SHOWING THE PROPORTIONS BY WEIGHT OF PERICARP AND SEEDS IN THE FRESH MOIST FRUITS OF THEOBROMA CACAO (COCOA).

A. In pounds (lbs.).							
Year.	Total number of fruits weighed.	Total weight of the fruits including seeds.	Total weight of seeds.	Average weight of a single fruit with seeds.	Average weight of seeds in a single fruit.	Weight-proportion of pericarp and seeds, the entire fruit being taken as 100.	
						Pericarp.	Seeds.
1906-7	41,728	36,319 lbs.	10,007 lbs.	0·87 lb.	0·24 lb.	72·5	27·5
1907-8	47,376	43,081 ,,	10,751 ,,	0·91 ,,	0·23 ,,	75·0	25·0
	89,104	79,400 ,,	20,758 ,,				
B. In kilograms (kilos.).							
1906-7	41,728	16,474 kilos.	4539 kilos.	0·395 kilo.	0·109 kilo.	72·5	27·5
1907-8	47,376	19,541 ,,	4877 ,,	0·413 ,,	0·103 ,,	75·0	25·0
	89,104	36,015 ,,	9416 ,,				

Note.—Two fruits tested by me in Grenada gave a mean pericarp-proportion of 75 per cent.

NOTE 16 (p. 337).

The two modes of drying of legumes, as illustrated by Pisum and Guilandina.

VERY different results are obtained from Peas (*Pisum sativum*) according as the pods are picked in the moist state and left to dry under ordinary air-conditions, or are first allowed to accomplish more or less of their drying on the plant. In the first case the dried pods

retain a greenish hue and are thickish in appearance. In the second case they are pale and parchment-like and relatively thinner.

This is associated with different behaviours in the balance, the first type showing in average pods a pericarp-proportion of over 40 per cent. of the total weight, the second type, on the other hand, a pericarp-proportion of only 20 per cent. The same indication is also afforded by the difference in the actual weights of the dried fruit-cases, those of the pods that dried after detachment averaging 15 or 16 grains, and those of the pods dried on the plant only from 7 to 9 grains.

By experiments we can determine that the pericarp or fruit-case of the detached fresh pod loses about 86 per cent. of its weight when dried; whilst if we know the shrinking ratio of the entire pod and the average proportion of parts in the fresh fruit and in the fruit dried on the plant, we can easily show that the pericarp then loses in drying about 93 per cent. of its weight. Thus, taking the shrinking ratio of the ripe moist fruit at 100 to 20 (involving a loss of 80 per cent.) and the pericarp-proportions of the moist and dry pods at 60 and 20 per cent. respectively, we obtain the following results for a typical six- or seven-seeded fruit:—

THE SHRINKING OF PARTS OF A RIPE SIX- OR SEVEN-SEEDED POD OF PISUM SATIVUM WHEN DRIED ON THE PLANT.

Pisum sativum.	Proportional weights of the pericarp and seeds, taking the entire pod as 100.		Actual weight in grains.		Loss of weight.		
	Moist fresh pod.	After drying on the plant.	Moist fresh pod.	After drying on the plant.	Moist fresh pod.	After drying on the plant.	Loss of weight.
Pericarp . .	60	20	120	8	100	7	93 per cent.
Seeds . . .	40	80	80	32	100	40	60 „
Entire . . .	100	100	200	40	100	20	80 „

The shrinking ratio can be obtained by comparing the average weights in the moist and dry condition of a large number of pods from the same plant and containing the same number of seeds.

The differences in the behaviour of the pods, whether dried in the detached condition or allowed to dry on the plant, may shortly be summed up from the previous remarks in the following manner:—

<i>Pisum sativum</i> .	Condition of the dry pericarp.	Proportion of dry pericarp to the weight of the entire pod.	Average weight of the dry pericarp in grains.	Loss of weight of pericarp in the previous drying process.
Pods dried in the detached condition in a room	Greenish and relatively thick	Over 40 per cent.	15 or 16	85 or 86 per cent.
Pods dried on the plant	More or less de-colourised and relatively thin	About 20 per cent.	7 to 9	91 to 93 „

Note.—With the exception of the average weight which here applies to six- or seven-seeded pods, the results apply to any normal pod.

It is thus obvious that the drying under ordinary air-conditions of detached moist ripe pods of *Pisum sativum* does not represent the drying which takes place on the plant. That peculiar partial bleaching which the drying pod displays on the plant is but little if at all produced by merely drying the detached green pod. It is not merely a question of colour but a question of weight, the dried detached pod being not only greener, but also, when deprived of its seeds, double the weight of the husk of the fruit that has dried naturally on the plant.

Two kinds of drying of the legume, determined by the detachment or non-detachment of the fruit, also came under my notice in other leguminous plants, such as *Cæsalpinia*, *Guilandina*, *Vicia*, etc. With *Guilandina bonducella* they were very conspicuous. Pods on the plant dried black or dark brown; whilst those in my room dried green. Green two-seeded pods allowed to dry on my working table on different occasions in Jamaica, Grenada, and Grand Turk gave closely similar results, both in the retention of more or less of their green hue and in the ultimate dry weight of the pericarp, which ranged only between 41 and 47 grains. The loss of weight experienced by the pericarp in four sets of experiments on single fruits in these three localities varied only between 74 and 78 per cent.

On the other hand, pods of *Guilandina bonducella* that had dried on the plant had not only lost their green colour but were very sensibly lighter in weight. In Grenada three double-seeded pods gathered dry and dehiscing from the plant had an average weight of 23 grains without their seeds. In the same way, five similar pods gathered dry in Grand Turk gave an average weight of 27 grains.

This difference in the weights of dried detached and undetached pods of this species of *Guilandina* must be reflected in the difference in the loss of weight experienced when drying. The average moist weight of the four detached pods without their seeds was 182 grains,

and their average dry weight was 44 grains, indicating a reduction of 76 per cent. Now if we assume that the eight pods gathered dry from the plant had about the same original moist weight as respects their pericarp, then their average dry weight of 25 grains represents a reduction in weight during the drying process of about 86 per cent. These results, though rough, are probably near the truth, experiments made in widely removed localities in the West Indies giving closely similar indications. They are summed up in the following table :—

Guilandina bonducella.	Condition of the dry pericarp or fruit-case.	Average weight of the dry pericarp in grains.	Loss of weight of pericarp in the drying process.
Pods dried in the detached condition in a room	Greenish and relatively thick	44	76 per cent.
Pods dried on the plant	Blackish or dark - coloured and relatively thin	25	86 „

I have here only touched the fringe of an interesting subject, and perhaps some investigator may be induced to take up this inquiry. The two changes in colour which green moist legumes experience whilst drying on and off the plant, a blackening or darkening as in *Faba*, *Vicia*, etc., and a partial bleaching as in *Pisum*, *Canavalia*, etc., may be brought into some kind of relation with the coloration of the seeds, a matter discussed in Chapter XVII. Such an inquiry would have to be approached from the physical and chemical as well as from the biological side.

NOTE 17 (p. 320).

COMPARISON OF THE CAPSULES OF PRIMULA VERIS (PRIMROSE) AND OF SWIETENIA MAHOGANI (MAHOGANY) AS REGARDS THE WEIGHT-PROPORTION OF THE PLACENTAL AXIS OR COLUMELLA, THE LIVING FRUIT OF THE FIRST-NAMED WEIGHING ABOUT 4 GRAINS AND OF THE SECOND ABOUT 6000 GRAINS.

	Proportional weight of the placental axis or columella, taking the entire fruit without the seeds as 100.	
	Living moist fruit.	Fruit dried on the plant.
Primula veris	63	56
Swietenia Mahogani	14	12

In *Primula veris* the placental axis in the living fruit is a fleshy pointed dome which loses about 85 per cent. of its weight as the fruit dries ; but owing to the presence of sugar it is hygroscopic and a little sticky in the dried shrunken state.

In *Swietenia Mahogani*, where the fruit belongs to the woody-capsule type, the axis or columella, though ligneous in appearance in the living fruit, loses about 72 per cent. of its weight in drying, though retaining its original regular prismatic form.

NOTE 18 (p. 395).

On the colour of embryos.

THE following additional remarks on the colouring of embryos may serve to supplement the results given in Chapter XVII. As respecting this feature of the embryo in resting seeds, which is the point to which systematists generally restrict themselves, one may quote from Mrs Hooker's translation of the *System of Botany* of Le Maout and Decaisne, where it states (p. 111) that "the colour of the embryo varies ; it is white in most plants, yellow in some Cruciferæ, blue in *Salpiglossis*, green in the Spindle tree and Maples, and pink in *Thalia*."

The coloration of the embryo is apparently constant enough to rank at times as one of the ordinal characters. It is noteworthy that of the five orders mentioned in the above-quoted work as possessing resting seeds with green embryos or green cotyledons, Zygophylleæ, Aurantiaceæ, Rhamnæ, Aceraceæ, and Meliantheæ, all belong to the Discifloral series of the *Polypetala* ; and although it does not seem to be a frequent character with the Celastrineæ, referred to the same series, *Euonymus*, which belongs to this order, possesses seeds with a green embryo. The embryos in the orders above-named have often large, flat, foliaceous cotyledons, and occupy most of the length and breadth of the seed-cavity ; but in *Melianthus* the green embryo is very small, lying in the midst of a copious albumen.

NOTE 19 (p. 453).

On the retrogression of plants under conditions of stress.

As bearing on the retrogression of plants under conditions of stress, one may recall Lord Avebury's remark on the frequency of small leaves reduced to scales in seedlings with subterranean cotyledons, rudiments

at present fulfilling no useful function and offering, as he adds, interesting indications of the past history of the plants (*A Contribution to our Knowledge of Seedlings*, Internat. Sci. Ser., vol. lxxix. p. 159). Though one can imagine repressive conditions where the plant would be driven to utilise these rudiments of leaves, it is necessary to remember Dr Goebel's warning that arrested organs do not necessarily represent organs that were fully developed in the ancestors of existing forms, and that it is invalid to assume that functionless organs are always only the vestiges of earlier completely formed ones, it being quite a general rule that many more primordia are laid down than become functional (*Organography of Plants*, i. 61). I am afraid, however, that the argument from rudimentary organs would not assist my theory, since one can point to cases amongst *Barringtonia* and *Guttifera*, where the hypocotylar axis becomes the storehouse of the food-reserve and the cotyledons are represented by functionless scales. The last word on the subject belongs to the student of development, and I notice with some satisfaction Dr Goebel's statement that cotyledons proceed from the unsegmented primordium of the embryo and not, as with later leaves, out of the vegetative point of a shoot (*Ibid.*, ii. 400).

It is possible that the results of future investigation will support the view that the retrogression may extend further back than the seed-stage as we know it on this planet, and that the dual organism that seems to be represented in the combination of endosperm and embryo in an albuminous seed may be split into its two primal parts, thus offering starting-points for two independent lines of plant-development in different worlds.

NOTE 20 (pp. 26, 35).

WHILST preparing the appendix after the rest of the work was printed, I found it more convenient to place the materials originally intended for this note in Note 28 (p. 494).

NOTE 21 (pp. 149, 183).

ADDITIONAL RESULTS SHOWING THE BEHAVIOUR OF DIFFERENT
SUBSTANCES AFTER EXPOSURE TO A TEMPERATURE OF 100° C.

	Original weight.	After exposure to a temperature of 100° C. for two hours.	Five or six days after the oven experiment.	Regained from the air.
Chlorite	100	99·6	100·0	0·4
Common opal	100	98·0	99·2	1·2
Rice of commerce	100	86·8	98·9	12·1
Veronica (species) fleshy living leaves	100	23·3	27·5	4·2
Corylus Avellana (Hazel) wood of living stem	100	56·7	64·2	7·5

These results will serve to bring out the contrast between mineral substances containing a little water, as chlorite and opal, air-dried vegetable substances, as rice of commerce, and living plant materials, as fresh leaves and green wood, when they are subjected to a temperature of 100° C. for some hours and are then exposed to the air for some days. The chlorite and opal had little to lose in the oven, and gained most or all of it back from the air. The rice behaves like other air-dried plant-substances in regaining from the air the water lost in the oven, the small deficit being probably connected with hygroscopic variation. On the other hand, fresh leaves and living wood gain back but a small proportion of what they lose in the oven. What is not regained is the water of vitality. What is regained is the water of hygroscopicity, and this is the only water the rice holds in the ordinary air-dried state.

I may remark that the data given in the table on page 183 in the case of the second experiment on Hazel leaves are merely resorption results after the oven test.

NOTE 22 (pp. 198, 324).

The drying régime of Swietenia Mahogani.

THIS is dealt with on p. 324 for the fruit as composed of pericarp and seeds. In Note 28 on p. 494 the placental axis or columella is differentiated from the pericarp in the process.

NOTE 23 (p. 205).

The rupturing of the coats of the germinating seed of Entada scandens.

It cannot be said that the splitting takes place in the weakest point in the coverings. As a matter of fact, it is in the thickest portion, namely, at the hilar scar, that the rupture occurs. If we dry the shell-like coverings of the germinating seed, we find that the thickness in and about the scar is about 3 millimetres, whilst the thinnest portion at the opposite border of the seed is only half as thick. Usually the shell thins away as we leave the base of the seed where the rupture takes place. In fact, there is all the appearance of a special provision for adding to the thickness and strength of the coats at this point, the micropylar opening being obliterated. Mere weakness in the coverings at any particular place does not result in their rupture at that spot. This is well shown in the fact that although all the seeds of this plant were filed half through the shell at the sides and top to procure germination, in no case did the splitting occur there when the process began. I may add that the splitting of the coats in the swelling seed is not necessarily followed by germination, as indicated by the protrusion of the radicle, and that therefore the question of any pressure from this cause does not arise.

NOTE 24 (pp. 208, 219).

The Hura difficulty.

THE difficulty with the seeds of *Hura crepitans* is that their coverings, which attain their maximum development and weight long before the kernel reaches its full size, lose weight as the kernel proceeds with its growth, the albumen and the embryo which make up the kernel growing well together as the seed matures. As the result of a number of observations on the later stages of maturation, it was ascertained that while the seed added but little to its size and weight, a considerable change occurred in the relative proportion of the coats and the kernel.

When the pre-resting seed is fully mature, the coats have already lost considerably in weight, whilst the kernel has just reached the maximum of its growth. This is the condition that had to be represented in the table on p. 219, which contains the data for constructing the shrinking and drying régime of these seeds as compared with other plants; and of course the full shrinkage of the seed-coats is not there indicated. This is clearly brought out in the comparison of the two régimes given below, the first for the mature pre-resting seed, where

the previous loss of weight of the seed-coverings is not taken into account, the second for the same seed where this loss is allowed for.

THE SHRINKING AND SWELLING RÉGIMES OF THE SEEDS OF
HURA CREPITANS.

		Pre-resting seed.	Resting seed.	Seed swollen for germination.
Mature pre-resting seed, from the data on p. 219 and in table below	Coats . .	100	25	77
	Kernel . .	100	77	130
	Entire . .	100	48	100
The same after allowing for the shrinkage of the coats before the seed is mature, from data given below	Coats . .	100	18	54
	Kernel . .	100	77	130
	Entire . .	100	48	100

Here we see that when determining the shrinkage for the mature resting seed we are ascertaining its full amount for the kernel but not for the coverings, which, instead of losing 75 per cent. of their weight in the shrinking process, really lose as much as 82 per cent. during the whole stage.

That the albumen and embryo which constitute the kernel increase in weight, and by implication in size, after the seed-coverings have begun to contract and dry, is clearly indicated in the table below. The growth in size of the embryo is not there shown, but it may be observed that when the coats have attained their maximum size and weight, the embryo, though completely formed, is only about one-fourth of the mature size and covers only a third of the surface of the albumen. That the growth of the albumen and the embryo is much behind the growth of the seed-coats becomes very evident when one handles the seeds, the embryo in its turn being less advanced than the albumen.

It is also brought out in the table that the shrinkage of the coats during the maturation of the kernel is confined to the inner layer, which is semi-crustaceous in the early stage and contracts and hardens as the kernel matures.

Another peculiarity in the seeds of *Hura crepitans*, which it shares with other seeds possessing oily kernels, is the small amount of water taken up when swelling for germination (see pp. 208, 214). Whilst in leguminous seeds displaying the same structure, as in *Poinciana*, *Cassia*, and *Bauhinia*, the swelling kernel on the average increases its weight by about 150 per cent., in *Hura* the kernel adds barely 70

per cent. to its weight, and in *Ricinus* a little over 40 per cent. But the relatively small amount of water absorbed by the kernel of a seed of *Hura crepitans*, when swelling for germination, is counterbalanced by the large amount taken up by the coverings, which increase their weight threefold, as already illustrated in the first table of this note (see also p. 212). In spite of this great absorption, however, the coats do not attain their original weight in the pre-resting seed, whilst the kernel exceeds it. Though the contrast in behaviour is here much exaggerated, it exemplifies a principle in operation in many seeds, as discussed in Chapter IX.

TABLE ILLUSTRATING THE CHANGES IN WEIGHT AND IN THE PROPORTION OF PARTS IN THE CASE OF SEEDS OF HURA CREPITANS AFTER THEY HAVE ATTAINED THE MAXIMUM WEIGHT AND SIZE IN THE PRE-RESTING STATE.

(W = weight in grains ; P = percentage.)

	Later stages in the maturation of the pre-resting seed.										Resting seed.		Seed swollen for germination.		
	I.		II.		III.		IV.		V.						
	W.	P.	W.	P.	W.	P.	W.	P.	W.	P.	W.	P.	W.	P.	
A {	Coats . . .	34·0	81	33·6	80	32·0	76	28·6	68	23·9	57	6·0	30	18·5	44
	Kernel . . .	8·0	19	8·4	20	10·0	24	13·4	32	18·1	43	14·0	70	23·5	56
	Entire seed	42·0	100	42·0	100	42·0	100	42·0	100	42·0	100	20·0	100	42·0	100
B {	Albumen . .	7·4	93	7·5	89	11·7	87	16·1	89	12·3	88	20·4	87
	Embryo . .	0·6	7	0·9	11	1·7	13	2·0	11	1·7	12	3·1	13
	Entire kernel	8·0	100	8·4	100	13·4	100	18·1	100	14·0	100	23·5	100
C {	Outer soft integuments	18·8	...	19·9	...	18·4	...	21·5
	Inner crustaceous shell	15·2	...	13·7	...	13·6	...	7·1
	Entire coats	34·0	...	33·6	...	32·0	...	28·6

A shows the progressive stages in the weight and proportions of the coats and kernel, beginning with the later maturing stages, when the pre-resting seed has attained its maximum weight and size, and going on to the resting state and to the swollen state immediately preceding germination.

B shows the changes in the weight and proportions of the albumen and embryo in the later stages of the maturation of the pre-resting seed, and also the changes in the resting seed and in the seed swollen for germination.

C shows that the shrinkage of the coats in the later stages of maturation is restricted to the inner crustaceous shell, which hardens as the process advances.

Note that the data given in column V. refer to the pre-resting seed when the kernel (albumen and embryo) has reached maturity. They are the data used in the table on p. 219.

NOTE 25. (See Chapter X. p. 236.)

OBSERVATIONS ON THE WEIGHT OF RESTING SEEDS OF PISUM, PHASEOLUS, FABA, AND RICINUS, SHOWING THAT THE INCREASE IN WEIGHT DURING TWO YEARS RECORDED BY VAN TIEGHEM AND BONNIER IS INCLUDED IN THE RANGE OF THE NORMAL HYGROSCOPIC VARIATION.

A. Pisum sativum, Faba vulgaris, Phaseolus multiflorus.										
	Variety.	Number of seeds.	Weight in grains.							Hygroscopic range or variation in weight.
			1910.					1911.		
			May 21.	May 28.	June 6.	June 13 and 14.	July 17 and 18.	April 8.	August 5.	
Pisum sativum	Early Sunrise Pea	19	102·9	102·7	103·8	104·6	104·4	...	101·9	2·6 %
Pisum sativum	Duke of Albany Pea	17	101·7	101·4	102·8	103·9	103·7	...	100·7	3·2 ,,
Faba vulgaris	Green Windsor Broad Bean	6	201·0	199·9	202·0	204·8	202·8	197·5	197·5	3·6 ,,
Faba vulgaris	Long-pod Broad Bean	8	207·9	207·1	208·9	211·7	210·0	205·2	204·5	3·6 ,,
Phaseolus multiflorus	Scarlet Runner	9	200·2	199·3	201·5	203·8	200·7	196·5	197·5	3·6 ,,

Note.—The Albany Pea has wrinkled seeds, whilst the seeds of the Sunrise Pea are nearly smooth.

All the above seeds were kept in a cool, rather damp room until the end of July 1910, when they were transferred to a warm, dry room. They were all eight to ten months old.

B. Ricinus communis.	
Number of seeds 152, with caruncle retained, six months old. They were kept in a cool, rather damp room for the first two weeks, and afterwards in a warm, dry room.	Number of seeds 39, with caruncle removed, twelve months old. They were kept in a cool, rather damp room for the first three weeks, and afterwards in a warm, dry room.
July 14, 1908, 385·9 grains	October 14, 1909, 66·7 grains
„ 25, „ 387·1 „	„ 18, „ 67·1 „
August 1, 1908, 385·3 „	„ 22, „ 66·1 „
September 2, 1909 382·7 „	March 15, 1910, 66·1 „
June 18, 1910 382·8 „	June 20, „ 66·2 „
April 8, 1911, 383·4 „	August 4, 1911, 66·2 „
August 5, „ 384·0 „	...
The hygroscopic range or variation in weight amounted to 1·1 per cent.	The hygroscopic range or variation in weight amounted to 1·5 per cent.

NOTE 26 (pp. 289, 325, 354).

The "replum" of Entada polystachya.

IN this genus the replum is the name applied to the persistent border of the legume by which the joints are held together. It is really a bifurcating fruit-stalk, the two branches thinning off considerably until they unite at the distal end of the pod. In the moist fruit it makes up about 12 per cent. of the weight of the pericarp (fruit less the seeds), and about 15 per cent. in the dry fruit.

NOTE 27 (p. 309).

THE WATER-CONTENTS OF THE COCO-NUT.

Materials.	Original weight.	Weight after air-drying.	Weight after exposure to temperature of 100° C.	Total loss of water.
Husk of green fruit . . .	100	20	16	84
Shell of ripe fruit . . .	100	93	83	17
Kernel of ripe fruit . . .	100	60	56	44
Embryo of ripe fruit . . .	100	31.5	23	77

It will be noticed that whilst the husk of the green full-sized fruit is employed, the other materials belong to the ripe fruit (see pp. 305, 307).

The data given for the air-drying of the kernel and embryo on p. 411 differ a little from those above, though the contrast between them is the same.

NOTE 28 (pp. 325-327).

Further details supplementing the materials given in the tables on pp. 325-327 and p. 26 for the determination of the drying régimes of fruits and seeds.

- (1) *Achras Sapota*, p. 325.—In two-seeded fruits the pericarp-proportion would be 98 per cent., and in ten-seeded fruits 88 per cent.
- (2) *Acrocomia*, pp. 26, 325.—See under Palms (p. 499).
- (3) *Æsculus Hippocastanum*, (pp. 323, 326). See also pp. 263, 269, 284, 303, 320.

- (4) *Albizzia Lebbek*, p. 327.—See pp. 334, 349 for a detailed treatment of these legumes.
- (5) *Aquilegia*, p. 326.—The data given in the table relate to a fruit-head with five follicles, each follicle with twenty seeds.
- (6) *Areca Catechu*, pp. 26, 326.—See under Palms (p. 498).
- (7) *Arenga saccharifera*, p. 325.—See under Palms (p. 498).
- (8) *Bactris*, p. 327.—See under Palms (pp. 499, 500).
- (9) *Barringtonia speciosa*, p. 325.—The drying régime is discussed at length on p. 294; the proportion of parts on pp. 302, 303; and the history of the fruit in Note 11 (p. 478) and on p. 318. Only one seed is usually matured in this fruit; but at times (perhaps in 10 per cent.) there are two seeds. In one fruit specially examined the two seeds were lying one on top of the other, the two contiguous sides being flattened together, as if both seeds had been developed in a single loculus.
- (10) *Bignonia, near æquinocialis*, p. 326.—The placental septum is not differentiated in the data given in the table. This is done below:—

Moist fruit	{	Pericarp proper	.	.	42 per cent.
		Placental septum	.	.	14 „
		Seeds	.	.	44 „
					100 „
Dry fruit	{	Pericarp proper	.	.	30 per cent.
		Placental septum	.	.	8 „
		Seeds	.	.	62 „
					100 „

These results may be compared with those for *Primula veris* (p. 500) and *Swietenia Mahogani* (p. 503), where a placental axis or columella is concerned.

- (11) *Cakile*, p. 327.—In both the species named below I have selected fruits where the lower joint as well as the upper joint contained a normal mature seed:—

(a) *Cakile æqualis*, dry fruit from Jamaica :

Upper joint, less seed	0·3 grain
Seed of upper joint	0·1 „
Lower joint, less seed	0·2 „
Seed of lower joint	0·1 „
					0·7 „

(b) *Cakile maritima*, dry fruit from England :

Upper joint, less seed	0·5	grain
Seed of upper joint	0·2	„
Lower joint, less seed	0·13	„
Seed of lower joint	0·07	„
		0·9	„

(12) *Canavalia gladiata*, p. 326.—This is *C. gladiata*, DC, the variety with red seeds (see Note 5, p. 471).

(13) *Canavalia ensiformis*, p. 326.—This is *C. gladiata*, DC, the variety (*ensiformis*) with white seeds (see Note 5, p. 471).

(14) *Canna indica*, p. 326.—The pericarp, which makes up 39 per cent. of the moist fruit, is thus composed :—

Outer soft tubercles or spines scaling off as the fruit dries and losing 90 per cent. of their weight in the process	10	per cent.
Pericarp proper, which loses 80 per cent. of its moist weight as the fruit dries	29	„
		39	„

(15) *Caryota*, p. 327.—Regarding the fruit as a berry, the pericarp-proportion would be 22 per cent. in the dry fruit.

(16) *Citrus*, p. 325.—In another moist fruit of the Common Orange (*Citrus Aurantium*), weighing 3500 grains and containing 15

PROPORTION OF PARTS IN DIFFERENT SPECIES OF CITRUS.

Ripe moist fruit.	Citrus Aurantium.		Citrus decumana (Shaddock).		
	Common Orange.	Mandarin Orange.	A.	B.	C.
Rind . .	19	20	25	41	34
Flesh . .	79	79	72	56	63
Seeds . .	2 [12]	1 [5]	3 [80]	3 [80]	3 [85]
	100	100	100	100	100
Total weight	3500 grains.	1870 grains.	14,000 grains.	12,700 grains.	15,300 grains.

Note that the number of the seeds is in brackets.

seeds (78 grains), of which 3 had aborted, the proportional weight of the pericarp was 97.8 per cent. The number of seeds varies greatly and affects the relation. Thus, if the Mandarin Orange referred to in the table had had a seed in each of its ten segments, the proportional weight of the pericarp would have been reduced from 99 to 98 per cent.

- (17) *Cocos*, pp. 325, 327. (See under Palms, p. 499.) The data here given for *Cocos nucifera* refer to the green coco-nut and to the completely air-dried fruit without water, and can only be used as indicated under Palms in this note.
- (18) *Elæis guineensis*, p. 327.—See under Palms (pp. 499, 500).
- (19) *Entada polystachya*, p. 325.—See Note 26 on p. 494.
- (20) *Erythrina corallodendron*, p. 327.—The beading of the pods, which is dealt with on p. 360, has an important effect here.
- (21) *Faba vulgaris* (Broad Bean), p. 326.—The pericarp-proportion of a two-seeded dry legume, weighing 55 grains, was 26 per cent.
- (22) *Gossypium* (Cotton plants), p. 327.

PROPORTION OF PARTS IN THE DRY DEHISCING FRUIT.

	<i>Gossypium barbadense</i> (weight of fruit 31 grains).	<i>Gossypium hirsutum</i> (weight of fruit 50 grains).
Pericarp . . .	28	24
Wool	20	33
Seeds	52 (16 seeds)	43 (23 seeds)
	100	100

The wool forms 28 per cent. of the resting seed in *G. barbadense*, and 43 per cent in *G. hirsutum*.

The influence of the hairs on the proportional weight of the seed-coats is shown in the table on p. 194. In all cases the fruits designated *Gossypium hirsutum* in this work are from the same plant, whether or not marked by (?) in the text.

- (23) *Hibiscus esculentus*, p. 327.—The data given in the table refer to a dry fruit weighing 100 grains with 10 carpels and 94 seeds. In a dry fruit weighing 62 grains with 7 carpels and 54 seeds the pericarp-proportion was 36.
- (24) *Hura crepitans*, p. 325.—The *Hura* difficulty is discussed in Note 24 (p. 490). The drying of the entire fruit is discussed on p. 289.

- (25) *Leucaena glauca*, p. 326.—See p. 334.
 (26) *Lonicera Periclymenum*, p. 325.—See p. 266.
 (27) *Mauritia setigera*, p. 326.—See below under Palms.
 (28) *Momordica Charantia*, p. 325.—The arils are included in the weight of the pericarp. Their proportion is shown below where the drying régime of a fruit is given.

	Moist.	Dry.	Loss of Weight.
Fruit-case or pericarp	234 grains	22·5 grains	90·4 per cent.
Arils	62 „	4·0 „	93·6 „
Seeds	38 „	24·5 „	35·6 „
Entire fruit	334 „	51·0 „	84·7 „

- (29) *Monstera pertusa*, p. 326.—Most berries have one seed, but quite 10 per cent. have two seeds.
 (30) *Opuntia Tuna*, p. 325.—See Note 10, B, on p. 478.
 (31) *Oreodoxa regia*, p. 326.—The small shrinkage of the fruit is due to the large quantity of oil in the pericarp.
 (32) PALMS.

- (a) *Areca Catechu*, pp. 26, 326.—There is reason for believing that, as in the Coco-nut, the seed reaches maturity after the pericarp has begun to dry.
 (b) *Arenga saccharifera*, p. 325.—The fruit is characterised as a drupe in the table, but the data there given are based on the view that it is a berry, and so I will take it. The pericarp-proportion is much reduced in 3-seeded fruits, as compared with 1-seeded fruits. Thus:—

Moist fruit, 1-seeded, pericarp-proportion	90 per cent.
„ 3-seeded, „ „	69 „
Dry fruit, 1-seeded, „ „	80 „
„ 3-seeded, „ „	55 „

- (c) *Mauritia setigera*, p. 326.—It would seem that the seed continues to ripen after the pericarp has begun to dry.
 (d) *The tribe Coccoineæ*.—The drying régime and the proportion of parts are represented in the following table for the drupaceous fruits of palms of this tribe.
 Explanatory remarks follow.

		Proportional weight of parts, taking the entire fruit as 100.		Loss of weight stated as a percentage of the weight in the moist condition. The first number refers to the moist state, the second to the dry state, the third is the loss.
		Moist.	Dry.	
<i>Cocos nucifera</i> (Cocunut), 50,000 grains (moist weight)	Husk .	83	57	100 to 20 or 80 per cent.
	Endocarp	6	21	100 ,, 93 ,, 7 ,,
	Seed .	11	22	100 ,, 60 ,, 40 ,,
	Entire .	100	100	100 ,, 29 ,, 71 ,,
<i>Cocos plumosa</i> (100 grains in moist state)	Husk .	56	39.7	100 ,, 45 ,, 55 ,,
	Endocarp	35.6	51.9	100 ,, 92 ,, 8 ,,
	Seed .	8.4	8.4	100 ,, 63 ,, 37 ,,
	Entire .	100.0	100.0	100 ,, 63 ,, 37 ,,
<i>Acrocomia lasiospatha</i> (550 grains in moist state)	Husk .	70	35	100 ,, 18 ,, 82 ,,
	Endocarp	22	50	100 ,, 82 ,, 18 ,,
	Seed .	8	15	100 ,, 68 ,, 32 ,,
	Entire .	100	100	100 ,, 36 ,, 64 ,,
<i>Acrocomia sclerocarpa</i> (200 grains in dry state)	Husk	44	...
	Endocarp	...	45	...
	Seed	11	...
	Entire	100	...
<i>Bactris</i> (species), 170 grains in dry state	Husk	22	...
	Endocarp	...	45	...
	Seed	33	...
	Entire	100	...
<i>Elæis guineensis</i> (120 grains in dry state)	Husk	29	...
	Endocarp	...	56	...
	Seed	15	...
	Entire	100	...

The following explanatory remarks refer to the above table :—

Cocos nucifera.—The data employed here are those given in the table on p. 501 ; and the method of obtaining them is explained in the footnote there appended.

Cocos plumosa.—On account of the hygroscopicity of the husk arising from its large amount of sugars, the drying process is always incomplete. If these substances could be removed by soaking in water, the contrast with the drying process of *Cocos nucifera* would not be so great.

Acrocomia lasiospatha.—Though very good materials were employed, there is some disturbing influence to be looked for in explanation of the rather small shrinkage of the seed and the rather large shrinkage of the endocarp as compared with *Cocos*. This will probably be found in the increase of the oil and the decrease of water in the maturing seed and in the fact that the husk tends to ripen rather before the stone and seed reach their greatest development. The husk of the ripe fruit is full of a mucii-

liginous fluid. The stones of *Acrocomia* are black, very hard, and thick, and are used as ornaments, as in the case of *Aleurites* in the Pacific. In *A. lasiospatha* the stone is 3 to 4 mm. thick, and in *A. sclerocarpa* 4 to 5 mm.

Bactris.—This is a species common at river-mouths in Trinidad. The outer husk is very watery, and probably the fruit will display the régime of the coco-nut.

Elæis guineensis.—A peculiar drying régime is probably displayed on account of the abundant oil in the fruit.

The characteristic drying régime of drupaceous fruits is illustrated in the table by *Cocos nucifera* and *Acrocomia* (see below under *Prunus*). The water in the cavities of the green fruits of this tribe of palms is discussed on p. 414.

- (33) *Poinciana regia*, p. 325.—Owing to the hard woody character of the dry pod there was considerable difficulty in ascertaining the data. A disturbing cause is to be found in the failure of some of the seeds, their place being occupied by ligneous tissue.
- (34) *Primula veris*, pp. 323, 326.—The columella is included in the pericarp-proportion and may be differentiated thus:—

Moist fruit	{	Pericarp proper . . .	17 per cent.
		Columella . . .	29 ”
		Seeds . . .	54 ”
		100	”
Dry fruit	{	Pericarp proper . . .	11 per cent.
		Columella . . .	14 ”
		Seeds . . .	75 ”
		100	”

The régime of the drying fruit, including the columella in the pericarp, is worked out on p. 323.

With regard to the number of seeds in a capsule, the average was placed at 62 for a fruit from the following data:—

Three sets of ten capsules from three	{	540 seeds
different localities . . .		630 ”
		680 ”
		1850
		”

- (35) *Prunus communis* (Sloe), p. 325.—The materials for determining the drying régime of this fruit are given on p. 325, where the

endocarp or putamen is not differentiated. However, highly interesting results declare themselves when we treat the endocarp separately. It will thus be seen that the drying régime of such a typical drupe as that of *Prunus communis* is closely reproduced in that of the drupaceous fruit of *Cocos nucifera*. The proportion of parts in the two types of the drupe differs somewhat, but the drying régimes agree closely.

COMPARISON OF THE DRYING RÉGIMES OF FRUITS OF PRUNUS COMMUNIS AND COCOS NUCIFERA.

		Weight in grains.		Loss of weight.	Relative weight taking the entire fruit as 100.	
		Moist.	Dry.		Moist.	Dry.
Prunus communis (Sloe)	Outer soft coverings	24·9	3·9	84·4 per cent.	83	49
	Endocarp or stone	3·6	3·3		12	41
	Seed	1·5	0·8		5	10
	Entire fruit	30·0	8·0		100	100
Cocos nucifera (Coco-nut)	Husk	42,750	8,550	80·0	83	57
	Endocarp or shell	3,387	3,150	7·0	6	21
	Seed	5,500	3,300	40·0	11	22
	Entire fruit	51,637	15,000	71·0	100	100

As shown on pp. 304-309, the husk, shell, and seed of the Coco-nut do not attain their greatest development at the same time. For purposes of comparison it is here assumed that they all grow together. To obtain these results the proportions given in D column of p. 305 were applied to a dry fruit weighing 15,000 grains; and the proportions of the moist fruit were obtained by then applying the loss-of-weight percentages given on p. 306. The proportional weights of parts in the moist fruit were then worked out to the nearest integer only. The results conform with those given in the tables on p. 305 as far as the different methods employed allow.

The ripe fruits of *Prunus communis* vary considerably in weight on different plants, namely, between 15 and 40 grains, the average weight being from 20 to 30 grains; but my data do not indicate that there is any marked difference in the proportion of parts. However, the tendency displayed is towards an increase in the proportion of the fleshy covering and a decrease in the proportion of the stone or endocarp in the larger fruits, the relative weight of the seed remaining about the same. (See next page.)

As regards the time occupied in drying, about four weeks are required for ordinary drying in a dry room, provided that the skin is pricked in places. With the skin intact the time needed would be considerably longer; whilst under natural conditions in the open air, the complete drying would be probably but rarely

PROPORTION OF PARTS IN MOIST RIPE FRUITS OF PRUNUS COMMUNIS OF DIFFERENT SIZE AND WEIGHT.

	About 35 grains.	About 20 grains.
Flesh, including skin . . .	85 per cent.	82 per cent.
Stone	10 "	13 "
Seed	5 "	5 "
	100 "	100 "

These represent the average results for ten large and ten small fruits.

accomplished. In the case of bared stones kept a year, I found then when split open, and the seed removed, moisture was deposited when the halves of the stone were placed with their inner surfaces downward on the cold brass pan of the balance. This did not, however, occur with the cut surfaces of the seed, such seeds preserving a stable weight when exposed to the air for days, subject only to ordinary hygroscopic variation. There is no doubt, however, that the seed dries through the stone; but the above accidental indication in the pan of the balance led me to think that ultimately the stone becomes impervious and that free moisture is thus locked up in the seed-cavity. However, this idea was disproved by a simple experiment. Of ten stones that had been kept for about two years bared of their flesh, belonging to the same set and possessing about the same weight, five were kept in water for a week and the rest left exposed to the air. At the end of that time it was found that whilst the seeds in the dry stones were dry, a little shrunken, and averaged 1.06 grain in weight, those in the wet stones were moist and swollen and averaged 1.46 grain in weight, the inner surface of the stone being quite moist.

- (36) *Pyrus Malus*, pp. 324, 325. — Another ripe fruit weighing 716 grains and containing 5 seeds (4 grains) gave a pericarp-proportion of 99.4 per cent. in the moist condition.
- (37) *Quercus Robur*, p. 326. — It is not possible to give the exact data for the acorn, as the seed continues its growth after the pericarp has ceased to grow, a matter discussed on p. 309.
- (38) *Ravenala madagascariensis*, p. 325. — The number of seeds refers only to those matured; but the total seed-weight employed in this table includes the aborted seeds, which are much more numerous (see pp. 282, 359).
- (39) *Ribes Grossularia*, p. 325. — See Note 10, A, on p. 477.

(40) *Ricinus communis*, p. 327.—If we differentiate the parts in a dry capsule weighing 12 grains, we obtain the following results:—

Outer shrunken soft spiny covering	. 1.3	grains.
Axis between cocci	0.2 ”
Three cocci	4.5 ”
Three seeds	6.0 ”
	—————	
	12.0	”

(41) *Sambucus nigra*, p. 325.—See p. 266.

(42) *Sparganium ramosum*, p. 325.—The drying régime is such as is found with other drupaceous fruits, as *Prunus*, *Cocos*, etc. (see pp. 499, 501).

	Weight in grains.		Loss of weight.	Relative weight taking the entire fruit as 100.	
	Moist.	Dry.		Moist.	Dry.
Husk	0.56	0.10	82 per cent.	56	22
Endocarp or stone	0.32	0.28	12 ”	32	62
Seed	0.12	0.07	42 ”	12	16
Entire fruit	1.00	0.45	55 ”	100	100

The pericarp-proportion (husk plus endocarp) is here 88 per cent. for the moist fruit, instead of 85, as in the table.

It is in the loss of weight of the respective parts that the drupaceous régime is here illustrated.

(43) *Swietenia Mahogani*, pp. 324, 325.—The placental axis may be thus differentiated from the capsular walls, with which it is included in the drying régime given on p. 324.

Moist fruit	{	Pericarp proper or capsular walls	73 per cent.
		Placental axis or columella	. 12 ”
		Seeds 15 ”
			————— ”
		100	”

Dry fruit	{	Pericarp proper or capsular walls	78 per cent.
		Placental axis or columella	. 11 ”
		Seeds 11 ”
			————— ”
		100	”

(44) *Terminalia Catappa*, p. 327.—A dry fruit weighing 100 grains would be thus constituted :—

Skin and fibro-suberose material	57.5	per cent.
Endocarp	38.0	„
Seed	4.5	„
	100.0	

(45) *Theobroma Cacao*, p. 325.—For very extensive materials supplied to me by Mr Anstead, superintendent of the Botanic Gardens, Grenada, see Note 15 (p. 482).

NOTE 29 (p. 436).

On the growth of the embryo in the drying seed of Crinum.

ONE often finds references to the vivipary of the seeds of *Crinum* ; and in this connection the reader should read what Goebel says on this matter in his *Organography of Plants* (ii. 618). It is noteworthy that this habit is associated with the absence of seed-coats. But the most remarkable feature is not that there is no rest-period, but that the embryo is able to continue its growth uninterruptedly under conditions that generally determine that period. In fact, as in the acorn (see p. 434), germination takes place in the drying seed. This again is not a new fact ; and those who have read Rendle's *Classification of Flowering Plants*, 1904, will remember the figure (after Van Hall) there given (i. 306) of "a dry seed of *Crinum capense* germinating on the edge of a board."

Some moist fleshy seeds of a species of *Crinum*, taken from the plant at the end of December, were allowed to dry on my table in Jamaica. At the end of January I was surprised to find that they had lost only 19 per cent. of their weight. This tardy drying of seeds in such an unprotected state led me to examine one or two of them, when I found that the embryos were much stouter and about double the weight of those in the seeds freshly gathered. On 9th February I packed them away with other seed-collections, and on examining them in England on 2nd April, nearly half of the seeds were germinating. Five weeks of this interval had been passed in the tropics. The other seeds I examined at the end of April, four months after they had been gathered ; and although they had lost 57 per cent. of their original weight and displayed no external signs of germination, the embryos were eight times as heavy and correspondingly larger than when the seeds were collected. Much of the albumen had been assimilated ; but, unable to

pierce the seed's substance, the radicular portion had bent down and continued its growth within. The results are given in the table at the end of this note.

The loss of weight during the four months amounted, as above indicated, to rather over half of the seed's original weight. When first obtained the seeds were almost saturated with water, one of them, when placed in water for some days, increasing its weight by only $1\frac{1}{2}$ per cent. The embryo contains much more water in the freshly gathered seed than when growing in the air-drying seed. Thus, in the fresh state, when weighing 1 grain and less, it lost about 74 per cent of its weight whilst drying naturally in the air in the detached condition. Some weeks afterwards, when its weight was increased to 2 grains and its size proportionately augmented, it lost 65 per cent.; and four months from the date of gathering, when it had added another 6 grains to its weight and had increased its size tenfold, it lost about 50 per cent.

The interesting point is that the embryo continues its growth whilst sharing in the general drying of the detached seed. In the fresh seed it is moist, fleshy, and delicate in texture. After growing in the drying seed it is firm, solid, and drier.

Cases like those of *Crinum* and the acorn (p. 434), where germination can take place in a drying seed, seem at first sight to militate

TABLE ILLUSTRATING THE GROWTH OF THE WEIGHT OF THE EMBRYO OF CRINUM WITHIN THE DRYING SEED. (For further explanation see text.)

Detached seed.	Total weight of seed.	Weight of embryo.	Relative weight of the embryo to the seed.	Loss of weight of embryo when detached and air-dried.	Size of embryo in millimetres.	Condition of embryo.
Fresh seed	120 grains	1 grain	0·8 per cent.	74 per cent.	15 × 2·5 × 2·5	Moist, fleshy, delicate in texture.
The same a month later	97 „	2·0 grains	2·1 „	65 „	17 × 4 × 4	...
The same after another three months.	51 „	8·5 „	16·7 „	50 „	35 × 5 × 5	Firm, solid, and drier.

The seed is much wrinkled at the end of the experiment, its length being reduced from 33 to 27 mm., so that it is now considerably shorter than the embryo, which adapts itself by flexing as it grows.

against the view that seeds must absorb a certain quantity of water in order to germinate. But the minimum amount of water requisite, as dealt with on p. 43, is the water needed to start the germinating process in a resting seed after a period of complete repose. The seeds of *Crinum* and the acorn never actually enter upon the rest-period. Accordingly the quantity of water requisite to sustain the growing process would, it is likely, be far less than the amount needed to rekindle the vital activity of a resting seed. This is consistent with the familiar principle that it takes more energy to start a machine than to keep it going.

From the above table it is to be inferred that whilst the seed in its entirety lost 57 per cent. of its weight during these four months, the embryo increased its weight $8\frac{1}{2}$ times. We also perceive that this change was accompanied by corresponding changes in the size of the embryo, and that notwithstanding its growth it participated in the drying of the seed. As the embryo grew in the drying seed the proportion of its water-contents decreased.

Correction.—For “ten or fifteenfold” in the *Crinum* paragraph on p. 436, read “nine or tenfold.”

NOTE 30 (p. 448).

The conditions for flowering.

THERE is much to support the view that the vegetative mode of reproduction in plants is based on purely terrestrial necessities and that the flowering and seeding stage represents the plant's effort to return to its general cosmic habit. When Schimper remarked that the correlation between the production of flowers and the seasons of the year is an adaptation to external factors on the part of physiologically necessary processes, and that this dependence in the reproductive domain is a secondary feature (*Plant Geography*, p. 252), he opened up this question. When also he observed that the cardinal degrees for the growth—and perhaps for the inception—of the primordia of flowers are often much lower than for the growth of vegetative shoots, so that the former are favoured by a relatively lower temperature, and the latter by a higher temperature, during development (p. 48), he showed clearly in which direction the inquiry lay. Warmth, shade, moisture, and a rich soil favour, as we may infer, the vegetative growth of a plant, and retard the flowering process. The association between water and reproduction is specially discussed by Schimper (p. 26); and he points out how highly instructive is the behaviour of aquatic plants derived from terrestrial forms, which, whilst accom-

modating themselves to water as regards their vegetative activity, remain with few exceptions subaerial plants as regards sexual reproduction.

A more recent contribution to this subject is to be found in a paper by Professor Klebs on the influence of environment on the forms of plants in *Darwin and Modern Science* (1910). The circumstances favourable to growth, he remarks, differ from those which promote reproduction. As he shows, the behaviour of a plant can be determined at will by increasing or decreasing the supply of water and mineral salts. In the first case, as in the ordinary treatment with manure and abundant water, there is a relative diminution in the production of organic substances, such as starch, sugars, etc., which favours vegetative growth at the expense of the flowering process. If, however, the supply of water and salts is diminished, as when the plant grows under ordinary poor conditions, a vigorous production of organic substances follows and flowering results.

In this connection I may refer to the behaviour of the Sweet Potato (*Convolvulus Batatas*), which rarely seeds except when grown in poor, sandy soil, and in dry, rocky situations. The Fijians, I found, were quite incredulous as to its maturing seed; but after much searching I found a solitary plant in seed and so relieved their doubts. Similarly, the coloured people of the Turks Islands in the West Indies were surprised when I showed them the seed from their own plants. In the arid, sandy soil of those islands I found the plant seeding freely.

NOTE 31 (see previous note).

Growing Stakes or Live-Fences in Jamaica.

NUMEROUS trees supply the Jamaicans with materials for living posts for the wire-fences. These posts are employed to take the place of the dead-wood posts of logwood. Limbs of such trees cut to a length of from 4 to 6 feet are placed in the ground, and in a few weeks they strike root and produce young leaves.

Several of them belong to the Terebinthaceæ, such as the Hog-plum (*Spondias lutea*), the Sweet-plum (*Spondias purpurea*), the Maiden-plum (*Comocladia integrifolia*), and the Birch (*Bursera gummifera*). Amongst other trees thus utilised may be mentioned the Cedar (*Cedrela odorata*), one of the Meliaceæ, the Calabash-tree (*Crescentia Cujete*), of the Cucurbitaceæ, the Cocoa-plum (*Chrysobalanus Icacó*), of the Chrysobalanæ, and the Physic-nut (*Jatropha Curcas*), of the Euphorbiaceæ. Amongst the Leguminosæ thus employed are the Sword-plant, a species of *Erythrina* (perhaps *E. corallodendron*), and the Cuba-plum, which may

be a species of *Andira*. A tree named the Hog-doctor, perhaps the terebinthaceous *Rhus Metopium*, supplies yam-sticks for trailing yams, the sticks soon rooting and producing leaves.

Several other Jamaican plants exhibit the same quality. Thus the malvaceous tree, *Paritium elatum*, is said to grow from branches stuck in the ground, whilst the Dagger-plant (*Yucca aloifolia*) readily strikes into the ground again when it is cut down. This not infrequently occurs with some of the trees above mentioned. Thus on one occasion I noticed that a tree of *Cedrela odorata*, which had been lying on the ground for some time after being cut down, was sending up shoots.

When in Fiji I found that the natives used the branches of *Barringtonia racemosa* in constructing live-fences. When stuck in wet soil they soon develop roots and foliage. Other trees are credited by the natives with the same capacity, such as *Thespesia populnea* and *Hibiscus tiliaceus*.

NOTE 32 (p. 12).

Twist Coco-nuts.

THIS name is applied by the Tobago natives to dry nuts where the kernel is loose and shakes when the fruit is handled. This may be normal in many palms, as it is in *Acrocomia* of the same tribe; but with the coco-nut it is the exception. I regard the peculiarity as exhibiting the tendency of the seed to enter upon a rest-period, the persistent vital connection between the seed and the pericarp being a requisite condition for true vivipary, as in *Rhizophora*.

In such fruits, when broken open, the loose kernel comes out readily, looking in its brown skin much like a huge Brazil-nut. When the kernel is cut across, it proves to be without water in its central cavity, is perhaps thicker than usual, though this is not always the case, and contains a sound normal embryo. Mr H. Matthes, a planter of "Bacolet," Tobago, kindly gave me the following particulars.

Taken at random, out of a heap of coco-nuts about 1 or 2 per cent. would display this character. Out of 1000 trees in one locality 10 produced these fruits. Generally a tree produces only twist-nuts, with occasionally a few normal fruits. Of these ten trees all but one stood in imperfectly drained situations, where water was apt to accumulate in the rainy season; and to this cause he is inclined to attribute their behaviour in this respect. This results in the retention of the fruit on the palm, such nuts seldom dropping from the tree, but undergoing all their shrinkage attached to the parent. When compared

with normal dry fruits, twist-nuts have a wrinkled appearance. These nuts, he says, never germinate, the kernel being always dry, but not thicker than the normal.

NOTE 33.

TABLE ILLUSTRATING IN THE CASE OF *ENTADA SCANDENS* THE METHOD OF DETERMINING THE WATER AND SOLID CONSTITUENTS IN THE PRE-RESTING, RESTING, AND SWOLLEN STAGES FOR A NUMBER OF SEEDS, FOR WHICH THE REQUISITE DATA ARE GIVEN ON PAGES 200, 201 FOR THE SHRINKING AND SWELLING RÉGIMES, AND ON PAGES 135 TO 137 FOR THE WATER-CONTENTS OF THE RESTING SEED.

The data required, taking *Entada scandens* as an example, are the weight of the resting seed (400 grains), the shrinking and swelling ratio (2.5), the proportional weights of coats and kernel in each of the three stages, and the water-contents of the coats and kernel of the resting seed, as determined by exposure to a temperature of 100° C.

Condition of seed.	Parts.	Weight in grains.					Percentages.	
		Total weight.	Solids.	Water in the resting seed (water of hygroscopicity).	Water lost in the shrinking process (water of vitality).	Water absorbed in the swelling process.	Solids.	Water.
Resting seed	Coats .	156	133.4	22.6	85.5	14.5
	Kernel .	244	224.5	19.5	92.0	8.0
	Entire seed	400	357.9	42.1	89.5	10.5
Pre-resting seed	Coats .	460	133.4	22.6	304	...	29.0	71.0
	Kernel .	540	224.5	19.5	296	...	41.6	58.4
	Entire seed	1000	357.9	42.1	600	...	35.8	64.2
Seed swollen for germination	Coats .	310	133.4	22.6	...	154	43.0	57.0
	Kernel .	690	224.5	19.5	...	446	32.5	67.5
	Entire seed	1000	357.9	42.1	...	600	35.8	64.2

The shrinking and swelling ratios are taken as the same, viz. 2.5, since one is sometimes a little larger and sometimes a little smaller than the other; and it would be arbitrary to make a distinction, more especially as all the other data are based on average results.

All the materials above given are worked out from the data given in the tables on pp. 135 and 202. Results for a considerable number of other seeds can be obtained in the same manner by utilising the data given in the table on p. 200 for determining the shrinking and

swelling régime, and by employing the water-percentages given in the table on pp. 135 to 137.

The results above given for *Entada scandens* clearly illustrate the principle laid down for leguminous seeds on pp. 202 and 203 that during the swelling of a resting seed the coats take up less water and the kernel more water than was lost in the shrinking process. In this case we see that the coats only regained half of their loss, whilst the kernel regained all and about 50 per cent. in addition.

However, the principal importance of this table lies in its illustration of the method of determining for all three conditions of the seed (pre-resting, resting, and swollen for germination) the absolute and relative quantities of the water and solids, not only for the entire seeds, but for its separate parts (coats and kernel) in all three stages.

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Note.—Many matters are worked up in this index which on account of the plan of the book could not be treated connectedly in the text. The reader is therefore advised to bear this in mind when consulting these pages.

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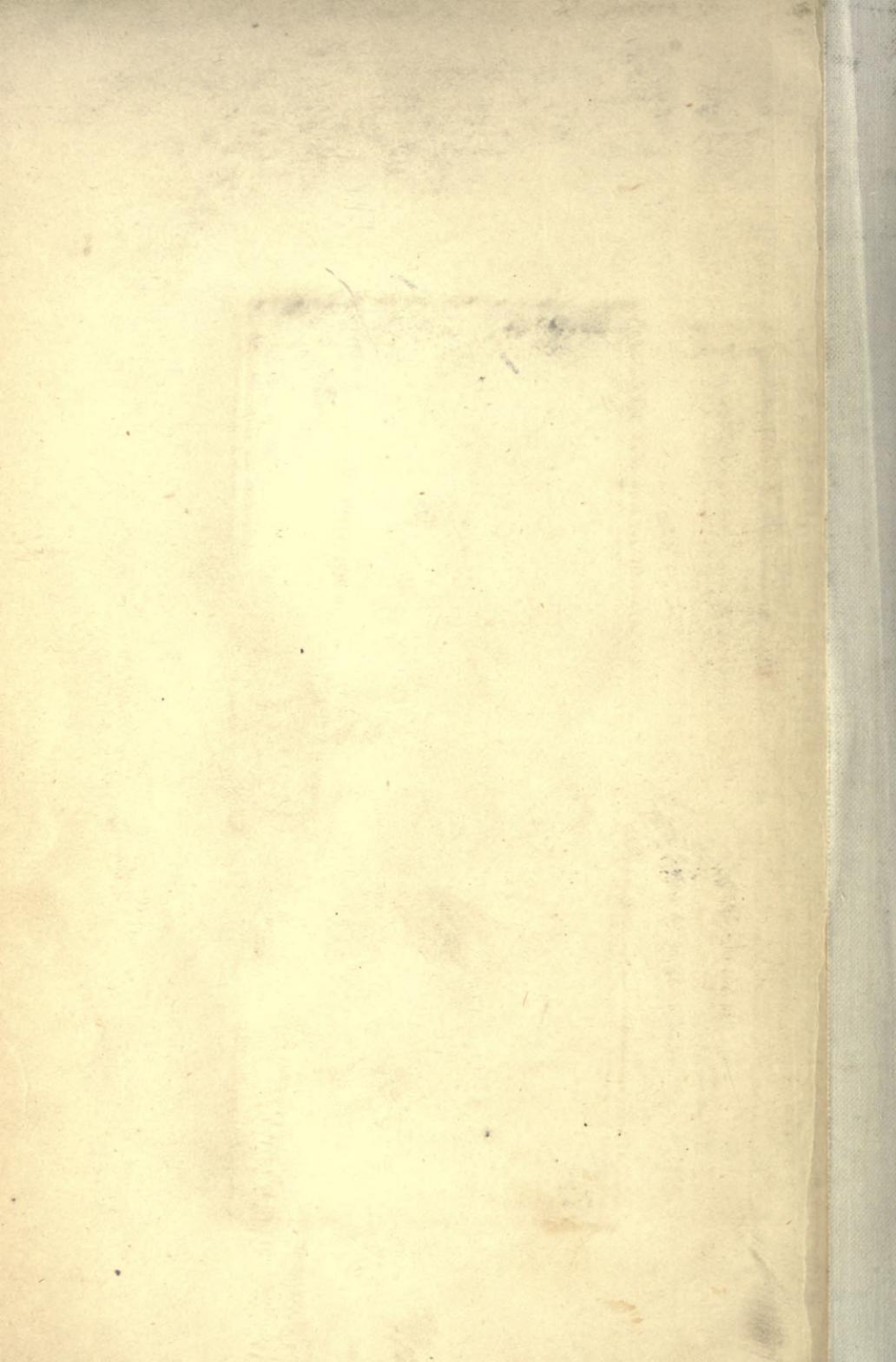
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Note.—See under Albuminous Seeds in index. Much importance attaches to the discovery by Dr Stapf of four species of bamboos with exalbuminous seeds, one of them viviparous. (*Nature*, May 17, 1906.)



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