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# THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION  
OF ECONOMIC BIOLOGISTS

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PHYSIOLOGICAL PRE-DETERMINATION<sup>1</sup>: THE INFLUENCE OF THE PHYSIOLOGICAL CONDITION OF THE SEED UPON THE COURSE OF SUBSEQUENT GROWTH AND UPON THE YIELD.

I. THE EFFECTS OF SOAKING SEEDS IN WATER.

By FRANKLIN KIDD, M.A. (CANTAB.), D.SC. (LOND.)

AND

CYRIL WEST, D.SC. (LOND.), F.L.S.

(With Plates I and II.)

INTRODUCTION.

In a survey of the literature of the last fifty years dealing with the Seed it is interesting to note that attention has been almost entirely concentrated upon the question of germination. The effect upon germination of every manner of treatment and of every sort of condition has been investigated in the case of the seeds of a great range of cultivated and wild plants.

In only a very few cases has attention been directed upon the question suggested by the title of this paper, namely, as to how far the physiological condition of the plant in the seed-stage (*i.e.* in maturation, dormancy and germination) may exert a pre-determining influence upon the whole subsequent course of growth and development. It is obvious from the point of view of crop production that this question as to the quality and size of the plants produced from any sample of seed may be even more important than the question as to what percentage of the sample is capable of germination. The degree of importance to be attached to this question appears when it is said that the yield from an equal number of plants of a pure line may vary to an extent of 50 per

<sup>1</sup> Balls, L. W. 'The Pre-Determination of Fluctuating Characteristics,' *Proc. Cambridge Phil. Soc.*, 1914; also, 'Analyses of Agricultural Yield,' Part III; 'The Influence of Natural Environmental Factors upon the Yield of Egyptian Cotton,' *Phil. Trans. Roy. Soc. (Lond.)*, B, 208, 1917.

cent., or even more, owing to the pre-determining influence upon the resultant plant of the physiological condition of the seed as effected by environmental conditions both previous to and also during germination.

The plant physiological problem which we are raising and with which we propose to deal in this and in following papers under the same general title, may be stated formally at the outset as follows: Presuming always a given equal number of plants, what are the limits of variation in growth and yield which may be pre-determined by the action of environmental conditions during the seed stage both previous to and during the course of germination; and how far may later environmental conditions during the course of growth affect the latitude of such variation?

The experimental work conducted by the authors dealing with the problem thus outlined is in progress. The present paper deals with the first results of experiments designed to test the effect of preliminary soaking of the seed upon its subsequent growth and development<sup>1</sup>.

In the next paper of this series the literature bearing directly or indirectly upon the subject will be reviewed. This review will clearly indicate the wideness of the field and the possibility of obtaining important results if experimental work on a sufficiently large scale be carried out both in the field and in the laboratory.

The stage of germination is obviously a very critical one in the life-history of the plant. By artificial control of the environmental conditions of the seed previous to and during the process of germination the cultivator may aim not only at the natural optimum, that is the yield produced by good seed under the most favourable conditions, but may even improve upon this.

#### EXPERIMENTAL.

##### *Experiment 1. Seeds sown on damp sand.*

Seeds of the following plants were used in this experiment, viz. culinary pea (*Pisum sativum*), dwarf bean (*Phaseolus vulgaris*), barley (*Hordeum*), and sunflower (*Helianthus annuus*). The seeds were soaked under 4 cm. of distilled water at an average temperature of 17° C. (*i.e.* the temperature of the laboratory) for periods varying from 8 to 72 hours and the result of this treatment upon the germination (Table I) and upon the subsequent growth of the same seeds (Table II) was observed. In this experiment both germination and growth occurred with the seed lying on damp sand in porous pots surrounded with water and loosely covered with glass.

<sup>1</sup> The experiments described in this paper were carried out during the autumn of 1917.

TABLE I. *Germination results.*

Name of plant	Number of seeds used	Germinations									
		2 days after sowing. Previously soaked					3 days after sowing. Previously soaked				
		0 hrs	8 hrs	24 hrs	48 hrs	72 hrs	0 hrs	8 hrs	24 hrs	48 hrs	72 hrs
<i>Pisum</i>	25	0	15	23	17	11	7	22	24	22	16
<i>Phaseolus</i>	25	0	18	18	8	5	10	24	23	15	5
<i>Hordeum</i>	50	31	48	43	41	26	46	49	48	49	37
<i>Helianthus</i>	25	11	14	10	10	6	22	20	15	21	10

The above table shows that soaking the seeds for periods exceeding 24 hours in general diminishes the rate of germination.

TABLE II. *Growth results.*

Name of plant	Hours soaked	No. of seeds	No. of plants	Average length of	
				After 12 days on damp sand at 17° C.	
				stem	root
<i>Pisum</i>	0	25	25	7.2 cm.	11.0 cm.
	8	25	23	7.0	8.2
	24	25	24	7.5	5.9
	48	25	18	3.0	2.0
	72	25	17	2.2	1.6
<i>Phaseolus</i>	0	25	23	6.4	7.4
	8	25	19	3.5	3.7
	24	25	15	1.3	1.1
	48	25	1 (very feeble)	—	—
	72	25	0	—	—
<i>Hordeum</i>	0	50	50	Dry weight (tops only)	
	8	50	50	0.555 g.	
	24	50	44	0.510	
	48	50	50	0.455	
	72	50	41	0.395	

*Pisum.* The soaking of seeds of *Pisum sativum* previous to sowing has a marked effect upon the subsequent course and vigour of development. The number of plants produced is not affected by soaking the seeds for periods of less than 24 hours. The retarding effect, however, upon the subsequent growth shows itself in the case of the roots of plants produced from seeds soaked even for the short period of 8 hours. After 48 hours soaking of the seed it is very marked. The size of the shoots is not greatly affected unless the period of soaking has exceeded 24 hours.

*Phaseolus*. In the case of *Phaseolus*, soaking the seeds previous to germination has an even more marked effect upon the subsequent course and vigour of development. Soaking for only 8 hours reduces the total growth after 12 days to 7.2 cm. as compared with 13.8 cm. for those sown dry on damp sand in spite of the fact that those which were soaked had a considerable start in germination and sprouted earlier.

The second point of importance brought out by these experiments is that the striking effects of soaking the seed upon its subsequent development are not visible in first observations upon germination. For instance, the seeds soaked for 24 hours showed a full percentage of germination and at first the radicles of these seeds appeared to be the largest and strongest of the whole series. At this stage the seedlings were such as would obviously be selected for physiological experiments, for example, on the rate of growth as influenced by temperature, etc. Nevertheless, on the twelfth day of the experiment half these plants had died and the remainder showed only about one-sixth of the growth of those plants which had arisen from seeds not soaked previous to sowing.

*Hordeum*. There is a progressive decrease in dry weight with time of soaking of seeds previous to sowing. The seeds, which had not been soaked at all, gave rise to the heaviest plants after 12 days in spite of the fact that during the first 4 or 5 days they were obviously behind the others owing to their slower germination.

#### *Experiment 2. Seeds sown in soil.*

In this experiment the following seeds were used:

- Wheat (Sutton's, Sept. 1917),
- Oats (Sutton's, Sept. 1917),
- White Mustard [*Brassica alba*] (Carter's, Sept. 1917),
- Dwarf Bean [*Phaseolus vulgaris*] (Sutton's, Sept. 1917),
- Broad Bean [*Vicia Faba*] (Carter's, Nov. 1916),
- White Lupin (Carter's, March, 1916).

Samples of the above-mentioned seeds were soaked for the following periods, 6, 24, 48 and 72 hours respectively under conditions similar to those of the previous experiment. They were then sown in potting soil in a greenhouse with an average temperature of 65° F., and were transferred to a greenhouse with an average temperature of 55° F. as follows: White Mustard after 4 days, Wheat and Oats after 5 days, Lupins after 7 days, Dwarf Beans and Broad Beans after 9 days.

The results obtained after 7 days are given in the following table:

TABLE III. *Germination results.*

Name of plant	Number of seeds used	Germination results	Seed soaked previous to sowing				
			0 hours	6 hours	24 hours	48 hours	72 hours
Wheat	100	}	Average height of seedlings 3 cm.	Average height of seedlings 3 cm.	Average height of seedlings 5 cm.	Average height of seedlings 5 cm.	Average height of seedlings 5 cm.
Oats	100		Few just sprouting	Average height 2 cm.	Average height 2 cm.	Average height 5 cm.	Average height 1 cm.
White Mustard	100		Average height 4 cm.	Average height 6 cm.	Average height 5 cm.	Average height 5.5 cm.	Average height 5 cm.
Dwarf Bean	25		0 showing above ground	4 showing above ground	1 showing above ground	0 showing above ground	0 showing above ground
Broad Bean	10		0 showing above ground	0 showing above ground	5 showing above ground	4 showing above ground	3 showing above ground
White Lupin	25		3 showing above ground	18 showing above ground	25 showing above ground	25 showing above ground	19 showing above ground

The results showing the effect of the various periods of soaking are given under separate headings for each crop.

*Wheat.* The five cultures were photographed after 4 weeks' growth (Pl. I, fig. 1) and showed a progressive increase in height from No. 0 (seed not soaked previous to sowing) to No. 2 (seed soaked 48 hours previous to sowing), but in No. 3 (seed soaked 72 hours) the plants were smaller than those in No. 2 and were obviously less vigorous. When the dry weight of the tops was taken (Table IV) the results confirmed this observation. The dry weight of the plants from seeds soaked for 48 hours was approximately 10 per cent. greater than that of the plants from seeds sown dry.

It appears also that the period of soaking bears no relation to the percentage of germination.

TABLE IV. *Growth results.*

WHEAT			
No. on Plate-fig.	Hours soaked	No. of germinations	Dry weight per 100 seedlings (tops only) after 5 weeks' growth
0	0	94	2.148 g.
1	6	92	2.065
1	24	96	2.119
2	48	95	<b>2.369</b>
3	72	97	2.206

*Physiological Pre-determination*

*Oats.* The oats were harvested 3 weeks after sowing. They show a result similar to that of the wheat. The number of germinations is not influenced by the period of soaking, but the dry weight of the seedlings from seeds soaked for 48 hours is 62 per cent. greater than that of the seedlings produced from seeds sown dry.

TABLE V. *Growth results.*

OATS		
Hours soaked	No. of germinations	Dry weight per 100 seedlings (tops only) after 3 weeks' growth
0	97	0.665 g.
6	96	0.966
24	95	0.954
48	99	<b>1.075</b>
72	96	0.833

*White Mustard.* The white mustard was harvested after a fortnight's growth. In this case the plants giving the highest dry weight were those from seed soaked six hours. The others form a graded series. The plants from the seeds soaked for 6 hours are about 25 per cent. heavier, but those from seed soaked for 72 hours are about 8 per cent. lighter than those produced from the dry seed. The number of germinations is apparently not affected by the soaking treatment.

TABLE VI. *Growth results.*

WHITE MUSTARD		
Hours soaked	No. of germinations	Dry weight per 100 seedlings (tops only) after 14 days' growth
0	96	0.535 g.
6	88	<b>0.657</b>
24	93	0.577
48	77	0.571
72	100	0.479

*Dwarf Beans (Phaseolus).* These plants were harvested 4½ weeks after sowing. Figs. 2 and 3, Plate I, show the appearance of the series at the time of harvesting. As in the previous experiment, even the shortest period of soaking (*i.e.* 6 hours) has a marked pre-determining influence in retarding growth in the course of later development to the extent of 26 per cent. as compared with the plants produced from seed sown dry, although both the number of germinations and the number of plants resulting are not affected. Preliminary soaking of the seed for 1 day

exercises a retarding influence upon the growth of the plants produced after a month's development to the extent of nearly 60 per cent. Longer periods of soaking has an even greater effect, whilst soaking for three days kills all the seed.

TABLE VII. *Growth results.*

DWARF BEAN		
Hours soaked	No. of germinations resulting in plants	Dry weight per 100 seedlings (tops only) after 4½ weeks' growth
0	22	27·41 g.
6	23	20·41
24	6	11·42
48	7	9·63

*Broad Beans (Vicia Faba).* Observations on the effect of the soaking treatment of the seed upon the subsequent development of the plant were made three weeks after sowing. The small number of these larger seeds used in the experiment does not allow us to place so much value on the results obtained. Those sown dry and those sown after only six hours' soaking did not complete their germination and moreover, the plants produced from the seeds which did completely germinate were very poor compared with those from seeds soaked 24, 48 and 72 hours respectively. The interest lies in the fact that a diametrically opposite result of soaking the seed appears in the subsequent growth of this variety of bean as compared with that obtained with the Dwarf Bean (cf. Table VIII with Table VII).

TABLE VIII. *Growth results.*

BROAD BEAN		
Hours soaked	No. of plants produced after 3 weeks in soil	Average height of plants after 3 weeks' growth in soil
0	7	4 cm.
6	4	3·5
24	10	8·4
48	10	8·4
72	10	10·4

*White Lupin.* In every member of the series the plants showed very uneven growth, but the effect, if any, of the soaking treatment of the seed upon the plants produced was not apparent to the eye.

*Physiological Pre-determination**Experiment 3. Effect of Temperature during soaking period.*

In this experiment the influence of the temperature obtaining during the period of soaking upon the degree and nature of the pre-determining influence of soaking upon subsequent growth and development was investigated.

25 seeds of Dwarf Bean (*Phaseolus vulgaris*) (Sutton's, Sept. 1917) were used in each experiment.

The seeds were soaked in distilled water for periods of 6, 24, 48 and 72 hours respectively at four different temperatures, viz.:

1. 10° C. (average)	}	In the dark.
2. 20°		
3. 25°		
4. 30°		

After the soaking treatment the seeds were sown in good potting soil in large wooden boxes which were placed in a greenhouse with an average temperature of 55° F.

The following table gives the results obtained when the beans were harvested 3 weeks after sowing:

TABLE IX. *Germination and growth results.*

DWARF BEANS				
Hours soaked	Dry weights per 100 plants produced from seeds soaked at			
	10° C.	20° C.	25° C.	30° C.
0	(24) 23·27 g.	(24) 23·27 g.	(24) 23·27 g.	(24) 23·27 g.
6	(10) 21·34	(16) 21·47	(17) <b>22·17</b>	(20) 21·74
24	(9) 20·05	(12) <b>21·04</b>	(18) 20·33	(16) 19·18
48	(8) 13·92	(15) <b>17·93</b>	(20) 16·28	(13) 11·54
72	(15) <b>17·80</b>	(16) 16·28	(12) 12·26	(0) —

The figures in brackets denote the number of plants produced.

The most obvious result of this experiment is that a deleterious effect is visible even after the shortest period of soaking (*i.e.* 6 hours) and that this deleterious effect progressively increases with longer periods of soaking at all temperatures.

The second result of importance from an economic point of view is that the temperature during the soaking treatment especially for the shorter periods does not have any *marked* effect upon the figures for the dry weight per plant.

Upon the number of germinations, however, and consequently, upon

the net yield, the effect of temperature during the period of soaking is most striking as is shown by the following table:

TABLE X. *Germination and growth results.*

Period of soaking	Temperature during the soaking treatment	Total No. of germinations	Actual dry weights of the plants produced	Dry weights per 100 plants
1 day	10° C.	9	1.805 g.	20.05 g.
1 day	20° C.	12	2.525	21.04
1 day	25° C.	18	3.660	20.33
1 day	30° C.	16	3.070	19.18

Considering these results from a plant-physiological point of view, it is curious to note that we do not obtain the simple result which might have been expected, namely, that both number of germinations and yield per plant should fall off, with increasing time of soaking, most gradually at low temperatures and most rapidly at high temperatures; in other words, we might have expected the highest values for plant weight and number of germinations at the lowest temperature for any given time of soaking. In Table IX the highest figures obtained for any given time of soaking are printed in heavy type and show at a glance that this is not the case.

*Experiment 4. Seeds sown on damp sand.*

In Figs. 4 and 5 (Plate II) the results of further experiments with another variety of Dwarf Bean are shown. In these cases a much longer subsequent growth period (*i.e.* 8–10 weeks) was allowed. The difference in the results from seeds sown dry (Figs. 4 A and 5 A) and seeds which had been soaked for 12 hours previous to sowing (Figs. 4 B and 5 B) is very marked.

Removal of the testas before soaking apparently has no effect upon the results of the soaking treatment (Figs. 5 A and 5 B).

DISCUSSION AND SUMMARY.

Three main conclusions may be drawn from the results obtained from the experiments described in this communication, although these were not carried through to the final stages of development of the various plants concerned. In the first place, soaking the seed in distilled water previous to sowing may have a marked effect upon the subsequent growth of the plant. In the second place, a germination test cannot be relied upon in the least to give any criterion of what this effect may be. And thirdly, the nature of the effect is strongly specific, quite different

results being obtained by similar treatment upon closely allied plants. Beans, which give the most striking results, illustrate these three points effectively.

Firstly, the result of soaking Dwarf Beans (*Phaseolus vulgaris*) even for a period of 6 hours becomes evident after a month's growth by a decrease in the dry weight yield of the tops of the plants of 26 per cent. as compared with the control crop produced from seeds planted dry (Exp. 2). Secondly, seeds of the same species, which were soaked for a period of 24 hours before sowing, showed by far the most rapid and vigorous germination (Exp. 1), while later, 12 days after sowing, the total length of these plants as compared with the controls set dry was as 2.4 : 13.8. Lastly, when the results obtained with the Broad Bean (*Vicia Faba*) are compared with the above (Exp. 2), an absolute reversal in the effects following soaking is observed. In the case of the Broad Bean the effect of soaking the seeds for periods up to 3 days was found to be increasingly beneficial, not only on the percentage of germination, but also upon the size of the plant produced. Thus, after an interval of 3 weeks the average height of the plants produced from seeds planted dry was only 4 cm. as compared with 10.4 cm. in the case of those soaked for 3 days before sowing.

The thanks of the authors are due to Mr W. Hales, A.L.S., Curator of the Chelsea Physic Gardens, for assistance in the culture of the seedlings.

## EXPLANATION OF PLATE FIGURES.

### PLATE I

- Fig. 1. Wheat plants from seeds sown dry (0), soaked in water previous to sowing for periods of 6 hours ( $\frac{1}{4}$ ), 24 hours (1), 48 hours (2), and 72 hours (3) respectively. Photographed 4 weeks after sowing.
- Fig. 2. Dwarf bean plants from seeds sown dry (0), soaked in water previous to sowing for periods of 6 hours ( $\frac{1}{4}$ ), 24 hours (1), and 48 hours (2) respectively. Photographed  $4\frac{1}{2}$  weeks after sowing.
- Fig. 3. A parallel series to that shown in Fig. 2. Photographed  $4\frac{1}{2}$  weeks after sowing.

### PLATE II

- Fig. 4. A. Dwarf bean plants from seeds sown dry.  
B. Dwarf bean plants from seeds soaked for 12 hours previous to sowing. Photographed 8 weeks after sowing.
- Fig. 5. A. Dwarf bean plants from seeds sown dry. The testas were removed.  
B. Dwarf bean plants from seeds soaked for 12 hours previous to sowing. The testas were removed previous to the soaking treatment. Photographed 8 weeks after sowing



Fig. 1



Fig. 2



Fig. 3

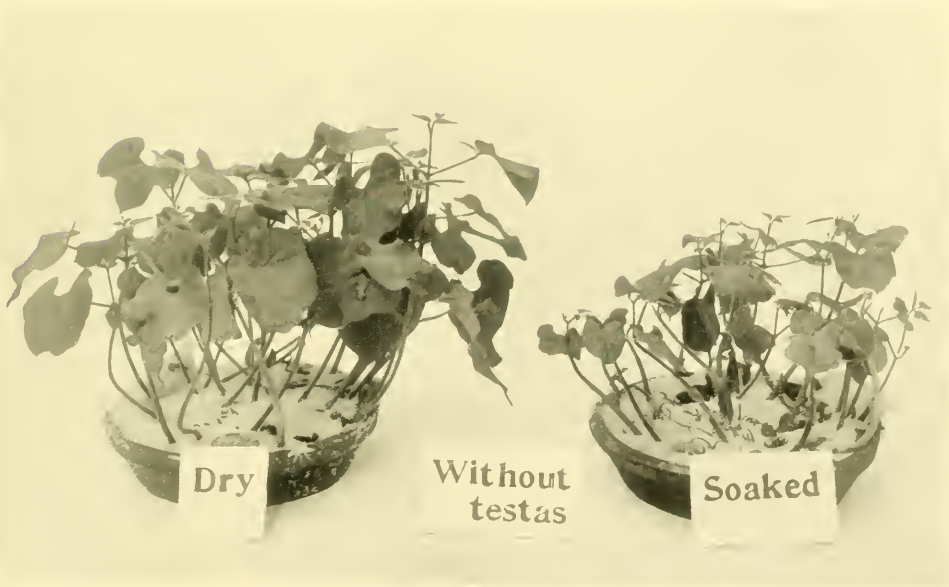




A

Fig. 4

B



A

Fig. 5

B



## “REVERSION” AND RESISTANCE TO “BIG BUD” IN BLACK CURRANTS.

BY A. H. LEES, M.A.

(*Plant Pathologist, Agricultural and Horticultural Research Station,  
Long Ashton, Bristol.*)

(With Plates III—VI.)

IN this paper owing to the apparently close connection between Reversion and Big Bud it is proposed to treat the two subjects together. It seems impossible to explain Reversion without discussing Big Bud and special cases of the latter necessitate for their explanation and therefore for the explanation of certain cases of Reversion, reference to the factors governing resistance to Mite attack.

For these reasons it has been necessary to combine in one paper material that would otherwise have been better suited for two.

### REVERSION.

This disease is known under various names, such as “Going wild,” “Running off,” “Nettle leaf” and possibly others. “Reversion” seems now to be the commonly accepted name and, being so, is used here. The name of course implies that the plant is reverting to the wild type. Scientifically the idea is extremely improbable and there is nothing to show from the observed facts that such a process has been or is going on. For lack of a better name however the term reversion will be used in this paper.

### CHARACTERISTICS OF THE DISEASE.

In a fully reverted bush the following points may be observed.

(1) The fruit “runs off”; that is, at picking time either no berries are found on the strig or only a very few generally undersized fruits instead of the many plump ones of the normal bush. These few berries may be at the base or at the tip of the strig.

(2) There is an extensive growth of the laterals resulting in a crowded, instead of an open, form of bush.

(3) The internodes are abnormally long and thin.

(4) The leaf is sharp pointed, abnormally narrow, with a more than usually serrate margin.

While in badly attacked bushes all these points may be observed at once it is much more common to find only some of them.

The disease is nearly always gradual in its appearance and frequently parts of a bush will show signs while the rest is quite healthy. Until the eye becomes trained it is easy to pass over bushes which are only beginning to revert.

While from the practical point of view the failure of the fruit is undoubtedly the most important point it is not in the author's opinion the most crucial for the elucidation of the disease. If the theoretical explanations afterwards to be considered are correct it is clear that the extensive outgrowth of lateral wood precedes the running off in point of time and may serve to explain the latter. In discussing the disease therefore and its association with Big Bud or otherwise the facts will be considered as affecting the outgrowth of laterals and not the failure of the fruit.

#### CHARACTER OF THE NORMAL GROWTH IN THE BLACK CURRANT.

For a correct interpretation of the pathological condition it is necessary to have a correct conception of the normal, and therefore no apology is needed for a description of what is perhaps already familiar to most.

A strong healthy twig of the current year's growth shows the following arrangement of buds in winter.

The lowest buds are generally weak and are often wood buds, that is buds having one single growing point surrounded by rudimentary leaves. The rest of the buds up to the terminal are flower buds. They vary in strength but all show the same structure. They consist of a median flower rudiment, made from the typical growing point present early in the summer, and two accessory, weak growing points.

The terminal bud is a typical but strong wood bud.

In the subsequent year growth takes place as follows (Pl. III, Fig. 1). A strong wood growth issues from the terminal bud forming the fruiting wood for the following year and the flower rudiments in the lateral buds unfold and bear fruit. One or both accessory growing points present in the fruit bud make a short spur-like growth and form fruit buds to give fruit the following season.

The wood buds at the base of the winter shoot remain dormant, make



Fig. 1. Whole of last year's growth and base of current year's in a normal shoot from Long Ashton. Most of the flower buds of last year have made a spur-like growth from the accessory growing points. Note absence of development of top buds of the last year's growth due to their original weakness as shown in Graphs I and II.



Fig. 2. "Oak Leaf" caused by mite attack on a strong growing terminal bud.



Fig. 3. A normal leaf, broad and blunt, and a "reverted" leaf, narrow and pointed.



Fig. 4. Normal leaves formed at the end of the season. They are smaller and more divided than the leaf formed during active growth.



a short or a strong growth depending on the vigour of the bush as a whole. Usually they remain dormant or make a short growth.

The normal growth of the black currant may therefore be said to be terminal and correct pruning and culture ensures a constant supply of long straight young wood.

#### CHARACTER OF ABNORMAL, REVERTED GROWTH.

*Case 1.* Associated with moderate or large numbers of Big Buds.

Since 1914 it had been noticed that Reversion often occurred amongst mite attacked bushes and frequent cases of such association came under the author's experience in visiting plantations in Worcestershire and Herefordshire. It was natural to suspect that the two were linked together in some way but the case was complicated by the fact that reversion often occurred amongst bushes where there was either no big buds or very few. A year or so after the connection had first been noticed, bushes began to revert at Long Ashton and it was possible to investigate the disease under good conditions. Here it was apparently associated with the Big Bud attack which had been increasing ever since the bushes were planted.

In order to discover how far the tendency to reversion corresponded with mite attack the bushes were carefully examined in June and marks given for the amount of reversion present. Four classes were recognised, normal bushes, slightly attacked bushes where the leaves tended to the pointed type, but with normal fruit, a worse condition where the fruit had partly run off and a still worse where the fruit had completely run off.

In the following winter the bushes were divided into four classes as regards numbers of big buds present. This was done for two years. In this time there were forty cases of reverted bushes in the two last classes which were also placed in the last two classes for Big Bud and only twelve such reverted cases that were placed in the second class for Big Bud (namely in the class showing a minimal number of big buds).

There was no case of definite reversion on bushes that showed no big bud the following winter. The evidence thus pointed to a close connection between the two diseases.

As was previously mentioned, one of the most characteristic signs of a reverted bush is the extensive growth of lateral wood, a condition which is usually associated with a lack of suckers from the base. This lateral growth proceeds largely from the lower buds of a yearly growth and not from the higher as occurs if the terminal be injured or removed

in summer time. Any cutting back of the terminal in summer time or hard cutting back in winter does not produce the same effect since wood growths then emanate from the buds immediately below the pruned part.

If the history of a mite attacked bush be followed in detail the following appears to happen in the case of a strong shoot. The terminal bud usually gets infested by migrating mites early in June. Generally only a few are present and the growth from the terminal appears normal. Should many mites succeed in getting in and the bush be in strong growing condition very characteristic leaves are developed. This type is generally known as “oak leaf” by growers. The leaf is thick and dark green and bears no resemblance to the usual shape of the normal leaf. It is a certain sign of a mite infested terminal (Fig. 2; cf. Figs. 3 and 4). In any case the growth from the terminal is checked to some degree.

This check is sometimes sufficient to force out some of the lateral buds lower down during the current year (Pl. IV, Fig. 5). The laterals of course will push according to their strength during the succeeding year. Most of them, where mite is fairly abundant, will also be mite infested, since they are formed at the time when mite migration is most active. They therefore cannot grow out at all. If any escape, and especially if they are not in the process of changing into fruit buds, as they would be normally, they will sometimes make a short outgrowth in the current year and in any case become stronger buds than they would otherwise be (Fig. 5). The lateral buds formed after June, that is those which during the next winter are situated just below the terminal, usually escape mite infection and develop into fruit buds having the structure already described.

The reason why these often fail to grow out under the stimulus of the check to the terminal bud may be explained thus. At the time of their formation the growth push of the plant is rapidly decreasing (see Tables I and II) and also that the two accessory growing points in the forming fruit bud are very weak. If however the check takes place comparatively early before the lateral buds have changed into flower buds out-growth often takes place (Figs. 5-8).

The position therefore at the end of the first year is that the terminal bud is “big” as also most of the lower laterals. A few of these have been abnormally strengthened or have made a slight outgrowth while the higher laterals are normal fruit buds.

The following year when growth begins the terminal, being mited, can make no further growth and there is consequently pressure put upon the buds below. As pointed out, the basal buds have been unduly



Fig. 5. Outgrowth of laterals formed during last year (about one inch of growth) due to strong mite check to terminal. In the current year growth has continued from these strengthened buds and shows a reverted type of foliage.



Fig. 6. Type of reverted growth at Long Ashton. Three years' growth on "French." Two year old wood bears fruit that has "run off." Forced lateral growth occurs each year either just below the then terminal or from wood buds low down on the year's growth.



Fig. 7. Shoot from Long Ashton photographed in September showing old terminal big bud (whitened to show up). In this case nearly all the buds below the terminal being mited only three shoots grew as shown in the figure. The leaves are reverted in type.



Fig. 8. Shoot from Long Ashton photographed in December, showing result of check to terminal during *early* summer.



TABLE I. *Growth Graph of Scabrook's Black.*

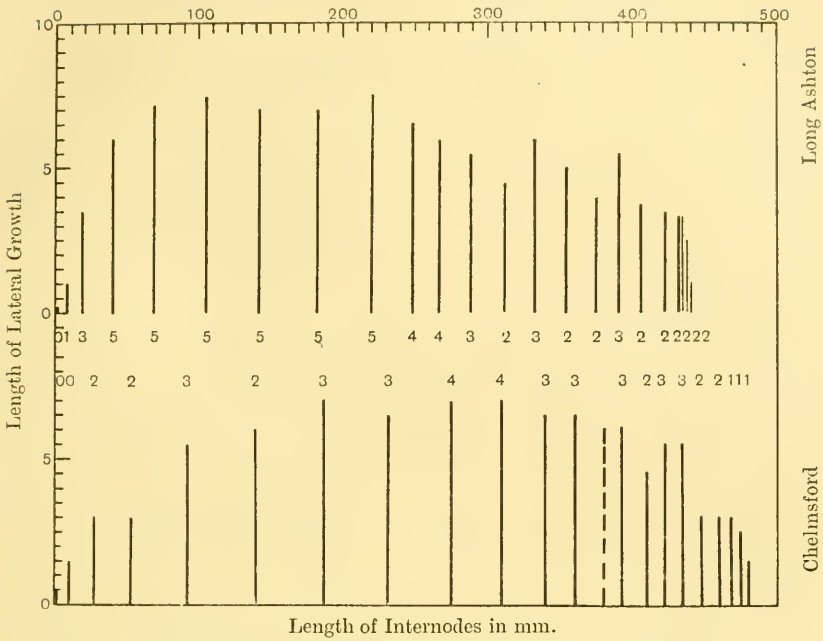
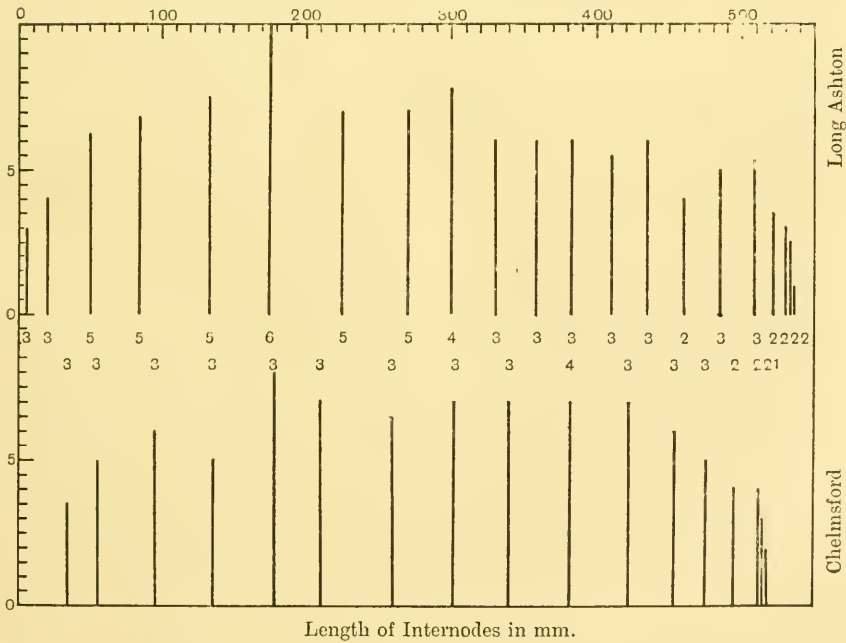


TABLE II. *Growth Graph of Boskoop Giant.*



strengthened during the previous season and it is they that now grow out into twigs of various lengths.

There is also often some growth made from one or both of the accessory growing points present in the highest fruit laterals. It is usually only slight and may be explained by the fact that though these growing points are weak the growth push of a fruit tree is always at its maximum at the top of the yearly growth. The previous year, when they failed to grow out, their growing points were still weaker and the growth push of the plant as a whole was decreasing, but in the spring of the current year not only are they stronger but the growth push of the plant is increasing to a maximum.

Weak shoots show a slightly different behaviour from that just described for a strong shoot. A weak shoot usually means that terminal growth ceases early in the season and that therefore when mites are fairly abundant nearly all the laterals become "big." Such shoots do not form wood buds at the base and therefore no growing out takes place from that region. Generally there is a small amount of outgrowth from any lateral bud that has escaped mite but often the shoot becomes entirely bare and all growth from it ceases.

Where mites are very abundant and the bush is still making strong growth a slight variation occurs from what has been described. Here the check to the terminal bud in the first year is so strong that it disappears altogether during the summer while growth is still active and the laterals immediately below are thus stimulated to strong outgrowth the same year. This case must be distinguished from the previous one where the terminal, though checked, continues growing during the current season and only fails to grow next season because it has become a big bud. As explained below in the section treating the growth graphs of the black currant removal of the terminal in the winter causes buds far below it to shoot while removal in the summer causes buds just below it to shoot.

*Case 2. Reversion of a Big Bud resistant variety.*

At first sight it would seem that if Big Bud were a necessary antecedent to Reversion, resistant varieties should be free from it. Through the kindness of Messrs Seabrooks of Chelmsford I have been enabled to study some very interesting cases of reversion on the variety known as "Seabrook's Black." As the term "resistant" implies the variety does not under ordinary circumstances become badly attacked. In the firm's experience some big buds are sometimes formed but they never increase seriously in numbers and the bushes as a whole remain practically free.

Reverted wood of this variety differed from Long Ashton material in

that the characteristic lateral outgrowths arose from fruit buds instead of from basal wood buds (Pl. V, Fig. 9). From comparative examination of material from Chelmsford and Long Ashton there appears to be a greater tendency to form wood buds at the latter place than at the former. This is probably connected with the different climates at the two places. The result is that outgrowths are more in number and weaker in growth since many weak buds are pushed instead of a few strong. In both cases however the effect of a bushy type of growth is produced instead of a thin type, though the manner of production is slightly different.

When such reverted shoots were examined it was found that many of the buds were abnormally small (Fig. 10). Instead of being the normal oval shape they were angular like an inverted V and were only 2 mm. in length instead of being about 6 mm. When such buds were dissected it was found that the growing point had been killed and only some brown dried up material left to mark its position.

From previous experience of growing points being killed by mite during the summer at Long Ashton it was impossible not to assume that the same cause had produced this effect, namely mite attack. This hypothesis was supported by the fact that big buds were often also present though these were confined to the lower portion of the shoot while the "killed" buds practically always occurred higher up. It is reasonable to look upon these "killed" buds as having been more strongly attacked or as being less resistant to mite than typical big buds and it is possible to trace a complete series of buds showing various stages of resistance to mite attack.

At the bottom of the series where presumably the mite attack is greatest and resistance is smallest come the "blind" buds (Fig. 10). In this case no trace of a bud can be seen though the scar of the leaf in the axil of which it should have been borne is clear. The bud above and below it are usually quite normal.

Next in the series come the inverted V-shaped buds. They are small and consist of only about half the normal number of scales surrounding the dead growing point. In this case presumably the attack was either later or less strong or the growing point was more vigorous. Such buds are not usually found low down on a shoot for reasons subsequently explained. The next stage is normal in shape but smaller than a healthy bud and shows a killed growing point. Such buds are not very common and indicate that the killing process took place later than the last stage but before any tendency to fruit bud formation had taken place.

The next stage consists of buds resembling "big buds" in shape but

much smaller (Fig. 10). The growing point has had time to change into a flower rudiment but the scale leaves are deformed, showing the characteristic semi-spherical shape of big buds. There is however no mite present though sometimes the flower rudiment shows brown areas where it has presumably been injured by mite. In extreme cases of this stage the flower rudiment has been killed and one of the accessory growing points has changed into a very weak flower rudiment.

The last stage is the “big bud.” Here the attack is so mild or the growing point so strong that the latter is not killed but is stimulated to irregular growth. In this resistant variety they occur almost without exception low down on the yearly growth.

The terminal bud may be either a “blind” one or a “killed” one but is only in the most rare cases “big.”

These killed buds cause an interesting pathological effect on the pith. Ever since the disease had first come under the author’s notice certain curious brown marks in the pith have been observed. They occur as smaller or larger streaks in the pith of the main stems but appear to start as spots just below a lateral bud.

I am indebted to my colleague Mr O. Grove, Oenologist at Long Ashton, for his investigation of it. He failed to find any organism microscopically and also failed to obtain any living culture from such spots. It is improbable therefore that they are caused by any organism. Microscopically they appear as brown gummy masses and strongly suggest degenerative changes.

When examining this mited material from Messrs Seabrook it was found that such brown spots were always connected with killed or blank buds. In a few cases the very beginning of the process could be seen consisting of a small spot only, immediately under the killed growing point. Not in every case of a killed bud could the spots be seen but wherever there was a brown spot a killed bud could be found close by from which the browning had started. It would appear probable therefore that such brown spots are due to degenerative changes in the pith cells consequent on the sap flow to the killed growing point being stopped. The phenomenon is an effect of the disease rather than a cause.

The presence of these “blind” and “killed” buds on shoots of “Seabrook’s Black” immediately suggests the reasons of its resistance. Strictly speaking it is not resistant but very susceptible, so much so that the mite kills the growing point in an attacked bud and as a consequence cuts off its own supplies and thus perishes. A few buds however become “big” and serve as a small source of infection the following year.



Fig. 9. Reverted wood from a Scabrook's Black grown at Chelmsford. Last year's terminal, situated in the photograph between two lateral growths, was killed by mite and its base whitened to show its position. This year's extension growth was formed from one of the high lateral buds.



Fig. 10. Parts of two shoots of Scabrook's Black. In the longer shoot 1, 3, 4 and 5 (reckon from the top) are killed buds of varying size. Lateral no. 2 resembles a big bud but is smaller in shape and contains no mites. The terminal is blank, having been completely killed by mite. The smaller shoot is photographed partly end on to show the minute bud formed from one of the accessory growing points originally present in the now killed terminal bud. The shoot also shows "round" buds and "killed" buds lower down.



Fig. 11. Reverted wood of Scabrook's Black grown at Chelmsford. The immediate cause in this case was the formation of a flower bud as terminal in the preceding season. The strig of the fruit formed from it can be seen on the left-hand side at the extreme base of the current year's wood.



Fig. 12. Reverted wood of Scabrook's Black grown at Chelmsford. The strig formed from the flower bud formed as last year's terminal is clearly to be seen at the top of the figure. Nearly all the lateral buds have made abnormal growth.



At Long Ashton where the variety has been under observation for three or four years bushes have been found to be losing their resistance and one or two are showing a considerable number of big buds. There is no reason to doubt that the variety is under ordinary circumstances resistant and Messrs Seabrooks' experience supports this contention. Their experience however seems to be practically confined to the drier portions of England and it is possible that the variety might alter its behaviour in a wet climate. Thus it is noticeable that very few killed buds are present on Long Ashton examples and that big buds seem to have taken their place.

In order to study the method of growth of the variety at the two places two series of measurements were made. The length of each internode on typical shoots was measured and also the distance, for each lateral bud, from the apical end of the leaf scar of the subtending leaf to the highest scale scar on the lateral bud. This latter figure gives a fairly true idea of the "strength" of any particular lateral bud being, strictly speaking, the distance it has grown out since its inception. Tables I and II give the result of these measurements. The abscissae show the distance of the nodes in millimetres from the base of the current year's growth and also the length of the individual internodes. The ordinates show the relative length of growth made by the lateral buds and serve to indicate the strength of the individual buds. In order to make a clear graph these values are multiplied forty times. The figures running across the graph indicate the number of scale scars shown by the corresponding lateral bud. Table I represents the graphs of typical shoots of Seabrook's Black at Long Ashton and at Chelmsford. The shoots were chosen as nearly as possible equal in strength, the Long Ashton one having a diameter of 9 mm. at the base and the Chelmsford one  $8\frac{1}{2}$  mm. The number of internodes also happens to be nearly equal, being 23 and 22. They may therefore be considered to be representative, especially as many other shoots from the two places showed the same general arrangement. The Chelmsford shoot showed a blank or blind bud at one node and this is indicated by the dotted line. It must be pointed out at the outset that the graphs are not necessarily strictly comparable in point of time; thus there is no indication that the two buds at about 185 were formed at the same time. Indeed it is known that growth continues at Long Ashton later than in drier climates, this period being in the case of apples three or four weeks. Looking first at the internodes in the Long Ashton specimen the normal summer check to growth begins at 220 and continues in a rather feeble way as indicated

by the comparatively long internodes until 430, the last three internodes being formed without any chance of elongation. It covers therefore a distance of eleven internodes. In the Chelmsford specimen the check begins at 330 and continues strongly, as indicated by the closeness of the internodes, until 460, a distance of eight internodes. The chief difference is therefore that the check at Long Ashton is gradual and weak while that at Chelmsford is sudden and strong. At the other end of the graph it may be noticed that the growth is more vigorous at Chelmsford than Long Ashton as the internodes are rather larger.

As a general rule the strength of the lateral buds is dependent on the vigour of the bush at the time of their formation and at first sight one would expect the Chelmsford figures to be higher than the Long Ashton ones whereas they tend to be slightly lower. An examination of the number of scale scars on the laterals, however, explains the situation. These numbers (running across the middle of the graph) show that whereas six at Long Ashton run as high as 5, at Chelmsford only two read 4 and it is clear from a superficial view that these average considerably less. From these figures one may draw the conclusion that the growth of laterals at Long Ashton continued over an extended period slowly, while that of the laterals at Chelmsford was characterised by a great push and a sudden check. The growth of the laterals therefore closely follows that of the internodes under the two different climatic conditions. These two kinds of growth can be very largely, if not entirely, accounted for by the different rainfall at the two places. Thus for a thirty-five year period the average monthly rainfall for June, July and August are shown in the accompanying table. July and especially August show a markedly increased rainfall at Long Ashton. The soil therefore in these months tends to be wetter and this tendency is increased owing to the factors encouraging evaporation, namely sunshine and air dryness, being less marked at Long Ashton than in the east of England.

TABLE III. *Rainfall in inches.*

Month	35 yr. av.	
	Chelmsford	Long Ashton
June	2·07	2·52
July	2·33	2·92
August	2·27	3·61
Total	6·67	9·05

Table II shows a similar graph for Boskoop Giant at the two places. In this case also the shoots are fairly comparable with each other and

with the Seabrook's Black graphs since they have a thickness at the base of  $9\frac{1}{2}$  mm. for the Chelmsford shoot and 9 mm. for the Long Ashton shoot. The influence of climate is here the same in all respects as in the Seabrook graph. The number of internodes however is less, being twenty-one and seventeen, though the length of the shoot is greater. The internodes are therefore, as can also be seen from a superficial glance, longer. Incidentally it may be remarked that Seabrook's Black is a better type for production of fruit, in that, in a given length of shoot, there are more lateral, that is fruit, buds than in Boskoop Giant. Comparing Seabrook's Black and Boskoop Giant under Chelmsford conditions the great concentration of internodes in the former at the end of the graph is in marked contrast to the corresponding part of the graph for the latter. It indicates an early check to growth, an indication which is borne out by the numbers of scale scars in the last nine laterals. These in the case of Seabrook's total eighteen while for Boskoop they are twenty-three. One may assume therefore that under the same climatic conditions Seabrook's receives a more decided check to growth than Boskoop.

If, as has been already assumed, the resistance of Seabrook's Black to Big Bud at Chelmsford is due to the fact that mites kill the bud growing points instead of forcing them into hypertrophied growth it should be possible to show that the conditions at Chelmsford are such as to bring this about more readily than at Long Ashton, where big buds are formed extensively on this variety. It has been shown above that the conditions at Chelmsford cause an early and marked summer check to terminal and lateral growth and therefore it is likely that mite attacked buds will have their sap supply very much curtailed at the time of this summer check. There will therefore be more tendency for these growing points to be killed by the mite attack than in the Long Ashton climate where growth continues longer. These facts also explain why some big buds are formed at Chelmsford and why they are practically always situated low down on the shoot. For it is just these buds that have been growing the longest and must have been, from their position, earliest attacked. A big bud therefore is formed from a growing point that has been attacked early and has had abundant and long continued sap supply while a killed bud is formed from a growing point that has been attacked late in the season and has a poor and brief supply of sap.

These considerations explain why some big buds are formed on Seabrook's and also why they do not increase in number. Probably it will be found that in wet years they do increase and in dry years disappear.

Transfer them however to a wet climate like Long Ashton and they continue to increase regularly and the variety apparently loses its resistance. If this theory is sound there should also be some explanation why Boskoop is not resistant at Chelmsford, since in that climate it has a more definite summer check than at Long Ashton. This is partly, at any rate, supplied by the fact that, as already pointed out, the summer check has much more effect on Seabrook's than on Boskoop. This habit of an early check to growth may be sufficient in itself to explain the mite-resistance but on the other hand there may be other factors which influence the result. There is however nothing in the evidence so far in the author's possession which would lead to any other conclusion. It would thus appear possible, by arranging the cultural conditions in such a manner as to get a marked and continued summer check, to cause "Big Bud" to disappear almost entirely from an infected plantation. Such a treatment will be tried in the near future.

The graphs of Table I serve to explain the character of the reverted wood in a typical shoot of Seabrook's Black. The terminal bud is either blind or a killed bud which means that it was attacked comparatively late in the season. The following year there is no strong terminal growing point to take the growth push so that this is distributed amongst the accessory growing points in the flower buds according to their strength and also according to their nearness to the apex of the shoot. The lowest buds (0 to 50) are not only weak but far from the apex and therefore are unremoved. The next two are stronger but being still fairly far from the apex usually make but a short growth. The next six are comparatively strong and usually make a considerable growth while the last five or six are so weak that, despite the extra push due to their nearness to the apex, they make but a short growth. Fig. 11 shows the kind of growth obtained in reverted shoots grown under Chelmsford conditions and agrees fairly well with the theoretical expectations.

*Case 3. A. No Big Bud present. Killed buds extremely few or absent.*

In addition to the material already described were shoots from Messrs Seabrook's from reverted bushes not showing any big buds. The terminals here were apparently normal and there were very few killed lateral buds. The fact that killed buds were to be found suggested the possibility that the original terminal had been killed and its place taken by one of the accessory growing points originally present in the terminal bud. This does sometimes undoubtedly happen, as may be seen in Fig. 10 which shows the killed terminal in a Seabrook's Black twig. The small bud immediately lateral to the blank terminal is one of the

accessory growing points. No such clear case could be found in the material coming under Case 3 and it is certainly not sufficient to account for the reversion there experienced.

TABLE IV.

Source of shoot	No. of terminals examined	Av. no. of internodes on shoot	Av. length of shoot in cm.	Av. length of internode in cm.
Sound Seabrook, Chelmsford				
Flower	17	15.5	32.0	2.06
Wood	12	16.6	49.9	3.00
Reverted Seabrook, Chelmsford				
Flower	29	15.8	38.3	2.42
Wood	4	16.7	41.7	2.50
Sound Seabrook, Long Ashton				
Flower	12	17.2	35.0	2.03
Wood	5	21.0	51.6	2.42
Sound Boskoop, Chelmsford				
Flower	—	—	—	—
Wood	10	17.9	54.1	3.02
Sound Boskoop, Long Ashton				
Flower	4	15.2	28.7	1.88
Wood	8	19.2	48.0	2.5

Examination of the terminals however suggested a possible cause. They were found in most cases to be flower buds. Thus (Table IV) out of thirty-three shoots examined twenty-nine had flower bud terminals and only four wood buds. In the spring these terminal flower buds would open and it would not be until an accessory growing point present in the bud was strengthened sufficiently that normal terminal wood growth could take place. While this process was going on however there would be a definite stimulus to growth on the buds situated below the terminal. In a fair proportion of cases the remains of the strig from the previous year's terminal flower bud (Figs. 11-13) could be seen and such an arrangement might easily lead to reverted wood being formed. In order to see how common this cause might be a number of shoots from different sources were examined and the results tabulated and averaged in Table IV. It shows that flower terminal buds are always associated with comparatively weak growth. Thus sound Seabrook's Black from Chelmsford showed an average length of internode of 2.06 cm. for flower terminals but 3.00 cm. for wood terminals. Long Ashton material gave corresponding figures of 2.03 and 2.42. Reverted Seabrook's Black from Chelmsford off bushes showing no big bud gave approximately equal

figures but nearly all fruit buds, indicating that the bushes as a whole were not growing as strongly as they should be. Sound Boskops from Chelmsford which were very strong shoots showed no flower terminals at all while Long Ashton material again gave the higher figure for shoots with wood bud terminals. From the evidence therefore it would appear that shoots making a weak growth from whatever cause usually end in a flower bud and such a condition might be expected to cause reverted wood the following season.

Weak growth in any twig may be caused by two conditions. The bush as a whole may be making weak growth or the twig itself may be in such a position as to get a poor sap supply. Suckers from a bush usually make a strong growth the first year, a moderate one the second year and comparatively weak ones in the third and fourth years. In the best pruning method therefore all fourth year wood (if any) and most third year wood is pruned away. Thus none of the weakest wood is allowed to fruit and only part of the rather weak wood, the best and most abundant fruit being obtained from the strong and moderately strong wood. In a healthy bush therefore it is not until the third or fourth year that the terminals are changed into flower buds and so the behaviour of the succeeding year's growth is of no consequence.

*Case 4. Aphis attack.*

The effect of aphis attack in summer is, as stated above, to cause two or three lateral buds immediately below the point of attack to break into growth. Fig. 14, Pl. VI, shows a typical example and is of course of comparatively common occurrence. True terminal growth has thus been lost and the terminal buds formed on these lateral outgrowths at the end of the season are practically always flower buds. Consequently next year there is a tendency for reverted wood to be formed. Reverted wood means more lateral wood and consequently less sap is available for the terminals. This results again in a tendency to form flower bud terminals and so the process continues. If however the bush as a whole is in very good condition the terminals on the wood formed as a result of the aphis attack may be wood buds in which case there is no immediate tendency to revert. If the growth is not quite so strong but still moderately so the bush may recover its condition in the year following aphis attack and form wood buds as terminals and so escape reversion. The immediate effect therefore of aphis attack will depend on the condition of the bush. It is possible that aphis attack may affect the bush in another way. If as usually happens three shoots appear where in unattacked bushes but one is present it is clear that, if every shoot on a



Fig. 13. Reverted wood of "French" grown at Long Ashton. The strig from last year's terminal flower bud can be clearly seen. The two accessory growing points originally present in the terminal flower bud have in this case both grown, giving the appearance of a divided terminal. Big Bud is present but was not the cause of reversion.



Fig. 14. Growth resulting from aphid check in summer. Specimen from Long Ashton. At the top is the original terminal much weakened by aphid attack. The strength of the shoot, in this case a strong sucker, was thrown almost entirely into the five buds immediately below.



bush behaved so, the total number of terminal growing points or extension shoots would be tripled. If this condition is not remedied at pruning time the bush becomes possessed of far more extension growing points than it can support properly.

*Case 5.* Through unknown causes.

In addition to the cases already described there is a form of reversion for which at present no explanation can be offered. It occurs in very young bushes that have been cut down immediately after planting and therefore cannot be accounted for by any interference with terminal growth. Instead of making the usual straight growth with broad leaves considerable branching occurs from the laterals made during the current season; at the same time the leaves are markedly pointed in shape. The following year the fruit runs off. This case is being investigated but at present there is no satisfactory explanation.

#### CONCLUSIONS.

In every case so far examined it has been shown that reverted wood has been caused by a check to the terminal bud. This check may be owing to the normal wood bud terminal being substituted by a big bud, a killed bud, a blind bud or a flower bud. In all cases an abnormal amount of growth from lateral buds situated below, takes place. The exact arrangement of this lateral growth depends on the time and manner of the check to the terminal and has already been discussed. There is at all events little doubt from the evidence given above that such a check does occur and that it suffices to explain the character of reverted wood. The connection between reverted wood and "running off" of the fruit is not quite so clear.

The amount of running off varies with the season. If it is wet the fruit on reverted bushes hangs on very much better than if it is dry, which would point to insufficiency of sap supply as the cause. This is supported by the behaviour of the berries. Usually it is the basal ones that remain but sometimes it is the apical or intermediate ones. In any case they do not drop until about half size, a behaviour which suggests that fertilization has taken place normally. The evolution of the fruit goes on as in a healthy bush until the summer drought begins to be felt and there is nothing to show up to this time that they will not reach maturity. The case may be compared with the June drop of plums where fruits already "set" are dropped in considerable quantities and only the more favourably placed ones are left. If drought in respect of the bush affects the holding power of the fruit it is not unreasonable to look for

some factor causing a local drought to the young fruits. The presence of an unusual number of growing points may supply the answer. They may absorb the sap that should go to the developing fruits and thus cause a local drought. It may be contended that normal bushes often show a considerable amount of branching and yet bear fruit but this case is entirely different. Here the branching is caused by excess of sap from the roots forcing out buds otherwise quiescent, while in truly reverted bushes the sap is diverted from the single terminal growing point into a number of laterals that would in the ordinary course of events have remained quiescent. In the first case there is enough sap for the fruit buds and more to spare for lateral wood growth and in the second a limited supply diverted from the fruits to an unusual number of new growing points. In addition, these extra lateral growths are usually formed comparatively low down on the year's growth and it is possible that as a result they secure the first call on the sap supply. The case may be compared with that of the peach whose method of fruiting is similar. Here also the flowers are borne along the preceding year's shoot and it is a text-book rule to leave a growing point beyond the developing fruits. Failure to do so is said to prevent the fruits from attaining their normal size and in practice often, though not always, does so. In gardening language there is nothing to “draw the sap” to the fruit, in consequence of which the fruits suffer from a local drought. It cannot be too strongly urged that the whole process of reversion is gradual and at no point can hard and fast lines be drawn. This is not surprising when it is considered what complex factors affect the sap supply to the fruits. It will be dependent on the variety, the climate, the condition of the rooting system, the number of active growing points, and so on. One of the most puzzling points about running off is the fact that the sap supply to the fruits would appear to be small at the same time when, to judge from the active growth made by the bush, the sap supply elsewhere is large. Apart from the argument outlined above that the abnormal number of sap drawers deprive the developing fruit of sap there is another point to consider. At the time when the outgrowth of laterals begins the growth push is vigorous (see graphs, p. 15). At the time when the fruit drops, which is somewhat later, the general growth push has slackened though the lateral growths are still actively transpiring and making vigorous calls on the sap supply. Strictly speaking therefore the sap supply to the fruits is small at a time when the sap supply *has been* large to the laterals.

## POSSIBLE REMEDIES.

Since there may be several causes of Reversion it is important to determine in any given case which are acting. Reversion caused by the presence of mite can obviously only be cured by the elimination of the mite. There is no satisfactory method yet of doing this though some means of control might be found by using the information afforded by Tables I and II. Investigation will be continued in this direction. Reversion caused by terminal fruit bud formation is evidence either of faulty pruning or of poor condition of the bush as a whole. Correct pruning assisted by judicious manuring or other necessary cultural operations should give a permanent cure. Reversion caused by aphid should be curable by pruning away superabundant terminals; at the same time care should be taken that the bush is making strong growth.

## SUMMARY.

1. Reversion is characterised by four symptoms:

- (a) "running off" of the fruit,
- (b) unusual amount of lateral wood growth,
- (c) sharp pointed leaves,
- (d) long, thin, internodes.

2. It is associated with and apparently caused by a check to the terminal growth through change of the terminal wood bud into:

- (a) a big bud,
- (b) a killed bud or blind bud,
- (c) a fruit bud.

It may also be associated with aphid attack.

3. Mite resistant varieties revert under conditions 2 (b) and 2 (c).

4. Seabrook's Black is mite resistant because in normal climates and seasons the mite kills the attacked growing point and thus starves itself. This only happens when both climate and variety favour an early and strong continued check to the growth of the bush.

5. There is a form of reversion occurring in young bushes before mite or aphid are present. This form is at present unaccountable.

## A "WITHER TIP" OF PLUM TREES

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(With Plates VII—IX.)

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## I. GENERAL OBSERVATIONS.

IN the summer of 1916, during the course of an investigation into the cause of, and means of controlling, a "Blossom Wilt" of apple trees which proved to be due to *Monilia cinerea* Bon., the attention of the writer was directed to the presence of a *Monilia* on certain withered leaves and dead twigs of Victoria plum trees in the fruit plantation at Wye College. On microscopic examination it was found that the fungus was morphologically similar to that producing the "Blossom Wilt and Canker" disease of apple trees. The colour of the pustules was the same and the dimensions of the conidia when the two forms were found under similar conditions were also in approximate agreement, but since the mode of attack was quite different in the case of plum twigs it was decided that the disease demanded special study.

Observations made on the affected trees showed that leaves actually bearing pustules of the fungus were not of very frequent occurrence, but

there were many leaves which, with the exception that externally no fungus was to be seen on them, resembled those with the *Monilia* pustules on their surface, in that they were dark brown, curled and withered. These diseased leaves were borne on the young green vegetative shoots, *i.e.* the twigs which had developed from buds during that spring. At the time that observations were begun (about the middle of June) the majority of the affected twigs were either wilting at the tip or were quite dead for several inches from the tip downward. Others showed clearly that generally, if not invariably, the damage did not actually commence at the extreme tip of the damaged twig and then extend backward towards the main branch, but that a discoloured (dark brown) area appeared at a node bearing a dead leaf, the node being situated some distance behind the apex. When the discoloured area had girdled the twig the transpiration current became arrested and the terminal portion of the twig thus becoming flaccid began to wilt and the leaves to flag; this flaccidity caused the soft green tip of the shoot to become more or less pendant and the curve produced is generally a characteristic feature of the diseased twigs (see Pl. VII, Fig. 1).

At a later stage the whole of that portion distal to the node where the attack originated is dark brown and withered and the discoloration extends downwards for a short distance below that node, the lower limits of the diseased tissues being distinctly marked off by the contrasting colours of the dead and living parts. As desiccation of the diseased tips becomes more pronounced the affected tissues indurate and the curved condition of the shoots persists through the winter. Since the shoots are often attacked quite early in the season the leaves wither before the absciss layer is developed and so remain on the tree after the normal leaves have fallen. These dead twigs with their persistent withered leaves may easily be recognized during the winter and early spring (Pl. VIII, Fig. 4).

The injury results in the production of gum which in many cases oozes out through the bark and appears at the surface as a rounded drop which hardens on exposure to the air (see Pl. VII, Fig. 2).

Instances were observed where a twig had been attacked through two nodes; thus, in the example shown in Fig. 2 the terminal portion had been killed by a girdling lesion at a short distance behind the apex, below this being a healthy portion followed by another diseased area at a lower node.

In addition to the newly killed shoots the affected trees usually bore a number of dead twigs which, from their situation on the branches,

must have grown out and become infected during the previous year. On the surface of these older dead twigs were numerous *Monilia* pustules and it appeared probable that these had served as sources of infection for the young growth.

When a twig is killed early in the season the buds towards its base which normally would have remained dormant until the following year may be stimulated to precocious development and several weak shoots with pale green leaves grow out. Thus the vigorous leading shoot, which, under ordinary circumstances, was destined to produce a normal supply of young "wood" for the production of fruit buds in the succeeding second or third year, becomes replaced by a number of feeble, immature "unripened" shoots which would probably be killed during a hard winter (Pl. VIII, Fig. 3).

It was noticed that the plum trees that year were suffering from a severe attack by aphides (*Aphis pruni* Réaumur) and these insects were also present in considerable numbers on trees affected by the "Wither Tip" in other plantations in Kent.

Although inoculation experiments carried out at Wye with pure cultures of the fungus have hitherto failed to induce infection of the leaves<sup>1</sup>, observations in the open appear to indicate that the young shoots must in many cases (*i.e.* in the typical "Wither Tip" disease) become attacked through infected leaves. Duggar(4) in reference to the "Brown Rot of Stone Fruits" states<sup>2</sup> that "The twigs are also susceptible, but it has been definitely shown that infection of the twigs results only when either flowers or fruit produced on the twigs have already fallen prey to the disease." I have pointed out however(10) that there are reasons for suspecting that the American Brown Rot fungus is a form of *Monilia* quite distinct in some respects from either *M. fructigena* or *M. cinerea* as occurring in this country.

Frank and Krüger(7) have described and figured an instance of infection occurring in the lamina of a cherry leaf, but in this case the leaf was in actual contact with an infected flower. In the "wither-tip" disease of the plum, infection of leaves far removed from any other source of infection is of frequent occurrence.

Aderhold(1) records and figures the wilting of young shoots but only when infected through a node bearing diseased flowers. Frank and Krüger also illustrate a similar instance.

<sup>1</sup> *Vide* p. 38

<sup>2</sup> *Loc. cit.* p. 189.

## II. THE FUNGUS.

## (a) ANNUAL CYCLE.

Although the newly killed twigs did not as a rule bear any fungous fructifications except in those comparatively rare instances where *Monilia* pustules appeared on the leaves, the presence of *M. cinerea* on the dead twigs of the previous season suggested that the fungus would appear at the surface of the young affected twigs if these were allowed to remain on the trees until the following year. This seemed all the more probable by analogy with the annual cycle of that form of *Monilia cinerea* which produces the "Blossom Wilt and Canker" disease of apple trees. In a previous paper it has been shown that in the latter the pustules are not generally produced at the surface of the cankers and the dead spurs until the approach of winter, but develop readily from about the beginning of December onward through the winter and spring.

In order to ascertain whether similar conditions obtained in the case of the "Wither Tip" fungus, labels were attached to a number of the dead twigs in the summer of 1916. As was anticipated, grey *Monilia* pustules began to burst through the bark of some of the twigs early in December (a few being found with immature pustules on December 6) and continued to appear throughout the winter. With very few exceptions all the twigs labelled as showing the typical wither tip condition in the summer, bore *Monilia* pustules in winter. Thus on one tree 31 withered tips had been labelled in August 1916. *Monilia* pustules were first observed on December 6 when one of the dead twigs was found bearing the fungus, as pustular tufts of conidiophores, on its surface; later, pustules appeared on others and by May 1917 they were present on all except two of the labelled twigs.

The length of the dead portion had been noted in the case of some of them and in no instance could evidence be found that the fungus had extended any further along the twigs from August 2, 1916, to May 11, 1917. In this again the habit of the fungus found on the plum twigs is comparable with that of the form found on apple spurs and cankers for it has been shown that although the blossom-wilt fungus of apple trees makes rapid progress for a few weeks immediately after infection of the flower occurs its further extension into the tree is inhibited after about the middle of July.

On another tree 25 withered tips had been labelled on August 5, 1916; the *Monilia* appeared at the surface of three of them by December 6 and all bore mature pustules on May 14, 1917, when the tree was in full

bloom. Many of these withered twigs retained their leaves throughout the winter; the presence of such twigs still bearing leaves at that season of the year is an almost certain indication that *Monilia* pustules are to be found.

When the trees were examined in spring a few cankers bearing pustules of the fungus were found on the branches; in each case the canker had arisen round a node, the branch having been invaded through a short shoot or flowering spur.

Since considerable numbers of the dead twigs bearing the fungus were present on the trees under examination it was expected that there would be an outbreak of the disease during the summer of 1917. Very few examples of the typical "Wither Tip" condition were to be found however and it was noticed also that very few aphides were present on the leaves. This suggests that the aphides either aid in the distribution of the conidia or that their presence on the leaves reduces the vitality of the latter to such a degree that they are rendered particularly susceptible to attack by the fungus. The wounds caused by the aphid probably enable the germ tubes to penetrate the epidermal layer.

That outbreaks of the "Wither Tip" disease are dependent on aphid attacks has not yet been established, but the observations made during the past two seasons are suggestive since, although in 1917 (when aphides were few in number) the sources of infection, in the form of withered twigs bearing *Monilia* pustules, were more numerous than in the previous season, instances of twigs killed that season were very few.

#### (b) CULTURAL STUDIES.

In order to compare the fungus obtained from the dead twigs with strains of *Monilia* from other sources it was necessary to grow the organism in pure culture, so that its behaviour when growing on varied artificially prepared media could be studied; cultures of the fungus known to be uncontaminated with other organisms were also required for the inoculation experiments described later in this paper. For this purpose infected twigs were obtained from various sources in Kent and in all eleven strains have been grown.

Cultures were obtained initially in two ways, viz.:

(1) If the fungus was producing conidia, as when occurring on the dead twigs in the winter and spring following infection, or as sometimes found on the newly killed leaves in the summer, the conidia were isolated on agar plates and the resulting sporelings which were found to be un-

contaminated were transferred to other plates. When each had reached a sufficient size sub-cultures were made as required.

(2) When the fungus was found as barren mycelium only, as it occurs within the tissues of the newly infected twigs, transverse sections were made through the lower portions of the affected parts, *i.e.* either across the node itself where infection had arisen or through the diseased tissues of the internode below<sup>1</sup>. Particles of the sections were teased out in sterile distilled water and placed on agar plates. The mycelium present in the sections usually grew out uncontaminated by other forms so far as could be seen, but to ensure absolute purity of cultures sub-inoculations were made from the outgrowths by placing peripheral portions of the resulting mycelium on sterilized potato, a medium which has hitherto proved the most favourable for conidia development, and when the conidia were being freely produced some of them were isolated on plates and pure sporelings obtained as described under (1).

Agar-agar, containing an extract of prunes, either as plates or as "slants" in test tubes, was used for studying the mode of growth, and sterilized potato in wide test tubes or in Roux's tubes was used when conidia were required for measuring or for inoculation experiments.

When placed on the nutrient agar the mycelium grows out readily, producing within a few days a regular, almost circular disc of hyphae; later the margin develops into broad lobes with narrow sinuses between them. As in the case of the Apple Blossom-Wilt strains, growth is usually arrested at about 2 cm. from the centre but is resumed as flabelliform outgrowths which generally originate at the sinuses.

It has been shown that the form of *Monilia cinerea* infecting the apple flower, as represented by some thirty strains from various sources, invariably produces a brown coloration when growing on agar-agar containing an extract of prunes. The eleven strains obtained from plum twigs have shown some variation in the intensity of this coloration. One has remained quite colourless in most of the plate cultures of the medium and colourless or almost so as slant cultures in test tubes; one has produced a coloration indistinguishable in intensity from that of the apple blossom strains, while the others are intermediate.

When growing on sterilized potato in test tubes or in Roux's tubes all the "Wither Tip" strains tested have produced a copious supply of conidia, numerous grey tufts of conidiophores, usually in more or less

<sup>1</sup> The terminal internodes, which wither because the transpiration current is interrupted by the death of the tissues actually invaded by the fungus, do not themselves necessarily contain mycelium.

continuous zones, being produced towards the upper end of the potato. In this respect these strains differ from those obtained from the apple since the latter have always produced but a scanty supply of conidia when grown on sterilized potato.

(c) DIMENSIONS OF THE CONIDIA.

The conidia obtained from a leaf bearing pustules in the summer of 1916 were found to range from  $10 \times 8.5\mu$  to  $23 \times 14.5\mu$ , the majority however were  $16-18 \times 12-14\mu$ . In subsequent cases 100 conidia were measured and an average taken. In two instances conidia were obtained in summer from twigs killed during the previous season; the averages for 100 conidia of each were  $14.0 \times 10.5\mu$  and  $14.0 \times 10.0\mu$  respectively. When conidia were taken from dead twigs in the winter or early spring their dimensions were considerably smaller; thus the average of 100 conidia taken from a twig in winter was  $11.0 \times 8.0\mu$ , and from another in early spring  $10.5 \times 7.0\mu$ , the size varying from  $5.5 \times 5.0\mu$  to  $17.0 \times 10.0\mu$ .

By analogy with observations made on *Monilia cinerea* as occurring on the flowering spurs of the apple it was considered that the variation was not due to specific differences in the various strains but was the result of modifications in the substratum (particularly the amount of moisture present), and perhaps also of differences in temperature according to the season during which the conidia were in process of development. To confirm this supposition the various strains were subsequently induced to produce conidia under approximately the same conditions by cultivating them on sterilized potato in the laboratory, and an average was obtained of the dimensions of 100 conidia taken from each culture. The size of the conidia formed under such conditions was found in each strain to approximate to that of conidia taken from infected leaves in summer. One strain, already referred to as producing in early spring conidia averaging  $10.5 \times 7.0\mu$ , was also inoculated into plums in the plantation while the fruit were green and still growing; the average size of 100 conidia taken from one plum was  $16.5 \times 12.5\mu$ , from another  $16.0 \times 11.0\mu$ .

The variation in the dimensions of the conidia of the various strains according to the substratum or to the time of the year is shown here in tabular form.

Table showing variation in the dimensions of conidia of various "Wither Tip" strains of *Monilia cinerea*<sup>1</sup>.

Strain	Source of strain (all obtained from plum trees)	Conidia on twigs killed previous year			Twig killed during current year: conidia on young leaves	Conidia on potato cultures	Conidia on plums artificially inoculated
		Taken in winter or spring	Taken in summer				
<i>a</i>	Dead twig killed previous year	—	14.0 × 10.5 (8 × 6.5—23 × 13)	—	16.5 × 12.0 (8.5 × 7—22 × 15)	—	
<i>b</i>	Young twig killed current year	—	—	—	17.0 × 13.5 (10.5 × 9—25 × 18)	—	
<i>c</i>	Young twig	—	—	(10 × 8.5—23 × 14.5 but mostly 16—18 × 12—14)	16.0 × 12.5 (9.5 × 8—22 × 18.5)	—	
<i>d</i>	Young twig	—	—	—	16.0 × 12.5 (9 × 7—22 × 20)	—	
<i>e</i>	Old dead twig	—	14.0 × 10.0 (8.5 × 6.5—25 × 14)	—	16.5 × 12.5 (8.5 × 8—22 × 18)	—	
<i>f</i>	Young twig	—	—	—	16.0 × 13.0 (9.5 × 8.5—23 × 18)	—	
<i>g</i>	Young twig	—	—	—	16.0 × 12.5 (8 × 7—21 × 19)	—	
<i>h</i>	Young twig	—	—	—	18.5 × 14.0 (9.5 × 8—23 × 20)	—	
<i>i</i>	Canker on a branch infected through a short shoot	10.5 × 7.0 (6 × 4.5—14 × 9.5)	—	—	16.0 × 11.5 (9.5 × 8—21 × 18)	—	
<i>j</i>	Dead twig killed previous year	11.0 × 8.0 (6.5 × 6—17 × 10)	—	—	—	—	
<i>k</i>	Dead twig killed previous year	10.5 × 7.0 (5.5 × 5—14.5 × 9)	—	—	16.5 × 12.0 (17.5 × 6—25 × 18.5)	July 18 16.5 × 12.5 (10 × 7.5—27 × 19.5) July 31 (another specimen) 16.0 × 11.0 (10 × 7.5—27 × 14.5)	

<sup>1</sup> The readings were taken correct to 0.5 μ and the averages were calculated also correct to the nearest 0.5 μ. The numbers within brackets show the range of variation observed in each case.

## (d) IDENTITY OF THE FUNGUS.

The fructifications found on the dead twigs during winter and spring were those of a *Monilia*; the ashy grey colour of these pustules, their size (not usually exceeding 1 mm. in diameter) and the dimensions of the conidia correspond to descriptions of *M. cinerea* Bon. as given by Aderhold and Ruhland<sup>(2)</sup> and by Woronin<sup>(12)</sup>. The size of the conidia obtained from *old dead twigs in summer* more nearly coincides with the dimensions given by Aderhold and Ruhland for the conidia of *M. laxa*; strains obtained from such twigs were however indistinguishable in their mode of growth and in the size of their conidia from those strains obtained from twigs producing *in winter* pustules with conidia considerably smaller and comparable with those of *M. cinerea* as given by the same authors, when the various strains are grown as pure cultures under laboratory conditions. It follows that, in considering the dimensions of the conidia as an aid to the identification of species of *Monilia*, the conditions under which the conidia have developed must be taken into account.

Although *Monilia fructigena* occurs frequently on the fruit itself, and in some orchards causes quite as much damage to the ripening and mature plums as *Monilia cinerea*, and although the former may be found commonly on trees affected with the "Wither Tip" disease, the writer has never found *M. fructigena* on the dead twigs nor isolated it from infected young shoots; its occurrence appears to be exclusively on the fruit.

The "Wither Tip" disease of plum trees is therefore to be attributed to *Monilia cinerea* Bon. The writer at present prefers to retain this, the name given to the conidial stage of the fungus, in preference to *Sclerotinia cinerea* for reasons already stated in a previous paper<sup>(10)</sup>.

The "Brown Rot" fungi are known to be responsible for great losses in other parts of the country where the plum is extensively cultivated, particularly in Cambridgeshire, the Evesham and Pershore districts of Worcestershire, and in Devonshire; not only are the fruit, blossom and twigs attacked, but the larger branches are often killed. Since the "Wither Tip" fungus readily attacks both fruit and blossom of the plum tree and may form cankers (as shown in this paper), it appears probable that the same form is the one chiefly responsible for the attacks in the districts mentioned. In Devonshire a disease which appears to be identical with the "Wither Tip" of plum trees in Kent is reported<sup>1</sup> as

<sup>1</sup> Vide, *The Fruit-grower, Fruiterer, Florist and Market Gardener*, June 15, 1916.

causing great damage; it is attributed to *Sclerotinia* (*Monilia*) *fructigena* but is probably caused by *M. cinerea*.

As there is still some confusion in respect to the nomenclature of the *Monilias* parasitic on fruit trees, and since the work recorded in the present paper affords evidence of the occurrence of biologic forms of *M. cinerea*, it is desirable that a comparison be made of the forms of *Monilia* from various fruit-growing localities; the writer therefore would be glad to receive specimens of affected fruit or branches from other counties that the fungus present on the diseased material may be compared with those strains obtained from trees in Kent.

### III. INOCULATION EXPERIMENTS.

During the spring and summer of 1917 inoculation experiments were carried out, using pure cultures of a strain of *Monilia cinerea* obtained from a dead twig bearing *Monilia* pustules, with the object of acquiring further knowledge relative to the mode of parasitism of the fungus, and the extent of the injury caused by it. Several strains had been isolated during the summer of 1916 and grown as pure cultures, but, as some organisms are known to become less virulent after continued growth on artificial media, it was thought desirable to start cultures of a strain isolated during the same season as that in which the inoculations were to be made. Since there was also the possibility of the occurrence of variation in the virulency of different strains of *Monilia cinerea*, particularly as it had been found that cultural variations were to be detected among the strains, it was decided to work throughout with one strain, known to originate in a single conidium and actually obtained from a "withered tip" of a plum tree.

The method adopted in isolating the strain used for the inoculation experiments was as follows:

Towards the end of March 1917, a twig, which had been killed during the previous summer and which bore a number of the grey pustules typical of the fungus, was removed from the tree and placed in a moist chamber. In 48 hours the pustules had become very pulverulent and conidia were removed by means of a sterile needle and placed in sterile distilled water in a watch glass; the conidia floated on the surface and drops of the water were transferred with a platinum wire loop to an agar plate. Some of the drops contained isolated spores and these could be examined under the microscope through the bottom of the plate. After

two days several of the resulting sporelings were seen to be uncontaminated and three were transferred to another plate. All three grew out in a similar manner and were indistinguishable in their mode of growth from other strains of *Monilia cinerea*; sub-cultures from one of these were used in the inoculation experiments. On the agar plates the fungus failed to produce conidia and as these were necessary when infection of flowers *via* the stigma was attempted, cultures growing on sterilized potato were obtained since on this medium conidia readily developed within a week.

(a) INOCULATION OF PLUM LEAVES.

Since observations in the open suggested that infection of the twigs arose in the leaves, attempts were made to produce the disease by inoculating leaves with the fungus. Experiments were made on the leaves of young growing shoots both in the greenhouse and in the open, conidia being placed (1) directly on the uninjured surface of the leaves, or (2) on the glands at the base of the lamina, or (3) on punctures made through leaves by means of a sterilized needle. In no case however did inoculation result in infection of the leaves and no difference could be detected between inoculated leaves and controls, repeated attempts giving invariably negative results.

It would appear that the leaves must receive some special form of injury before the fungus is able to invade the tissues and the results lend support to the hypothesis that aphides provide the kind of injury necessary for the fungus to establish itself in the leaf.

(b) INOCULATION OF PLUM FLOWERS.

*Experiment 1.* Inoculation of flowers on a Victoria plum tree in the College Plantation.

A culture of the fungus growing on sterilized potato in a test tube was prepared and when numerous conidia had developed the potato block was transferred from the tube to a sterile petri dish; small portions bearing tufts of conidiophores were cut off with flamed scalpels and transferred to another dish which was then taken to the tree where the experiment was to be carried out. The actual inoculation of a flower was made by removing from the dish one of the particles of potato on the point of a sterilized mounted steel needle, and the conidia-bearing surface was applied to the stigma of the flower.

The tree selected was free from diseased twigs or "mummied" fruit.

Five branches were chosen and in all eighteen umbels of flowers were inoculated; one of these umbels consisted of three flowers, the rest of two flowers each, so that thirty-seven flowers were inoculated. The umbels so treated were mostly at alternate nodes, the intermediate ones being used as controls. Within three days all these flowers showed evidence that infection had occurred, by a brown coloration of the stigmas and in most of them by the discoloration extending also down the style.

At this stage no other flowers on these branches showed any discoloration of the styles or stigmas, thus indicating that the infection was the direct effect of inoculation with the *Monilia* conidia. The results obtained are given below in detail for Branches I and III, on each of which four umbels of two flowers each were inoculated; these, being also typical of the results obtained on the rest, show the progress of the disease after inoculation of the stigmas until the branch itself is invaded.

The inoculations were made on May 11; the nodes bearing the treated flowers were labelled *a, b, c, d*.

*Results on the 3rd and 4th days after inoculation.*

Branch I.

MAY 14	MAY 15
(a) Stigma of each of the two flowers brown	Styles brown for 2 and 5 mm. respectively
(b) Stigma of each flower brown: in one the discoloration had extended for 2.5 mm. down the style	Styles brown for 2 and 7 mm. respectively
(c) Stigmas brown: in one the style was also brown for half its length ( <i>i.e.</i> for about 5 mm.)	Styles brown for 6 and 8 mm. respectively
(d) Stigmas brown: styles also brown for 1 and 5 mm. respectively	Styles brown for 5 and 7 mm. respectively
<i>Controls:</i> No discoloration, even of the stigmas on the rest of the flowers on the branch	No discoloration of the stigmas

Branch III.

MAY 14	MAY 15
(a) Both stigmas brown and both styles for 2 mm.	Styles brown: one for 5 mm. the other to the base (about 10 mm.)
(b) Both stigmas brown; styles brown for 3 and 4 mm. respectively	Styles brown for 5 and 7 mm.
(c) Both stigmas brown; styles brown for 2.5 and 4 mm.	One style brown for 6 mm. the other to base
(d) Both stigmas brown; style of one flower brown for 2.5 mm.	Style brown for 5 and 8 mm.
<i>Controls:</i> No brown stigmas	No brown stigmas

## Results on the 6th and 8th days after inoculation.

## Branch I.

MAY 17	MAY 19
(a) 1. One flower with style brown for 5 mm.	1. Style brown to its base; base of pedicel brown and sulcate for 2 mm.
2. The other flower with style brown to base; ovary brown, and a brown discoloration is evident on the exterior of the flower at junction of pedicel and calyx tube	2. Whole flower brown and withered, calyx lobes recurved; pedicel brown to base and longitudinally sulcate, discoloration extending upwards into the base of the other flower (No. 1 above)
(b) 1. Flower with style brown for 6 mm.	1. Style brown to base
2. Style brown to base, ovary also brown	2. Nearly the whole of the calyx tube and 2 mm. of the pedicel are brown
(c) 1. Style brown to base	1. Style and ovary brown, calyx lobes discoloured and recurved, base of pedicel brown for 5 mm.
2. Style brown to base, ovary brown, base of calyx tube brown	2. Whole flower withering, calyx lobes recurved, pedicel brown to base and discoloration extending upwards in the other pedicel
(d) 1. Style brown to base	1. Style and ovary brown
2. Style brown to base, ovary and base of calyx tube also brown	2. Whole flower withered and inclined on its pedicel; pedicel brown to base and longitudinally sulcate
<i>Controls:</i> Of the rest of the flowers on this branch some stigmas show a slight discoloration	Most of the non-inoculated flowers now show a slight discoloration of the stigmas; three also show a browning for 1 mm., while one flower has its style brown to base

## Branch III.

MAY 17	MAY 19
(a) Both flowers with brown styles, the discoloration beginning to extend into the ovary	Style and the whole of the ovary brown in both flowers
(b) One flower with style brown for 6 mm. the other with style brown to base	Both styles brown to base; in one flower the discoloration also extends through the ovary and is to be seen on the outside in the basal part of the calyx tube
(c) Both flowers have styles brown to base and the ovaries are also brown; one is also discoloured at the base of the calyx tube	Both flowers brown and withered with recurved sepals; pedicel of one of them brown and sulcate for half its length, the other brown to its base
(d) Each flower has style brown to base and ovary also brown; one has a trace of brown at the base of the calyx tube	Both flowers brown and withered with recurved sepals; pedicel of one brown and sulcate for 1 cm., the other to its base
<i>Controls:</i> One flower at the node next below (c) has its style brown for 1 mm.; otherwise there is no distinct discoloration on any of the non-inoculated flowers of this branch	Some of the non-inoculated flowers still show no discoloration whatever, others have brown stigmas and one has its style brown for 3 mm.

*Results on the 10th and 12th days after inoculation.*

## Branch I.

MAY 21	MAY 23
(a) 1. The discoloration at base of pedicel extends for 1.5 cm. upwards 2. This flower bears small grey <i>Monilia</i> pustules	Both flowers are withered to base; the leaves round the base of the umbel are wilting
(b) 1. Style, ovary and base of calyx tube brown 2. Pedicel brown for 3 mm. from the calyx downwards; the stamens bear <i>Monilia</i> pustules; the flower is detached at its base but is attached to the other flower by its stamens	1. Flower itself brown; pedicel still green but somewhat sulcate 2. Stamens still entangled with those of No. 1
(c) The pedicels of both flowers are brown to the base and bear <i>Monilia</i> pustules	Both flowers quite withered to base; pedicels bear pustules
(d) 1. Calyx tube and 1 mm. of pedicel brown 2. The pedicel now bears pustules	1. Flower brown to base of the pedicel 2. No further evident change
<i>Controls:</i> The non-inoculated flowers have discoloured stigmas and some have styles brown for about 1 mm., but only one flower is quite dead	The non-inoculated umbels are setting into fruit, except the one at node distal to (a) and one other flower which is dead

## Branch III.

MAY 21	MAY 23
(a) Umbel broken off (probably during a thunderstorm of previous evening)	—
(b) 1. No further change evident  2. Calyx tube and half the pedicel brown	1. Style brown to base and the discoloration is extending in the upper half of the ovary, which however has increased in size 2. Broken off
(c) One flower is detached; the pedicel of the other is brown for three-quarters of its length	Flower withered to base of pedicel
(d) Both flowers brown to base of pedicels; one pedicel bears <i>Monilia</i> pustules	Both flowers quite withered; the leaves round the base of the umbel are wilting and their petioles are brown at the base only ( <i>i.e.</i> they are being invaded from the point of insertion on the fruiting spur)
<i>Controls:</i> The non-inoculated flowers generally show a discoloration of the stigmas and a portion of the style (usually about 1 mm.)	The non-inoculated umbels are now setting fruit

*Result five weeks after inoculation.*

On June 14 the five branches treated showed results of inoculation to be as follows:

## Branch I.

This branch was dead at node *c* and from this node distally to the tip of the branch, which has evidently been girdled by a canker at node *c*.

At node *d* the spur was dead but no canker had arisen round its base.

## Branch II.

The branch was dead from node *b* to the tip (*i.e.* branch girdled at *b*). Gum was oozing from the dead spur at node *c*.

## Branch III.

- (a) Spur dead but no canker present on the branch.
- (b) and (c). Both spurs alive (*i.e.* leaves showed no signs of wilting) but the flowers had been killed so no fruit had set.
- (d) Spur dead: there was no evident canker at this node but gum was oozing through the bark just below the node.

## Branch IV.

- (a) Spur dead: a canker half girdled the branch: a large gum globule was present on the branch near the insertion of the spur.
- (b) The leaves at this node were alive: the dead flowers were still persisting and the spur was gumming round the base of the flowers.
- (c) Spur dead: a gum globule was present near the insertion of the pedicels: no canker had developed.

## Branch V.

This branch was dead from node *e* to the tip: at *d* gum was present and an incipient canker was indicated by a slight depression of the bark on the branch round the base of the spur.

On the rest of the tree at this stage there were only five dead spurs altogether and no branches had been killed except in the case of those produced by artificial inoculation.

*General Results of the Inoculation of the Thirty-seven Flowers.*

After inoculation the flowers were not examined until the 3rd day; by that time all the stigmas were brown and, with the exception of six flowers, the discoloration had extended from the stigmas down the styles to a distance of 1 to 5 mm. By the following day the browning had proceeded several millimetres further so that in some flowers it had reached the base of the style and in two cases was encroaching on the ovary itself.

On the 6th day the ovary in several of the flowers was brown to the base and the discoloration was also to be seen on the exterior of the flower at the point of insertion of the flower on the pedicel and was extending downwards along the pedicel and upwards towards the tips of the calyx lobes.

8th day: many of the flowers were withered, the calyx lobes being brown and withered, and the pedicels brown and longitudinally sulcate to the point of insertion on the receptacle of the umbel (*i.e.* the tip of the flowering spur); in a few the tissues of the spur itself were invaded as shown by the fact that the discoloration had reached the base of the pedicel of one flower of the pair and was extending *upwards* from the base of the pedicel of the second flower.

At this stage the rest of the flowers on the tree showed generally only a normal discoloration of the stigmas; in a few it had extended for a short distance down the style. Two umbels however showed a browning of style and ovary with the discoloration extending to the pedicels, and it was evident that these had become infected also, the infection probably having arisen by conidia carried by bees from artificially inoculated flowers. There were no flowers quite withered except among those on which conidia had been placed at the beginning of the experiment.

10th day: the disease had extended further into the flowers and pedicels and on some of them *Monilia* pustules with conidia were present. In three cases the fungus had advanced into the tissues of the spurs and by cutting off supplies to the leaves round the bases of the flowers, produced a wilting of the leaves.

12th day: the leaves of other spurs were also wilting and examination showed that the discoloration began at the base of the petiole, thus showing that the disease was invading the leaves from the spur.

With regard to the flowering spurs which had not been artificially inoculated (some hundreds in number) on the same tree, only two at this time bore withered flowers and leaves and one other had dead flowers. These three spurs were all in the neighbourhood of inoculated umbels, being from 9 to 15 inches from the nearest flowers inoculated from the culture; their proximity to the artificially inoculated flowers suggests that bees had carried conidia from the stigmas of the latter to those of neighbouring flowers.

5 weeks: all the inoculated flowers had been dead for some time; at some of the nodes the disease had not only killed the flowering spur but had reached the branch and girdled it (so causing the death of the distal portion) or had produced a canker partly girdling the branch. In some instances gum had issued from the bases of the infected spurs.

It is evident therefore that the strain of *Monilia cinerea* used in this experiment, a strain obtained from a twig affected with the "Wither Tip" disease readily infects plum flowers, invades the spurs, and is able to produce cankers on the branches.

*Experiment 2.*

While the experiment recorded in the preceding pages was in progress, the stigma of a single flower, one of an umbel consisting of two flowers on a young plum tree growing in a pot in the open, was inoculated for the purpose of obtaining a photographic record of a diseased flower at various stages after infection. Unfortunately a storm removed the flower on the ninth day after inoculation and by that time there were no other flowers available suitable for a repetition of the experiment. However, three photographs were secured and these show the earlier stages of the disease after inoculation of the stigma with conidia of the fungus (Pl. IX, Figs. 7, 8 and 9). The second flower of the umbel served as a control and in the photographs is seen to the left of the infected one.

Inoculation was effected by bringing a particle of potato bearing conidial tufts into contact with the stigma as in Experiment 1, on May 14. The condition of the flower on the days on which the photographs were obtained was as follows:

May 19: style of inoculated flower brown for 3 mm.; the control flower showed no discoloration even of the stigma; the petals of both flowers had fallen by this time (Fig. 7).

May 21: style of inoculated flower brown to base and the discoloration had extended into the ovary (Fig. 8).

May 23: whole of pistil brown, the calyx lobes were becoming withered and recurved: stamens collapsed (Fig. 9).

(c) INOCULATION OF IMMATURE PLUMS ON TREES IN THE  
PLANTATION.

*Experiment 1.*

The experiment was carried out on young green plums (variety Victoria) at a stage when they were about 2 cm. in length, the date when the inoculations were made being June 20.

Method: conidia were removed with a sterilized scalpel from the surface of a culture on steamed potato and floated on sterile water in a watch-glass which had been previously passed through a flame and allowed to cool. The inoculations consisted in applying with a flamed platinum wire loop drops of the water containing conidia.

The plums were treated in one of three ways:

(1) A drop of the conidia-containing water was applied to the stalk end of the plum (junction of stalk and fruit) without injuring the fruit,

(2) Pairs of plums were selected in which the two of each pair were in contact; one plum of each pair was inoculated by pricking with a sterile needle (a single puncture being made in each case), piercing the skin, and applying a drop of the water with conidia to the wound.

(3) Controls: these plums were each wounded with a single puncture but no conidia were placed on the wound.

The fruiting spurs at which the inoculations were made were labelled and numbered as follows:

1 } Treated as in method (1); both plums at each of the two nodes  
2 } were inoculated without wounding by conidia in a drop of water  
   } placed on the uninjured skin.

3 } At each of these four nodes, one of each pair of plums was  
4 } inoculated as in method (2); the other plum of each pair was  
5 } left untreated in any way.  
6 }

c } Controls: both plums at each of the two nodes were pierced by  
c } a single prick with a sterilized needle but not inoculated.

The above were all on one tree; on the next tree in the row a similar series of inoculations were made, *i.e.*:

7 }  
8 } Treated as nodes 3-6.  
9 }  
10 }

11 } Treated as nodes 1 and 2.  
12 }

c } Controls treated as c, c on other tree.  
c }

Thus in all eight plums were treated in each of the three ways.

No rot occurred throughout the experiment on any of those inoculated by placing conidia on the uninjured skin (*i.e.* plums at nodes 1, 2, 11 and 12), nor on those which had been punctured only.

On those inoculated by placing drops of water containing conidia on the punctures the results were as follows:

June 23: no change to be detected in any of them except No. 6 on which a discoloured<sup>1</sup> area extended for 2 to 3 mm. round the wound.

<sup>1</sup> The rot was indicated externally by a dull purple brown discoloration of the skin which was distinctly marked off from the green of the portion to which the rot had not extended.

The progress of the disease to the end of the month is shown in the table:

	JUNE 26	JUNE 28	JUNE 30
3.	Rot extends 2-10 mm. from the wound	Three-quarters of surface discoloured, numerous small grey pustules present	Whole surface discoloured and bearing pustules; skin sulcate
4.	No change	No change	No change
5.	No change	No change	No change
6.	More than half the surface discoloured; numerous minute pustules present	Whole of the surface discoloured and bearing numerous pustules	The other plum of this pair is attached to the inoculated one by a thickened pad of hyphae and a discoloration extends over it for 2-5 mm. from the point of contact
7.	Rot extends 4-10 mm. from the wound	Three-quarters of the surface affected; numerous pustules	Both plums had fallen to the ground
8.	About half the surface discoloured; no pustules	Whole surface affected; numerous pustules	Surface sulcate; a hyphal pad attaches the other plum to the affected one, though former shows no rot
9.	No change	No change	No change
10.	Nearly half the surface affected; no pustules	Nearly the whole of the surface is discoloured and bears numerous small pustules	Whole surface affected; no hyphal pad and the other plum is not attached and is not infected

The later stages of the disease in the same plums are shown in the next table:

	JULY 3	JULY 11	JULY 20
3.	Inoculated plum much shrunken and sulcate	Inoculated plum fallen; the other shows no rot	The plum not inoculated still healthy
4.	Drop of gum at wound; slight discoloration	No further change	The gum has dried; black spot 2 mm. diam. round wound
5.	No change	No change	No change
6.	Inoculated plum much shrunken and sulcate; three-quarters of the surface of the second plum is discoloured and bears numerous pustules	Both plums dry and shrivelled; stalk of inoculated plum brown to base, stalk of the other brown nearly to base	Stalks of both brown to base; gum is issuing from the apex of the spur
7.	(Plum fallen)	—	—
8.	Inoculated plum shrunken and sulcate; the other is discoloured over three-quarters of its surface	Both dry and shrivelled; pustules present; stalks brown to base	No further evident change
9.	Drop of gum at wound	No rot	No rot
10.	Inoculated plum shrunken and sulcate; no rot on the other	Hyphal pad present at point of contact of the two plums and the rot is invading the second plum	Both shrunken and wrinkled; surfaces bear numerous pustules; stalks brown to base

*Experiment 2.*

On June 26, when the plums were about 2.5 cm. long and still quite green, a series of inoculations, similar to that described under Experiment 1, was carried out on two other trees, the only difference being a modification in the manipulation when applying the conidia to the fruit. The inoculations in this instance were made by placing the conidia-bearing surface of a culture on steamed potato (the potato being cut up into small pieces and used as in the experiments on plum flowers) on the fruit; in the case of those plums inoculated through wounds the conidia were brought in contact with the punctured skin and the needle then inserted again in the wound to ensure contact of the conidia with the cells surrounding the wound.

As in the previous experiment no rot occurred except in those plums which had been punctured and conidia placed in the wounds. The modification of the former method of inoculation resulted in more uniform results and each of the eight plums showed distinct evidence on the second day after the treatment that a rot had set in; thus at each of the nodes numbered 3 to 6 the inoculated plums showed a purple discoloration extending for 2 mm. from the wound, while at nodes 7 to 10 the result was similar except that the colour of the affected tissues was not so distinctly marked.

The rapidity with which the rot extended through the infected plums is shown in the accompanying tables. As in Experiment 1, plums at nodes 1, 2, 11 and 12 were inoculated by conidia being placed on the uninjured skin, and again eight plums were punctured but not inoculated; these are not shown in the table since they showed no signs of rot throughout the experiment.

Extent of the affected areas on the 2nd, 4th and 7th days after inoculation made by placing conidia in punctures: the figures indicate how far the discoloration had extended from the wound:

Node	JUNE 28		JUNE 30		JULY 3	
	2 mm.		9-15 mm.			
3	2 mm.		9-15 mm.		Whole surface a dull purple brown and bearing pustules	
4	2		5-15		Whole surface a dull purple brown and bearing pustules	
5	2		8-12		Whole surface a dull purple brown and bearing pustules	
6	2		10-15		As in No. 3 but the other plum of the pair is attached by a pad of hyphae	
7	2		5-10		Whole surface discoloured and bearing pustules	
8	2		8-12		Whole surface discoloured and bearing pustules	
9	2		5-10		Whole surface discoloured and bearing pustules	
10	2		7-12		As in No. 6	

Later results were as follows:

JULY 11	JULY 20
3. Inoculated plum shrivelled, the other plum attached to it by hyphal pad and discoloured for about one-third of its surface. These two plums were removed and photographed on this date (see Pl. IX, Fig. 5)	Both plums quite dry, wrinkled and much shrunken, surface of both bearing numerous pustules with powdery conidia; stalks brown to the base
4. Inoculated plum dry and shrunken, stalk brown to base; the other plum wrinkled, its whole surface discoloured and bearing numerous pustules; browning extending along stalk for 2 mm. from the plum	No further change evident; no rot on the second plum
5. Inoculated plum with stalk brown to base	Inoculated plum detached from spur but remains suspended by its attachment to the other
6. Both plums shrunken and wrinkled; stalk of each brown and sulcate	No further change noticeable
7. Inoculated plum wrinkled and shrunken, numerous pustules present, stalk brown to base, and detached from the spur but fruit supported by its attachment to the other plum; the latter shrunken, bearing numerous pustules scattered over the discoloured surface, stalk brown to base	Inoculated plum wrinkled and shrunken, stalk brown to base and detached from spur but plum remains suspended by attachment to the other
8. Inoculated plum shrunken, stalk brown nearly to base, the other plum attached by hyphal pad but not showing any rot	Still no rot in the second plum
9. Inoculated plum on the ground, surface wrinkled, no rot in second plum	Both plums fallen
10. Inoculated plum wrinkled and shrunken, stalk brown to base; the second plum is somewhat shrunken, has numerous pustules scattered over the surface, stalk brown nearly to base	

The experiments prove conclusively that the strain of *Monilia cinerea* obtained from a withered plum twig was able to produce a "brown-rot" of the fruit when the conidia have access to wounds through the skin; conidia placed on the uninjured skin gave negative results in all cases and it would appear therefore that conidia falling on uninjured plums are unable to produce the rot. When however a healthy plum is in contact with an infected one the mycelium in the latter may produce a dense pad of hyphae at the point of contact, thus enabling it to penetrate the skin at that spot and set up a rot in the adjacent plum. When two plums are in contact the cuticle is probably injured by the frequent chafing resulting from the motion of the branch in the wind, for it was noticed that round the point of contact the waxy "bloom" was removed from the skin.

To supplement Experiment 2 another experiment was carried out at the same time in which one plum of a cluster of five was inoculated at a puncture. The disease extended rapidly through the plum primarily infected, then from that to the two in contact with it and from those to the remaining two so that eventually all five were affected. The result as seen on July 21 is shown in Pl. IX, Fig. 6, the plum in the middle being the one inoculated through a puncture on June 26.

It is evident therefore that the twigs affected with the "Wither Tip" disease are a source of danger to the fruit, for although wounds are necessary to enable the fungus to gain an entrance in the first place, observation has shown that injuries severe enough to rupture the skin are not infrequent; bruises and abrasions occur during storms and biting insects pierce the skin and leave open wounds.

#### (d) INOCULATION OF APPLE FLOWERS.

Since the strain of *Monilia cinerea* obtained from the plum twig and used in the experiments described in the preceding pages was morphologically similar to the form which produces the "Blossom Wilt and Canker" disease of apple trees it was to be expected that it too was capable of producing the "Blossom Wilt" when inoculated into apple flowers, although it is to be observed that the particular strain used in the experiments on plum flowers and fruit could be distinguished *in culture* from that which so readily infects the flowers of the apple, in that the former remains hyaline<sup>1</sup> in agar cultures containing prune juice while the latter always produces a dark brown coloration when growing on that medium. Experiments were therefore carried out to ascertain whether this hyaline strain from the plum could attack the flowers and spurs of the apple.

#### *Experiment 1.*

Young trees of the Worcester Pearmain variety growing in pots were used. A similar experiment on this variety carried out in 1917 but using a strain obtained from a *Monilia* canker of an apple tree resulted in the typical blossom wilt condition in two out of six flowers inoculated. In the present experiment, using the hyaline strain employed in inoculating the plum flowers and fruit, seven flowers were inoculated, viz., the central flower of each of seven umbels. Newly opened flowers (*i.e.* those

<sup>1</sup> One tube culture of this strain did give rise to irregularly distributed brownish patches but even then it was easily distinguished from the much darker cultures of the various strains obtained from apple trees.

which had expanded their petals during the preceding 24 hours) were selected, for in the experiments of the previous years it had been found that such flowers had been more readily attacked than older flowers.

Three of the flowers (numbered 1, 2 and 3) were inoculated on May 14; two others of the same age were left untreated and labelled as controls ( $c_1$  and  $c_2$ ). By the following day other flowers had opened and four of these were inoculated (numbered 4, 5, 6 and 7); three similar ones were kept as controls ( $c_3$ ,  $c_4$  and  $c_5$ ). No difficulty was experienced in obtaining conidia for the inoculations as this strain of *Monilia* produces numerous conidia on sterilized potato.

The result is shown in the table (p. 51).

The early inception of a brown discoloration of the inoculated flowers afforded evidence that infection had occurred. Later, all the inoculated flowers fell away and in no case was there any evidence that the disease had passed from the infected flowers into the tissues of the spur, and the leaves borne on these spurs remained green and healthy. It would appear therefore that the strain of *Monilia cinerea* used in this experiment is able to infect and cause the death of apple flowers but is unable to penetrate further than the base of the pedicels.

This result was particularly interesting as it suggested that there were strains within the same morphological species, *Monilia cinerea*, with different powers of infection. For confirmation of this it was decided to repeat the experiment side by side with one in which a strain from an apple tree was used. To obtain results strictly comparable one tree was selected, one of the Warner's King variety growing in the College plantation; umbels on one side of the tree were inoculated with the plum strain, those on the other with the apple strain. Each of the two strains had been isolated during the previous winter so that there was no question that either had lost its virulency from long continued growth on artificially prepared culture media and it had been already ascertained that the plum strain readily attacked plum flowers and spurs.

### *Experiment 2.*

*Method.* Particles bearing conidial tufts were cut from a culture of the "Wither Tip" strain growing on sterilized potato. These particles were placed in a sterile petri dish and taken to the plantation, where, by means of needles (previously flamed), they were inserted in the flowers to be inoculated in such a way that the conidiophores were brought in contact with the stigmas. That many of the conidia adhered was evident,

*Table showing result after inoculating apple flowers with a strain of Monilia cinerea obtained from a withered plum twig.*

	MAY 19	MAY 21	MAY 24	MAY 29
1	Styles brown for half their length (about 4 mm.)	Styles brown to base	Stamens collapsed; calyx lobes becoming desiccated and brown	Flower had become detached
2	Styles brown for 4 mm.	Styles brown to base	Some of the stamens collapsed; calyx lobes becoming desiccated	Calyx and stamens withered
3	Styles brown for 1-2 mm.	Styles brown to base	Stamens collapsed; calyx lobes becoming desiccated	Flower had become detached
c <sub>1</sub>	Slight discoloration of stigmas only	Stigmas brown; one style with slight discoloration	Styles brown for about half their length; stamens upright	Calyx and stamens withered
c <sub>2</sub>	No discoloration even of the stigmas	Stigmas and one style brown	Styles brown for about half their length; stamens upright	Calyx and stamens withered
4	No discoloration	Stigmas brown	Styles brown for about half their length	Calyx and stamens withered
5	Distinct browning of the stigmas and of one style for 1 mm.	Styles brown to base	Styles brown to base; some of the stamens collapsed	Calyx and stamens withered
6	Distinct browning of the stigmas	Styles brown to base	Styles brown to base; stamens all collapsed except two	Calyx and stamens withered
7	Stigmas brown	Stigmas brown	Styles brown to base; stamens spreading	Calyx and stamens withered
c <sub>2</sub>	No discoloration even of the stigmas	Slight discoloration of the stigmas	Stigmas brown; slight browning of styles; stamens upright	Calyx and stamens withered
c <sub>3</sub>	No discoloration even of the stigmas	Slight discoloration of the stigmas	Stigmas brown; slight browning of styles; stamens upright	Calyx and stamens withered
c <sub>4</sub>	No discoloration even of the stigmas	Slight discoloration of the stigmas	Styles brown for half their length; stamens upright	Calyx and stamens withered

for in some cases it was seen that the stigmas were greyish after the application.

Four umbels were so treated, the central flower (which opens first) and one or two others in each umbel being inoculated. The spurs bearing these umbels were numbered and labelled, and notes were made respecting the situation of the inoculated flowers in the umbels.

*Umbel No. 1.* Three flowers inoculated.  
 „ *No. 2.* Two „ „  
 „ *No. 3.* Three „ „  
 „ *No. 4.* Two „ „

Thus in this experiment ten flowers were in all inoculated with the "Wither Tip" strain of *Monilia*.

In order to avoid any inter-contamination between the two strains, the particles of potato were replaced in the dish and taken back to the laboratory. The needles were re-flamed and particles of a potato culture of the "Blossom Wilt" strain of *Monilia* from apple trees were then prepared and inoculations made on flowers on the opposite side of the same tree. In this case only one flower of each of four umbels was inoculated.

The inoculations were made on May 17 and the results as observed at intervals of a few days are here shown for comparison:

*Apple Flowers inoculated May 17.*

"Wither Tip" strain obtained from a plum twig                      "Blossom Wilt" strain obtained from an apple tree

MAY 20

All the inoculated flowers had brown stigmas; some of the styles were also discoloured for 1 mm.	All the inoculated flowers had brown stigmas and the styles were brown for 1-3 mm. No other flowers on these branches showed any discoloration
The rest of the flowers of the same umbels and those of other umbels in the vicinity showed no discoloration whatever	

MAY 23

The styles of the inoculated flowers were brown for from one-half to the whole of their length.	The styles of all the four inoculated flowers were brown to the base.
Most of the untreated flowers showed no discoloration at all; in a few cases a slight browning of the stigmas was seen and one style was brown for about half its length	Uninoculated flowers on the same side of the tree showed a slight discoloration of the stigmas only

MAY 26

<i>Umbel No. 1.</i> Styles of all three inoculated flowers brown to base; in two of the flowers the discoloration was also extending into the ovary and the stamens were drooping or quite collapsed	<i>No. 1.</i> Inoculated flower was brown with collapsed stamens, pedicel brown and shrunken (longitudinally sulcate), bases of filaments with pustules of the fungus
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## May 26 (cont.)

- No. 2. The styles of one flower were brown almost to the base; in the other flower the styles were brown throughout their whole length
- No. 3. All styles of the three flowers brown to base; stamens upright
- No. 4. Styles of both flowers brown to base; stamens upright. Uninoculated flowers had, in general, brown stigmas only but in some the discoloration extended half-way down the styles; no drooping stamens observed
- No. 2. Flower with stamens collapsed, calyx lobes withering, leaves round base of umbel beginning to wilt
- No. 3. Stamens collapsed; calyx lobes withering; leaves show a slight wilting
- No. 4. Stamens collapsed, but no wilting of leaves noticeable. Control flowers of the same age in the vicinity had styles brown for about half their length, there was no withering of calyx lobes and the stamens were all upright

## MAY 29

- No. 1. Two of the flowers had fallen away, the third had remained apparently unchanged since the 26th
- No. 2. Styles brown to base, and in one flower the calyx lobes were withered
- No. 3. No further change noticeable except that in one flower the stamens were drooping
- No. 4. No further change noticeable. Many of the control flowers by this time had styles brown to base; stamens generally upright; calyx lobes not withered
- In all four the infection had by this date extended from the inoculated flower into the tissues of the spur as shown by the fact that in each case the leaves round the base of the umbel of flowers showed a distinct wilting, were turning brown and their margins were more or less curved inward

## JUNE 6

There was no wilting of the leaves on any of the four spurs; the inoculated flowers had all failed to set into fruit, they had become withered and *fallen off*; of the uninoculated flowers some were setting into fruit:

- No. 1. One flower setting into fruit
- No. 2. None setting
- No. 3. Two flowers setting
- No. 4. Two flowers setting
- The young fruit on these spurs were 1-1.5 cm. in length

## JUNE 4

All the flowers (those untreated as well as those inoculated) and the leaves of the four spurs were quite withered; the dead flowers *remained in position* on the spurs, this condition being typical of the "Blossom Wilt" disease of the apple tree

- No. 4 was removed and mycelium was found in the tissues of the spur

## JUNE 7

The other three spurs were removed and cut longitudinally; in each case the young growth of the spur (bearing the leaves and flowers) was quite brown throughout and the browning had extended along the bark of the older portion for a distance of about 3 cm.

## (e) DEDUCTIONS FROM RESULTS OF INOCULATION EXPERIMENTS.

The experiments show that the particular strain of *Monilia cinerea* obtained from the plum twig is less virulent as a parasite on the apple than the apple blossom strain itself since it was unable to establish itself in the spurs of the trees inoculated, and this in spite of the fact that the method of inoculation adopted favoured the "Wither Tip" strain; thus in the second experiment ten flowers were inoculated with this strain as

against four treated with the apple "blossom-wilt" form, and the conidia of the culture used in the inoculations were more abundant, so there could be no doubt therefore that conidia were successfully applied to the stigmas.

The progress of the disease was almost the same for both (the "blossom-wilt" strain advanced a little more rapidly than the "wither tip" strain) until the base of the pedicel was reached, then in the one case the infected flower fell off without causing any further injury, in the other the flower not only remained in position but the disease extended from it into the tissues of the spur and affected the whole cluster of flowers and leaves.

In this connection it is to be remarked that Woronin<sup>(12)</sup> in his inoculation experiments with *Monilia cinerea* and *M. fructigena* was unable to produce with *M. cinerea* any infection of apple flowers except on the stigmas themselves. Thus he states<sup>1</sup>: "Die Gonidien der *Sclerotinia cinerea* wachsen auch unter der Einwirkung des Narbensaftes in Keimfäden aus, dieselben können aber nur den Griffel etwas angreifen und sind gar nicht im Stande weiter in die Apfelblüte einzudringen." It is probable therefore that Woronin worked with a strain of *M. cinerea* obtained from either cherry or plum, since I have had no difficulty whatever in infecting flowering spurs and branches of apple trees by inoculating the stigmas of the flowers with a strain of *M. cinerea* from an apple tree.

Whether other strains of *Monilia cinerea* found on "stone-fruit" trees behave as the "wither tip" strain used in the experiments has not yet been determined and it is proposed to carry out other experiments to ascertain whether there are strains occurring on plums and cherries capable of infecting the spurs of the apple through the flowers. The economic aspect of this problem is involved in the fact that plum trees are often interplanted with apple trees in mixed orchards and the possibility of the former proving sources of infection for the latter or *vice versa* is a point of importance to the fruit grower.

As already stated the "wither tip" strain used was one which usually remains quite hyaline when growing on prune-juice agar; others which have been isolated have more nearly approached the apple "blossom-wilt" form in that they produce a brown coloration when growing on that medium; one in particular (strain *g* of the table on p. 35) is in this respect practically indistinguishable from the apple strains. The "wither tip" strains which have been isolated and cultivated all produce

<sup>1</sup> *Loc. cit.* p. 25.

conidia readily when growing on semi-cylinders of sterilized potato in Roux' tubes, the tufts of conidiophores being produced in more or less continuous dark-grey parallel zones on the upper (thinner) half of the potato. The apple "blossom-wilt" strains on the other hand have always produced but a scanty crop of conidia when growing on potato, the conidiophores developing in relatively few isolated tufts.

The results afford evidence of the occurrence of biologic forms within the species *Monilia cinerea*. That forms morphologically similar but distinct in their biological relations with the host plant, occur among the obligate parasites, the *Uredineae* and the *Erysiphaceae*, has been fully proved<sup>(9)</sup> and there is evidence that such forms occur also in other groups; thus Grossenbacher and Duggar<sup>(8)</sup> conclude that *Botryosphaeria ribis* occurs as two forms, one parasitic on currant shoots, the other apparently saprophytic only and they find that the two forms can be distinguished by cultural characters.

In *Monilia cinerea* the two strains which have behaved as biologic forms can also be distinguished culturally and this suggests that biochemical methods may throw some light on the physiological relations of biologic forms in those fungi which, like *Botryosphaeria ribis* and *Monilia* spp., allow of culture on artificially prepared media. Alsberg and Black<sup>(3)</sup> working with several species of *Penicillium* pointed out in 1913 the desirability of applying biochemical methods in distinguishing the lower forms of fungi which are not readily to be distinguished by their morphological characters.

In the case of the two strains of *Monilia cinerea*, the difference in coloration suggested a differential action of some oxidising enzyme and preliminary experiments have shown that one strain produces a substance of an enzymic nature, probably an oxidase, much more readily than the other. These experiments are being continued for these two strains and will be amplified by application to other strains.

#### IV. CONTROL MEASURES.

From the inoculation experiments recorded in this paper it is evident that the form of *Monilia cinerea* which occurs on the dead twigs of plum trees is capable of infecting the flowers and causing a "brown rot" of the fruit of the plum tree, and that such twigs if not removed serve as sources of infection since they produce pulverulent pustules of conidia by the time the trees are in flower. Although inoculation of the leaves with pure cultures of the fungus have, up to the present, given negative

results it would seem that the young leaves also become infected from the dead shoots under certain conditions not yet understood. In severe attacks many of the leading shoots are killed and fruit-buds are replaced by the weak "unripe" twigs, that are induced to grow out. The diseased twigs should therefore wherever possible be removed from the trees together with all rotting and mummied fruit.

Some growers, at the time the fruit is gathered, encourage their pickers to remove all the plums affected with "brown rot." If this system became more general and could be extended to the pinching off of all "withered tips" also, the amount of fruit destroyed each year by "brown rot" would be reduced considerably. As an alternative the dead twigs could be removed in winter when, as a rule, they are easily distinguished by the recurved apex and by the persistent withered leaves. Where practicable they should be removed and burnt but in any case they are far less dangerous on the ground than if left on the tree. To test this point thirty-nine withered tips were removed from three trees and placed on the ground under the trees in September 1916; when examined in the spring of 1917 five of them only had pustules of the fungus, whereas of those left on the trees all, with very few exceptions, produced pustules.

As in the case of the "Blossom Wilt" disease of apple trees spraying with ordinary fungicides is not likely to prove nearly so efficacious as the removal of the dead twigs and diseased fruit. The stigmas of the open flowers are liable to become infected and these cannot be covered with a spray fluid without great risk of injury to the blossom. The fruit becomes infected through wounds and therefore again spraying cannot prove sufficiently protective. A spray that would kill the pustules or render them sterile might be effective but since the diseased twigs are very slender and often at the extreme tips of the branches great care would be necessary during the application to cover them with the spray and large quantities of the fluid would be wasted.

Experiments however were carried out to ascertain the effect of fungicides on the pustules borne by diseased twigs, attention being confined to preventing the pustules from shedding their conidia during that period of the year when new infection occurred. Twigs bearing pulverulent pustules were taken from the trees and atomized with the various spray fluids, then placed in the open, that they might be subjected to ordinary atmospheric conditions, and examined from time to time.

It was found that the commonly employed fungicides such as Bordeaux Mixture, soda Bordeaux ("Burgundy" Mixture), cupram, eau

celeste and lime-sulphur, were almost useless in this respect since, as a rule, they failed even to wet the pustules. They became more effective however when prepared so as to contain 1 per cent. soft soap<sup>1</sup> for then the pustules were wetted and the surface layer of conidia was killed. Ammonium sulphide with soft soap, as recommended by Eyre and Salmon (5, 6) for use against the oidium stage of the *Erysiphaceae*, was also tried with similar result. The pustules were thus prevented from shedding conidia for some time but they were not killed and during a period of wet weather the pustules evinced a tendency to grow out through the superficial barren layer and once more become powdery. Under favourable dry atmospheric conditions therefore such fungicides, when used with soap to reduce their surface tension and increase their wetting properties, would tend to check the spread of the disease if applied just before the flower buds open, to render the pustules non-infective during the flowering period, and again when the fruit has set to prevent the dispersion of the conidia while the fruit is growing. They are not to be relied on however from the fact that the pustules themselves remain alive and re-develop, producing fresh crops of conidia, during periods of moist weather.

Better results were obtained with a solution consisting of 1 per cent. caustic soda and 1 per cent. soft soap, the pustules remaining dark brown for fully three weeks after the application of the mixture; this solution would in practice be used as a "winter-wash" as its caustic properties would cause serious damage to growing shoots. Experiments with this spray-fluid have not been carried out in the open on plum trees, but results of trials on apple trees bearing similar pustules of the "Blossom Wilt" *Monilia* were not such as to warrant its recommendation.

#### V. SUMMARY AND CONCLUSIONS.

1. In the summer of 1916 many plum trees in Kent were affected with a disease which caused the wilting and death of the tips of young twigs.

2. On each diseased shoot one or two leaves became infected and the disease extended into the tissues of the shoot causing the wilting and death of that portion distal to the node bearing the withered leaf.

3. Such twigs bore pustules of *Monilia cinerea* Bon. during the following winter and spring.

<sup>1</sup> It was found that soft soap could be successfully mixed with each of the sprays mentioned except lime-sulphur.

4. Inoculation of plum leaves with pure cultures of a strain of the fungus obtained from a withered twig gave negative results.

5. Inoculation of the stigmas of plum flowers resulted in every case in infection and consequent death of the flowers; in some instances the infection not only killed the flowering spur but invaded the branch and formed a canker.

6. Inoculation of the fruit gave negative results on uninjured plums, but when the conidia were applied to wounds they produced a "brown rot" which rapidly extended through the fruit and infected other plums which were in contact with those primarily inoculated.

7. Inoculation of apple flowers with conidia of the "wither tip" strain resulted in the death of the inoculated flowers only; these fell off and infection extended no further. On the other hand inoculation of apple flowers with a "blossom wilt" strain from an apple tree not only caused infection of the treated flowers but the fungus extended also into the tissues of the spurs and killed all the flowers and leaves borne by these spurs.

8. The two strains of *Monilia cinerea* used in these experiments are indistinguishable morphologically and, since they are dissimilar in their powers of causing infection of the apple blossom, are to be considered as "biologic forms" or physiological strains. They can be distinguished by applying cultural and biochemical methods.

9. Spraying as a means of controlling the "Wither Tip" disease is not to be recommended. All diseased twigs and fruit affected with "brown rot" should be removed from the trees, otherwise they will prove sources of infection for the flowers and fruit of the following season.

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Fig. 1



Fig. 2





Fig. 4



Fig. 3





Fig. 8



Fig. 9



Fig. 7



Fig. 6

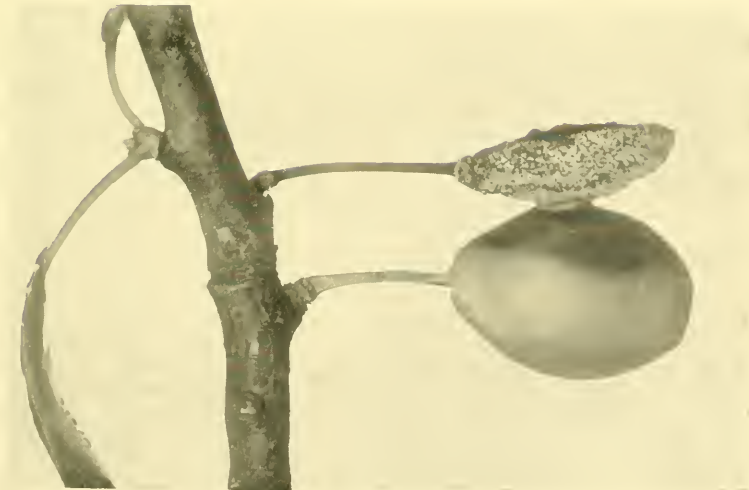


Fig. 5



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#### DESCRIPTION OF PLATES VII-IX.

- Fig. 1. A typical instance of "Wither Tip." Infection arose in the leaf on the left and, extending into the shoot, caused the wilting of the terminal portion.
- Fig. 2. In this case infection had occurred in two places; the apical portion is withered from infection through one of the upper leaves; a later attack originated in the second leaf from below, where a drop of gum is seen at the base of the affected leaf.
- Fig. 3. The death of the leading shoot has resulted in the outgrowth of two weak shoots with small pale leaves.
- Fig. 4. The "withered tips" as seen in winter and spring (photographed March 18, 1917); remains of dead leaves still present and *Monilia* pustules have appeared.
- Fig. 5. The plum on the right was inoculated on June 26 with conidia of a "wither tip" strain of *Monilia cinerea*. Result on July 11—the inoculated plum is covered with pustules of the fungus and the rot has extended into the other plum in contact with it; the pad of mycelium connecting the two is seen.
- Fig. 6. A group of five plums with *Monilia cinerea*. One of these plums was inoculated on June 26; the rot gradually extended through it and infected the rest. Result on July 21—all were infected and bore pustules of the fungus.
- Fig. 7. The upper flower was inoculated with conidia on May 14. Result on May 19—style discoloured for 3 mm.
- Fig. 8. The same on May 21: style brown to base.
- Fig. 9. The same on May 23: calyx lobes withered and recurved; stamens collapsed

## OVIPOSITION IN THE CELERY FLY.

BY T. H. TAYLOR.

(With one Text-figure.)

THE habits of the Celery Fly are comparatively easy to study, for, besides being conspicuously coloured and of fairly large size, the flies are obliging enough to proceed with their occupations when the observer approaches, gaily sporting their dappled wings and seeming but little embarrassed by his presence. A sunny afternoon is a favourable time for watching the flies lay their eggs, and although the details of the process are too minute to be seen from a distance, its general features can be followed without much trouble. After sunning itself on the upper surface of a leaf, a fly about to lay, crawls over the edge to the underside of the leaf, and, testing the surface with its tongue, proceeds to drive the tip of the ovipositor into the interior of the leaf. In a few seconds, the boring action ceases and is shortly followed by more generalised movements of the body such as in an insect are commonly associated with the process of egg-laying, and whose purpose is clearly to disengage an egg and pass it to the outside. Visiting other and often adjacent parts of the leaf, the insect lays two or three eggs one after another in quick succession, and then without displaying any further interest in the results of its labour flies off to fresh ground. If the leaf be now plucked and the lower surface examined with a lens, the punctures made by the ovipositor can be seen and also the eggs themselves each lying beneath the cuticle in a separate space in the parenchyma.

By imprisoning a fly in a glass tube or capsule and giving it a piece of celery leaf, one can watch the process of egg-laying under the microscope. After the pointed end of the ovipositor has pierced the epidermis, the body of the tube, two-edged and file-like, forming an efficient boring apparatus, passes into the tissue beneath and breaking down the cells around it prepares a cavity for the reception of the egg. Having cleared a suitable space, the fly charges the tube which, still extended into the leaf, has become for the moment relaxed and inert, and then, with a final effort expels the egg through the terminal opening and crawls away. The process from the insertion of the tube to its withdrawal lasts from about

35 to 50 seconds, the duration being influenced no doubt by the species and age of the leaf, the vigour of the fly and other factors. In captivity, a fly sometimes oviposits in a leaf while crawling on the upper surface, and on these occasions, probably because the tissue is more compact on this side, the process lasts somewhat longer. For example, it was noticed that a fly which spent about 50 seconds in passing an egg into a piece of celery leaf from above, required about 10 seconds less when inserting an egg from below.

At hatching, which takes place in about six days, the larva breaks through the egg-shell at the end pointing away from the puncture in the cuticle, and burrowing forwards, eats out at first a narrow gallery in the tissue, but after a few days changes its mode of attack, and mining in all directions gives rise to a wider cavity less regular in shape. Increasing in size as the larva feeds, the cavity thus produced often coalesces with others of the same kind, and, with these additions, forms a compound blister containing it may be several larvae—a circumstance which has perhaps given rise to the existing impression that the Celery Fly, like *Pegomyia* and other blister-making flies, lays its eggs upon the surface, whereas it resembles more closely such flies as the *Phytomyzidae*, which lay their eggs in the interior of leaves.



Celery-fly Egg in leaf of *Heraeleum*. showing puncture made by fly.  
(Drawn by Miss E. M. Wright.)

## AN EPITOME OF BACTERIAL DISEASES OF PLANTS IN GREAT BRITAIN AND IRELAND.

BY SYDNEY G. PAINE.

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THE study of bacteria in relation to plant diseases is a branch of plant pathology which has been largely neglected in this country. In fact it is unfortunate that plant pathology as a whole has not received the amount of attention at the hands of English botanists that its importance in agriculture and horticulture demands. Bacteriology in particular has suffered from neglect to such an extent that the knowledge of bacterial diseases of plants occurring in this country is limited to a very few diseases only. It would indeed be fortunate if this were due to the non-existence of others, but there is no reason to believe that the activities of bacterial parasites are less here than they are in other countries with a temperate climate. The unsatisfactory state of affairs was deplored by Prof. Potter in 1910<sup>(35)</sup> and since that time very little has been done to improve the position. The question calls for the urgent attention of botanists in order that this, which can only be described as a national disgrace, may be immediately remedied. Until quite recently no one in this country has applied himself solely to the study of bacterial diseases.

The leaflets of the Board of Agriculture include only six diseases attributed to bacteria<sup>(25)</sup> whereas in a general conspectus of bacterial diseases E. F. Smith<sup>(45)</sup> has compiled a list of 140 genera distributed through more than fifty families in which such diseases are known to occur.

Our present knowledge of bacterial diseases is mainly due to the American plant pathologists and the main reason why we in this country are so far behind the Americans in this respect is that we have no state-aided department of plant pathology which is in the least comparable with that of the American Bureau of Plant Industry. Other reasons are to be found in the facts that plant pathology and plant bacteriology in particular as a general rule form either no part or only a very subsidiary part of the curriculum of the botany student and that where such training is included in his curriculum the student is more attracted by the

mycological than by the bacteriological side of plant pathology. The investigation of bacterial parasitism in plants above all things demands of the plant pathologist an extremity of patience with which few perhaps are gifted. The difficulties met with in the isolation of the parasite from diseased plant tissues are infinitely greater than those encountered in the isolation of an animal parasite. The animal pathologist has in the blood a very specialised medium which excludes almost entirely the invasion of saprophytic forms; on the contrary, the sap of the plant cells is eminently suitable as a medium for the growth of many common bacteria, and, situated as the plant is in a soil containing upwards of five million organisms per gram, when once its defence against parasitism has been broken down by the entry of a parasite, many of these common soil organisms enter the diseased tissue and multiply luxuriantly often to the partial, and sometimes even to the total, exclusion of the original parasite. In attempts to isolate the parasite from potato stems affected with "Blackleg" the author spent several months battling with a multitude of saprophytes before success attended his efforts, and then only by chance was a colony of the parasite discovered on a plate containing some 200 others of which thirty had been already investigated and proved to be saprophytic organisms. In one investigation upon which he is at present engaged more than 400 cultures have already been made and many more will be necessary before the investigation is satisfactorily concluded. Again Smith and Townsend<sup>(44)</sup> worked most patiently for three years upon the "Crown Gall" disease before the causal organism was tracked to his lair. Another instance may be cited in emphasis of the difficulties encountered in this branch of pathology; Schiff-Giorgini<sup>(41)</sup> in investigating the Olive Knot disease worked for two years upon an organism thought to be *B. Oleae* which was later shown by Smith<sup>(43)</sup> to be a common soil organism and incapable of producing the disease. To quote from Smith<sup>(45)</sup>, "The labor involved is enormous and exacting to discouragement at times, the results come so slowly, so much must be done to be certain of so little, all because the organisms dealt with are very small—*how small*, we seldom realise!"

The British literature on bacterial diseases is so scattered and so fragmentary that it seems advisable to collect together the fragments and to "take stock" of our position. An attempt is therefore made in this article to bring together the known facts about our bacterial diseases in the hope that it may be useful to those engaged in diagnostic work, and that it may in some measure stimulate the advancement of this important branch of phytopathology.

## WHITE ROT OF TURNIPS AND OTHER VEGETABLES.

This disease investigated by Prof. Potter in 1900<sup>(36)</sup> was the first disease of bacterial origin to be recognised in this country. It is characterised by the complete rotting of the tissue attacked, the bacteria secreting an enzyme which has the power of dissolving away the middle lamella from between the cells thus destroying the coherence of the tissue and giving rise to the condition of a "Soft rot."

*Symptoms of the disease.* The first symptoms of disease appear in the autumn as a wilting and yellowing of the oldest leaves which droop to the ground, shrivel up and finally rot away. During a fortnight or three weeks the signs of disease progress inwards from the oldest to the youngest leaves until at the end of this period the plant has completely gone to the ground as a rotting, stinking mass. The root is found at this time to be partially or wholly reduced to a greyish white or brown pulpy mass.

*The parasite.* Potter was the first to isolate an organism in connection with this disease. He described a small unflagellate rod under the name *Pseudomonas destructans*. Johnson and Adams<sup>(19)</sup> isolated an organism from rotted turnips in the West of Ireland which they believed to be Potter's organism, and also found it to be unflagellate. They, however, draw attention to the close similarity of this to *Bacillus Oleraceae* isolated by Harrison<sup>(16)</sup>. Jones<sup>(22)</sup> obtained a culture of a second isolation from Potter and found the organism to be a bacillus, and Harding and Morse<sup>(22)</sup> have shown that under similar cultural conditions both Harrison's organism and Potter's second isolation are identical with *B. carotovorus* Jones. The writer obtained in 1912 a culture of *P. destructans* from Král's laboratory and a slide stained by Loeffler's method showed flagella very indistinctly but each organism appeared to have a single flagellum. In 1916 it was restained by Steven's modification of Van Ermengen's stain and it was then clearly seen that the majority of the organisms were unflagellate but that some, perhaps 10 per cent., were bacilli. That the number of flagella in bacteria is somewhat variable has been pointed out by Johnson and Adams<sup>(19)</sup> and the writer has found that *B. atrosepticus* grown on living turnips, and also sometimes on living potato, is present mainly in a unflagellate condition. Potter has agreed<sup>(37)</sup> that his organism may have been a bacillus. Upon the evidence, therefore, it seems well to abolish the name *P. destructans* until a definitely unflagellate organism answering exactly to the description given by Potter shall be again obtained from rotted turnips or other tissue.

The causal organism is then *B. carotovorus*, a rod-shaped organism of varying length motile by 3-6 peritrichous flagella. It stains well with the usual stains and is Gram negative<sup>1</sup>.

*Host plants and distribution.* The distribution of the disease seems to be general throughout Great Britain and Ireland and a great variety of hosts are liable to attack. *B. carotovorus* has been found by several investigators to be capable of producing rot in a great variety of plants, in the roots of carrot, white turnip, parsnip, rape, radish, salsify, in onion bulbs, hyacinth corms, cabbage, cauliflower, celery stalks and potato tubers. No rot has been produced in young carrots or parsnips, apple, pear, beetroot, sugar beet, swede turnips or tomato stems.

#### HEART-ROT OF CELERY.

A soft rot of celery, in which sometimes the petioles of the outer leaves only, but in more serious cases the heart and subsequently the whole plant, are reduced to a yellowish brown decaying mass, was described by Wormald in 1914(49) and an organism was isolated and named *B. apiovorus*. The disease had previously been observed in Ireland by Johnson and Adams in 1910(49) who had isolated an organism but had not studied it fully. In a later paper Wormald(50) gives the results of a comparison of his organism with a strain of *B. carotovorus*, which we have had growing in this laboratory since 1912 when it was obtained from America through the courtesy of Dr E. F. Smith. As the result of this later work Wormald concludes that the two organisms are identical and that "Heart-rot" of celery is the work of that omnivorous organism *B. carotovorus*.

#### "BLACKLEG" OF THE POTATO.

This is a disease which produces entire destruction of the plant when the attack occurs early in the season and a disastrous soft rot of the tubers during storage when, following a late attack in the field, a certain percentage of the tubers are so slightly affected at the time of lifting that their diseased condition goes unnoticed. The rot spreads from these diseased tubers to neighbouring healthy ones and the loss of the whole or a considerable part of the store frequently results.

<sup>1</sup> In order to save space no attempt is made in this article to give the full description of the cultural and physiological characters of the various organisms dealt with. These are readily available in the literature and where a full description of an organism is given in any paper to which reference is made an asterisk has been placed against the reference in the list of literature cited.

*Symptoms of the disease.* The first sign of disease is to be observed in the foliage. The leaves turn yellow or much paler green than healthy leaves and diseased plants can readily be recognised in the early stages by this character alone. At the same time they retain a rather erect position on the stem instead of spreading out horizontally and the edges exhibit a rolling towards the mid-rib. The rolling should not be confused with that of "Leaf-roll" since it is of cylindrical form rather than funnel shaped and there is entire absence of the pink or purple pigmentation characteristic of this disease. In the later stages of disease the leaves wilt and the whole plant assumes a brown to black colour and a very dejected appearance. The plants remain standing in the field in virtue of a special hardening of the three main vascular bundles of the stem. These quite early become browned for a considerable distance up the stem and are so hard that a sharp knife is needed to cut them transversely. The name "Blackleg" is derived from a characteristic blackening of the tissues of the stem commencing in the underground portion and extending to a height of two to three inches above the soil level. In the lower portion of the stem the pith is completely rotted away leaving a cavity in which fungal mycelium, easily recognised as that of saprophytic forms, is frequently present. The tissues in the upper portion of the stem appear sound except for the browning of the vascular bundles above mentioned and for a water-logged appearance of the pith for a centimetre or so above the upper limit of the cavity caused by the destruction of the pith cells of the lower portion. If the attack has occurred early in the season no tubers or only very small ones will have formed and anchorage in the soil is so slight that the least pull is sufficient to lift the plant. If, however, the plant is attacked after the tubers have well formed these will be infected by the organism through the vascular system of the underground stems. Such infected tubers will in warm moist weather rot off completely in the soil, but it more frequently happens that at the time of "lifting" the organism has not advanced from the vascular system and outwardly the tuber appears quite sound. These infected tubers give rise to the trouble in storage mentioned above and it is to them that the chief losses incurred through this disease are attributable. The organism may remain localised in the vascular ring of the tuber throughout the winter and the planting of diseased "sets" is believed to be the chief cause of dissemination of the disease.

*The parasite.* Several organisms have been described as giving rise to this disease but recent work by Morse<sup>(31)</sup> has shown that they are in all probability all strains of one species *B. atrosepticus*. Previously the name

*B. phytophthorus* was most frequently employed and Johnson<sup>(18)</sup> states that he isolated this organism from diseased potatoes in Ireland in 1906. His evidence however has not been published, and the differences between *B. phytophthorus* and another strain *B. melanogenes* isolated in the West of Ireland by Pethybridge and Murphy<sup>(34)</sup> are so slight that it is conceivable that they were overlooked by Prof. Johnson. The *B. melanogenes* strain was isolated by the author<sup>(32)</sup> from potatoes grown in Lancashire and it is possible that it is the only one present in the British Isles<sup>1</sup>.

*B. phytophthorus* was not included in the strains examined and found to be identical by Morse but he had before him a culture of *B. melanogenes* and this under similar cultural treatment gave identical reactions with *B. atrosepticus*.

*B. atrosepticus* is a medium-sized bacillus with rounded ends motile by 3-6 peritrichous flagella and does not stain by Gram's method.

*Distribution.* This disease has been reported from all parts of the British Isles but the causal organism has been isolated only in the three instances mentioned above. It is a disease which seems to be definitely on the increase and unless some efficient means of control can be found may cause a great deal of trouble in the near future.

*Host plants.* Carruthers<sup>(9)</sup> isolated an organism from beans (*Vicia Faba*) which he believed to be identical with *B. atrosepticus* and the author has found that this organism is strongly parasitic towards *Vicia Faba*, and Appel<sup>(4)</sup> has shown that besides beans, carrots, turnips, cucumbers, tomatoes, sugar beet and mangolds are also liable to attack.

#### BROWN ROT OF POTATO AND TOMATO.

A disease which has been very fully described by E. F. Smith<sup>(42)</sup> in which the vessels of potatoes and tomatoes become blocked with bacteria,

<sup>1</sup> Johnson has stated (20) that he has isolated three other organisms from diseased potato plants in Ireland, namely, *B. caulivorus*, *B. solanincola* and Kramer's bacillus to which Migula gave the name *B. solaniperda*, no evidence in support of the identification is however produced. *B. caulivorus* has been considered by Laurent (24) to be identical with *B. fluorescens liquefaciens* the pathogenicity of which still remains rather doubtful and is being investigated at the present time in this laboratory; it was found that from a prick infection with *B. atrosepticus* of a bean stem without special precautions to sterilise the epidermis the resulting rot gave a pure culture of a fluorescent bacillus and it is possible that whenever *B. fluorescens* has been isolated from diseased plants its existence is a saprophytic one following initial attack by some other organism. The pathogenicity of *B. solanincola* has been called in question by Smith (42) and there is some doubt expressed by Appel (2) as to whether the experiments of Kramer (23) are sufficient to establish the pathogenicity of his bacillus also.

an accompanying brown stain rendering the vascular bundles clearly discernible through the cortical tissue. The organisms enter the potato tuber through the stolon and produce there a brown stain in the vascular ring. From this the disease spreads as a brown rot into the storage tissue which is finally completely destroyed.

Massee<sup>(28)</sup> states that the disease has been recorded from several districts in the North of England and in Scotland. He gives a drawing which is strongly suggestive of Smith's disease and it is highly probable that the disease exists in this country, though in the absence of any evidence of the isolation of the causal organism it is still uncertain whether the English disease is etiologically identical with the American.

#### IRIS ROT.

The leaves become yellow, wilt and die. The underground portion of the plant becomes completely rotted. Massee<sup>(29)</sup> states that the disease is quite common in this country and the author has seen it in the beds at the Chelsea Physic Garden though the causal organism has not been isolated in this country. van Hall<sup>(15)</sup> found *B. omnivorus* and two species of *Pseudomonas* responsible for the disease on the continent.

#### YELLOW DISEASE OF HYACINTH.

Wakker's Disease of Hyacinth due to *P. Hyacinthi* and fully described by Smith<sup>(42)</sup> occurs in our nurseries but, so far, not to any great extent. The organism was isolated by the writer from a diseased corm, recently imported from Holland, growing in one of our large nurseries in 1915 and was found to give all the characteristic reactions of *P. Hyacinthi* and to give rise to the characteristic symptoms of the disease in a corm of Roman Hyacinth (*Hyacinthus orientalis*) when the cut surface of this was smeared with a loopful of the organism from an agar slope.

#### BLACK ROT OF CABBAGE AND OTHER CRUCIFEROUS PLANTS.

The bacteria enter the leaf through the water pores causing a yellowing of the neighbouring tissue. They pass then to the veins, which become strongly blackened, and travel by way of the vascular bundles to the root which may become almost entirely hollowed out by the rot. The disease is also spread by slugs and this is probably the more usual method of infection.

The symptoms of the disease and a very full account of it are given by Smith<sup>(42)</sup>. The disease was observed in England in 1901<sup>(30)</sup> and investigated by Potter<sup>(38)</sup> who isolated a *Pseudomonas* and in Ireland in 1910 by Johnson and Adams<sup>(19)</sup> who state that they isolated *P. campestris* though their published evidence is insufficient to establish this identity. Miss Doidge<sup>(13)</sup> has found *P. campestris* in diseased cabbages raised from English seed.

*The parasite.* *P. campestris* is a short rod-shaped organism with rounded ends, motile by means of a simple polar flagellum.

*Host plants.* Practically all members of the Cruciferae are attacked by this organism, cabbages, brussels-sprouts, turnips, swedes, radish, rape, etc.

#### BACTERIAL BLIGHT OF FRUIT BLOSSOMS.

The blighting of pear and other blossoms and the consequent loss of fruit has long been recognised as one of the worst evils with which the fruit grower is beset. This had almost universally been considered to be due to the effects of frost or of cold winds until the matter was investigated by Barker and Grove<sup>(3)</sup>. That these agencies, especially the former, do cause a considerable amount of loss is indisputable, but probably the greater part of the blossom blight is due to bacterial infection. The bacterial origin of the disease was discovered in 1913 by Barker and Grove who succeeded in obtaining in pure culture from diseased blossoms an organism which readily reproduced the diseased condition when placed upon or injected into various parts of flower buds borne upon healthy young shoots.

*Symptoms of the disease.* The first symptoms of disease vary considerably in individual flowers according to the flower part first attacked. Infection may take place in the sepals before the opening of the flower bud. These first turn grey at the tips and soon commence to blacken downwards towards the flower stalk: subsequent infection of this rapidly leads to death of the whole bud. The same result is often to be observed if the petals receive the infection, but in this case it frequently happens that the attacked petals fall prematurely before the other flower parts have become involved and the young fruit may then set normally. The receptacle frequently bears the onset of the disease, and being an internal structure the diseased condition is liable to be overlooked, the resulting failure of the fruit to set being attributed to lack of fertilisation. Small greyish-black spots appear which in a short time spread over the whole receptacle and the disease is conveyed to the ovary. Finally, the disease

may originate in the stigma, this becomes discoloured and the disease rapidly passes down the style to the ovary. Attacked blossoms showing very little obvious sign of disease may remain attached to the fruit spur for some considerable time and only fall when the tree is shaken by wind or otherwise, the slightest shaking being sufficient to bring down a shower of blossoms in all stages of development. After the fall of the flowers of a truss the spur may remain as a barren stump or may die back, this latter being in all probability due to subsequent attack by fungi such as *Nectria ditissima* or *Sclerotinia fructigena* since inoculation experiments with the causal organism on woody branches showed only slight damage. The organism may remain viable over the winter in the tissues of the spur left standing on the branch and thus may carry the disease over to the following spring.

*The parasite.* The causal organism is a medium sized rod with rounded ends motile by 2-5 polar flagella with lophotrichous arrangement. It stains well with the usual stains and is Gram positive. The cultural and physiological have been investigated by the above named authors and amplified by Miss E. M. Doidge<sup>(12)</sup> who obtained a culture of their organism from Prof. Barker in order to make comparison of this organism with one isolated by her from diseased pear blossoms in South Africa. Miss Doidge found certain marked differences between the two organisms which seem to justify the founding of two separate species, but, in view of the work of Morse<sup>(31)</sup>, which showed that quite as marked differences may disappear when two organisms are "trained" on the same media for some considerable time, it would seem desirable that treatment on the same lines should be applied to these two strains producing Blossom Blight before arriving at a definite separation. Miss Doidge's paper does not make it clear whether any previous training had been submitted to the two organisms before the parallel series of cultures was made.

*Host plants.* Barker and Grove found all the varieties of pear grown at the Long Ashton Research Station were susceptible to the disease, but that some were much more so than others; Beurre d'Amanlis and Catillac being specially susceptible. The bacillus has also been isolated from certain varieties of apples, plums and cherries. Barker<sup>(4)</sup> has also isolated an organism from gooseberry bushes which is believed to be identical with the organism causing pear blossom blight though no cultural evidence of this has as yet been given.

*Distribution.* The organism has been isolated from affected flowers from Gloucestershire, Devon, Middlesex, Sussex, Essex, Staffordshire and

Herefordshire, and is probably wide-spread throughout the country although no statistics are available as to its occurrence in the North or in Ireland.

#### BACTERIAL BLIGHT OF TOMATOES.

*Symptoms.* When the tomato is quite small a minute blackish patch appears at the base of the style and from this focus the disease spreads until finally the whole fruit is reduced to a blackish soft decayed mass. It has been stated<sup>(27)</sup> that infection takes place during the flowering period and that needle prick infection from diseased tissue will set up disease in a healthy tomato.

In view of the fact that Brooks<sup>(8)</sup> holds that bacteria are not the primary cause of disease the matter badly needs further investigation in this country.

#### LEAF SPOT DISEASE OF ORCHID.

Prof. Potter has described a bacterial blister on the leaves of *Odontoglossum uro-skinneri*<sup>(39)</sup>, the epidermis being raised by an accumulation of brown mucilaginous substance caused by the action of some organism which is not fully described.

#### BACTERIAL DISEASE OF PISUM SATIVUM.

An interesting closed bacterial disease somewhat analogous to the closed smut of barley. The organism is present in the cotyledons of the seed, germinates with the seed, enters the plumule and passes up the stem of the plant in the motile stage and is to be found in the seed and the seed pod. It has been investigated by Miss D. M. Cayley<sup>(10)</sup> at the John Innes Horticultural Institution where for some years it has caused much trouble.

*Symptoms of the disease.* In the worst cases the badly infected seed fails to germinate, but usually the primary shoot develops from the infected seed, soon turns brown at the tip, aborts, and lateral shoots develop prematurely to take its place. Sometimes on the youngest shoots brown streaks are to be seen but otherwise there is no sign of disease until the flowering period. The disease develops most rapidly in hot dry weather, the stem becomes brownish and has a water-soaked appearance, brown longitudinal streaks appear on the stem at the base of the petioles, the leaves become spotted and yellowish with darkened veins and the surface of the pod is sometimes roughened or embossed. Except in bad cases the plants grow to full height, flower and set a fair crop of seed but

on examination of the seed the cotyledons are found to have brown spots or bacterial cavities at the centre of each.

*The parasite.* *P. seminum* is a large rod motile by a single polar flagellum. It stains well with the usual stains and is Gram positive. On solid media it readily forms oval bodies which may occur strung together in chains giving the appearance of beaded rods. These oval bodies are thought by Miss Cayley to be involution forms which contain certain particles, these stain as spores and are believed to be spores though their germination has not as yet been observed.

*Host plants.* At present the disease has been found only in *Pisum sativum*, all varieties of which would seem to be susceptible to more or less extent. The most susceptible varieties on the soil of the John Innes Institution being Ne Plus Ultra and Duke of Albany. The dwarf earlies Chelsea Gem and Little Marvel are also specially susceptible, while Sutton's Improved Petit Pois has proved on this soil to be least affected. In this variety, however, only about 50 per cent. of healthy plants were obtained.

*Distribution.* The disease is believed to be fairly common, at least throughout the South of England, and to be steadily on the increase. Miss Cayley reports that it is each year becoming more difficult to find seed for experimental purposes which can be relied upon to be free from this disease.

#### POTATO SCAB.

The well-known corky patches or scabs on the skin of the potato are the result of the response of the cortical cells of the tuber to the stimulus of an invading organism and not, as has been frequently stated, the result of mechanical injury or of the attack of wire-worms or other animal parasites. In its defence against the parasite the tissue of the potato is so far successful as to limit the attack to a few of the outer layers of cells only. Successive layers of cork are formed as the organism penetrates into the tissue and these may extend to a depth of half a centimetre, but the internal storage cells remain unaffected. Bolley<sup>(6)</sup> isolated a small bacterium from scabbed potatoes in Indiana and with it produced scabs by artificial infection. Later however<sup>(7)</sup> he expressed doubt as to whether this organism is responsible for the disease under natural conditions, since, in subsequent efforts, he was unable to confirm his original work, but had no difficulty in showing that the usual cause of the disease is an organism which was isolated by Thaxter<sup>(8)</sup> and described as *Oospora scabies*. The disease was included amongst those

of fungal origin until 1912 when Cunningham(11) showed the relation of *Oospora scabies* to the bacteria. In 1914 this organism was referred by Lutman and Cunningham(26) to *Actinomyces chromogenus* a species previously described by Gasperini(14).

Lutman and Cunningham have obtained four strains of *Actinomyces chromogenus* Gasperini from scabbed potatoes in America. Whether the cause of the disease is the same in this country is still uncertain, and the investigation of this matter is one of the many problems in plant bacteriology which call for elucidation. It is very unsatisfactory that a disease so long-established in the country should not yet have been attributed to a definite organism.

#### CROWN GALL.

An intumescence disease on the roots of various plants has been fully described by Smith and Townsend(44). The same symptoms of disease have been found on the roots of Paris daisy(25) (*Chrysanthemum frutescens* L.) grown at Kew; although the organism has not been isolated here there seems little reason to doubt that the disease is etiologically identical with that in America.

A very large number of host plants have been found to be affected with this disease. In this country they have been observed also in plum, rose, raspberry and loganberry and in the United States on peach, apricot, almond, prune, apple, cherry, poplar, chestnut and blackberry.

#### SO-CALLED PHYSIOLOGICAL DISEASES.

A number of obscure diseases have been attributed to a derangement of the normal physiological condition of the plant without the intervention of a parasite. This is in all probability a lame way of hiding our ignorance, and the possibility of the existence of ultra-microscopic organisms in these cases should always be kept in the fore-front.

The "Leaf-roll" disease of potatoes has been investigated thoroughly by Quanjer(40) who finds a pathological condition of the phloem elements of the stem to which he ascribes the visible symptoms of disease. The facts that the disease is communicable to a scion by grafting a disease-bearing stock and *vice versa* and that it is transmissible through the soil would seem to point strongly to a bacterial origin of the disease, and further investigation is advisable before any cause other than a parasitic one is accepted for this disease.

The "Mosaic Disease of Tomato" has also been shown to be transmissible through the soil and the same argument applies in this case also.

"Sprain" in potatoes is another of these obscure phenomena and there would seem to be several different kinds of "sprain." One form has been attributed<sup>(25)</sup>, upon what evidence the author is unable to discover, to an arrested condition of Winter-Rot. Another form which has been described as "Internal Disease" by Horne<sup>(17)</sup> is believed to be similar to a disease which the writer is now investigating and which he has found to be due to a bacterial parasite<sup>(33)</sup>.

"Silver-Leaf Disease" in plum has also been suggested as due to a bacterial parasite<sup>(5)</sup> and Smolâk<sup>(47)</sup> observed bacteria in the vessels of the leaf although the relationship of these to the disease was not determined.

The need for further investigation of bacterial diseases and for more workers in the field is vital, how vital has recently been shown by the discovery in America of two diseases of cereal crops, a bacterial blight of Barley<sup>(21)</sup> and a disease of Wheat<sup>(46)</sup>; the latter is stated to be "not as destructive as the rusts but more destructive than the smuts and very likely more difficult to control." The means of control in bacterial disease are very difficult and necessitate a vast amount of research. Possible lines of attacking the problem have been so ably set out by Smith<sup>(45)</sup> in his *Conspectus of Bacterial Diseases* that little can be added in the present state of our knowledge.

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## “INTERNAL RUST SPOT” DISEASE OF THE POTATO TUBER.

(Preliminary communication.)

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THROUGH the courtesy of Mr A. D. Cotton of the Kew Gardens Pathological Laboratory the writer has obtained from two farms in the South of England specimens of potatoes suffering from a disease which had been diagnosed as of bacterial origin. From one farm at Dunstable the disease was so bad as to render the crop quite unsaleable, over 90 per cent. of the tubers being badly affected, and from the other farm at Christchurch came the report that at least 33 per cent. of the tubers had to be wholly rejected, so that it is safe to assume that upwards of 50 per cent. were affected to some extent.

The symptoms of the disease were thought at first to indicate *Pseudomonas solanacearum* as the cause. On further examination of diseased tubers, however, appearances were discovered which were quite different from those described by Smith<sup>(6)</sup> as characteristic of the attack of this organism. There is, for instance, no appearance whatever of a milky slime in the affected part of the tissue and the potatoes do not rot off during the winter. The tuber remains perfectly hard and appears sound except for a few brown patches on the skin and a certain appearance of “scabbiness.” Around some of the lenticels the skin is raised and cracked, and on removal of this there is revealed a darkened sunken area of corky tissue resembling somewhat the appearance of an old *Spongospora scab*.

On cutting a tuber discoloured patches of tissue of varying size are found scattered over the surface. These are typically of a brownish-red colour resembling that of iron rust or, perhaps, more nearly that of ginger-bread. They are distributed promiscuously through the tuber and only occasionally seem to have developed in proximity to the vascular

ring. In some of the first potatoes examined the patches had a greenish-black water-soaked appearance and seemed to have arisen from the vascular bundles suggesting *P. solanacearum* as the causal organism; it is, however, probable that the water-logging is secondary being due to the presence in the diseased tissue of certain saprophytic bacteria.

The size of the patches varies enormously from a small island of brown tissue of the size of a pin's head to an irregular-shaped patch spreading through several centimetres of the tissue. In certain cases the large patches can be traced to lenticels which show the "scabbed" appearance described above, indicating that the exciting cause has found entry into the tuber through the lenticel and that "the scabbing" is the result of its action on the surrounding cells.

Attempts to prepare diseased tissue for microtome sectioning have, so far, been unsuccessful, strong lignification of the walls of the attacked cells making them very difficult of penetration by fixing and other fluids. Hand sections through a small patch show a group of normal cells packed with starch grains and surrounded by a ring of brown tissue. In the brown zone the cells have thickened walls which stain red with phloroglucin and this coupled with their resistance to cutting has led to the conclusion that they are strongly lignified. As contents, these cells show brown protoplasm in which starch grains may be embedded or the starch may be replaced by globules of various shape and size which appear to be of oil or possibly of tannin. In certain of the cells there may be recognised masses of small bacteria intermingled with the starch grains. In some sections, however, bacteria could not be distinguished, either by motility or shape, from minute globules of the fat-like substance. The brown ring which gives the characteristic appearance to the patch is surrounded by a zone of colourless cells in which the starch has entirely disappeared and given place to more or less colourless oily globules. Frequently a small patch is found to be cut off from this zone of starch-free cells by the formation of a typical cork callus.

Sections through one of the larger patches show essentially the same cell characters as described above except that the inner cells are much disorganised, or they may have dried up and broken down leaving a cavity surrounded by cells with the characteristic brown and lignified walls.

By inoculations of diseased tissue into sterile potato broth an organism has with difficulty been obtained and shown to be the cause of the disease. Inoculations of sterile potato slices using pure cultures of the organism have repeatedly given successful infections, and from the diseased area,

which was thoroughly characteristic of the disease in the original tuber, the organism has again been isolated. Occasionally inoculations of potato broth with pieces of the original diseased tissue have failed entirely to produce turbidity in the broth. This sterility is believed to be due to the weak parasitism of the causal organism, the plant tissue having by cork formation confined the parasite within narrow limits in which it has died out during the winter.

The symptoms of the disease here dealt with correspond exactly with those described by Horne(3) for "Internal Disease" and by Mayer(4), Frank, A. B.(1), Sorauer and Rörig(5) and Frank, B.(2) under the names "Buntwerden," "Eisenfleckigkeit," "Buntheit," or "Stockfleckigkeit." There seems little doubt that these workers have described one and the same disease. All the German workers have come to the conclusion that the disease is not of parasitic origin and have sought for the cause in the physiological condition of the soil. Horne alone suggests that further search for a parasite might be advisable. The question of the identity of their disease with the one dealt with in this paper, for which the name "Internal Rust Spot" is suggested, is therefore of some considerable interest. Further discussion of this relationship and a full description of the causal organism of the "Internal Rust Spot" disease are reserved for a later paper.

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## A SHORT SUMMARY OF OUR KNOWLEDGE OF THE FRIT-FLY.

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*Communicated by Mr J. C. F. Fryer.*

THE fact that very extensive damage to corn crops throughout Northern and Central Europe may be the work of the frit-fly has been recognised for the past century and a half, the first record being published by Linné in 1750, but in the British Isles it is in only comparatively recent years that public attention has been directed to the losses caused by these depredations, though in many parts of the country the crops (especially of oats) are always liable to be attacked, and in some years the damage done is enormous.

A very large amount of literature on the subject has been published, chiefly continental, and much of it appears in periodicals or reports of only a limited circulation. In the following pages an attempt is made to collate all the more important facts concerning the frit-fly contained in such of this literature as has been accessible, with a view to arriving at some idea of what has been discovered up to the present time of the life history, and methods of combating the attacks, of this destructive little insect. Much of the information contained in Russian publications has been extracted from *The Review of Applied Entomology*.

On the Continent two species of *Oscinis* (*O. frit* and *O. pusilla*) are considered to be responsible for frit-fly attacks, but as the *O. pusilla* Meig. which several economic entomologists have professed to recognise is certainly not the form or species described by Meigen under that name, and as most authorities of the present day on Diptera consider *O. frit* to be a species exhibiting very considerable variation in the colour of its legs and in its size, reference to any such varieties (including *O. pusilla*) are incorporated in the present summary.

## DISTRIBUTION.

Frit-fly damage has been recorded from Norway, Sweden, Denmark, Finland, practically all Russia, Bulgaria, Austria, Germany, Holland, France, and the British Isles; while attacks by the larvae of Oscinids on cereal crops (though the species of *Oscinis* attacking are supposed to be different) have been recorded from Canada (Criddle, 1916) and Minnesota, U.S.A. (Washburn, 1905).

## DISTRIBUTION IN ENGLAND AND WALES.

Roughly speaking, the species is very troublesome in the whole of the south of England from Cornwall to Kent, in the Eastern Counties (except in the Fen District), and up through the counties between Wales and the Midlands to Lancashire and Yorkshire, with a few records from Northumberland. It appears to be especially destructive in the counties bordering on the Thames and the Severn, and in Hampshire, Dorset, E. Devon, and the Isle of Wight. In Wales it has been noted as a pest from counties on the English border such as Glamorgan, Radnorshire and Flintshire, and it has been recorded as doing damage in Ireland and Scotland.

## EXTENT OF DAMAGE.

The following few quotations from published and unpublished correspondents' reports will give some idea of the damage that may be caused by *frit* attacks.

"A field planted in the autumn with two bushels per acre, so entirely eaten the following spring as not to have left one healthy plant in a yard. They have robbed me of about fifteen bushels per acre on nearly fifty acres of fallow wheat." (Creese, Teddington near Tewkesbury, *vide* Ormerod, Report for 1881.)

"Nothing could have been more luxuriant than our Oat-crop at an early stage, but at present the whole aspect has changed, the fields being one mass of patches, getting worse and worse daily." (Bulteel, Ivybridge, S. Devon, *vide* Ormerod, Report for 1888.)

"The crop [of oats] came up and looked well until the latter part of May, what promised to be a heavy crop will only be a third." (Stick, St Columb, Cornwall, *vide* Ormerod, Report for 1888.)

"A very large area [of oats] in this part of the country has suffered." "The crop is practically destroyed except for hay." "The damage is quite appalling—90% of crop gone." (McCracken, Royal Agricultural College, Cirencester, *vide* Ormerod, Report for 1888.)

Letter from a Gloucestershire farmer in 1917: "Two of the [last] ten years I lost the entire crop, and the remaining eight I lost more than half, entirely through

Frit-fly. . . the loss to the country I consider is very much greater than either Anthrax, Sheep-Seab or Swine Fever. In 1913, 1914 numbers of farmers in the district have turned stock into their oat fields just before harvest as they found it was not worth cutting."

Letter from a Wiltshire farmer in 1917: "I have had my crop [of oats] depreciated at least a third on several occasions in recent years, making a loss of £320 on the oat-crop alone by Frit-fly, and the sample is always of an inferior quality which is much more noticeable in white oats."

"All growth practically stopped in a field of barley in Shropshire sown May 4th." (Roebuck, June 1917.)

"Three acres of spring wheat in S. Shropshire totally destroyed by Frit-fly." (Roebuck, July 1917.)

"Spring wheat sown end of April totally destroyed in Radnorshire." (Roebuck, July 1917.)

"Winchester, oats put in late, the whole would have been ploughed up but for clover, no oats at all." (Theobald, June 1917.)

"Frit-fly attacks during the last five or six years have been so general and destructive in the county that many farmers have stopped growing the crop." (Blaud, June 1917.)

In addition to the damage to the young oat plants, subsequent damage to the corn in the panicles is often very great, probably much greater than is generally realised. The following may be taken as a sample of the result of an attack of this nature:

In Wiltshire in 1917 five acres were sown at the end of April with Scotch seed of "Abundance" oat bought direct from Garton's. The yield of this field was 40 sacks of corn, very light in weight. An examination of an undressed sample of the corn gave the following result:

<i>Grains examined</i>	<i>Obvious frit damage</i>	<i>No grain or very light grain, probably largely due to "frit"</i>	<i>Sound corn</i>
358	74	70	214

The Returns published by the Board of Agriculture of the average yield of oats in England for the years 1910-1915 are instructive because they include the year 1912 when frit-fly attacks were exceptionally bad (*vide Journ. Board Agric.* Sept. 1912, p. 482) and a comparison may be made with other years when frit-fly damage was normal<sup>1</sup>.

<sup>1</sup> To arrive at the normal annual loss due to frit-fly one must take as a basis the average yield per acre of oats when free from frit-fly attacks, a figure difficult to arrive at as oats have been known to yield anything up to 120 bushels per acre. A yield of 60 bushels is considered by agricultural experts a satisfactory crop, and one of 80 bushels a very good crop. Taking 50 bushels per acre as a standard for England one arrives at an average annual loss of about 8 bushels per acre for the ten years 1901-1910, being equivalent to 16 per cent. or nearly 15,000,000 bushels per annum.

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### *Average yield in bushels per acre of Oats in England.*

1910	41·87	1913	38·50
1911	39·03	1914	40·01
1912	35·56	1915	40·52

Average yield in England for ten years 1901–1910 = 42·07.

Taking the ten year average to 1910 as a basis it will be seen that in 1912 when frit-fly attacks were very bad the yield was reduced by no less than  $6\frac{1}{2}$  bushels per acre and as the acreage under oats that year was 1,865,569 this would represent a loss of 12,126,198 bushels.

### PLANTS ATTACKED.

Rye, oats, barley, wheat, maize, and various grasses (*Bromus* sp., *Poa annua*, *Poa pratensis*, *Triticum repens*, *Triticum cristatum*, *Phleum pratense*, *Alopecurus pratensis*, *Milium effusum*, *Lolium perenne*, *Festuca pratensis*, *Avena flavescens*, *Arrhenatherum avenaceum* and its var. *bulbosum*). In England spring oats are chiefly attacked, though attacks have been recorded on winter oats, winter and spring wheat, barley, rye and grasses. Attacks are most common (or most noticeable) on the young plants, and these plants must not be far advanced in growth (Ritzema Bos, 1891); but the larvae of the third brood will feed in the panicles of oats still hidden in the sheath (*Board of Agric. Rep. on Inj. Ins. in 1892*), or in the young corn in the panicle, more rarely so far as the British Isles are concerned in the ears of barley (*vide* under "Imago" and Theobald (1906), and *Text Book Agric. Zool.* 1899), while the only records traced of larvae living in the ears of wheat are the breeding of *O. granarius* from a wheat kernel by Curtis (*Farm Insects*) and Carpenter's record (1909) of *O. frit* received "early in October from Queen's County where they had been found on newly threshed wheat." According to Ritzema Bos (*Zeitschr. f. Pflanzenkr.* 1, 1891, p. 347) the females of the second brood will only lay their eggs on the blossoming oats, and when oats have been attacked in the spring the flies produced from the larvae making this attack are very rarely on the wing in time to find the oats in blossom, and consequently have to oviposit on wild grasses<sup>1</sup>. It would appear that the flies when able to choose between oats and barley prefer the oats, for Miss Ormerod in her Report for 1888 stated that where "dredge corn" (barley and oats mixed) is planted, the maggot

<sup>1</sup> This was not the case in experiments carried out by the Department in 1918, late sown oats growing in the same field as those sown earlier being badly attacked both in the young plant and in the ripening grain.

will attack the oats and leave the barley; again, in the same Report, she quoted a letter to the effect that oats, drilled about the middle of April on part of a field after roots fed off by sheep, were badly attacked; the other part of the field being planted with barley did not appear to have been attacked. The same discrimination on the part of the fly was noted in Part II of the *Annual Report of Intelligence Division of the Board of Agriculture* (1911). Ritzema Bos (1894) quoted a case where it appeared that the fly preferred oats to wheat.

On the Continent, the larvae appear to winter mainly in rye, but also in winter wheat and wild grasses (Baranov, 1914) or rye, wheat, and winter barley (Rörig, 1893); so far as England is concerned little information is available, but the larvae have been found in winter wheat (Ormerod, Report for 1881, and Petherbridge, *Ann. Appl. Biol.* 1917), winter oats (Ormerod, Report for 1889), rye (Roebuck *in litt.* 1918), and in wild grasses, rye-grass, *Avena flavescens* and *Arrhenatherum avenaceum* (Edmunds, *Rep. Harper Adams Agric. Coll.* 1912). Winter wheat has also been known to be attacked in the spring, the flies hatching out at the end of June and beginning of July (Roebuck *in litt.* 1918).

#### NUMBER OF BROODS DURING THE YEAR.

The majority of writers are satisfied that there are three broods, though some Russians consider there may be four or even five in S. Russia. In the laboratory at Kiev four generations were reared (Dobrovliansky, 1915) as follows:

Date when flies were placed in insectary	Appearance of damage to plants	Appearance of Imago
1. May 9	May 29	June 13-23
2. June 15	July 3	July 23
3. July 24	Aug. 11	Aug. 27
4. Aug. 28	Sept. 26	Oct. 16 (two flies only)

Kulagin (1913) considered there to be three broods with smaller intermediate ones, a fourth brood being doubtful and only if weather conditions are favourable. Schesterikov (1910) stated that the appearance of the insect is governed by weather conditions. In the Board of Agriculture Report on insects injurious to crops in 1892 (London, 1893) it was suggested that there may be a constant succession of broods dependent upon the state of food plants and the weather, and this view would appear to be supported by the statements made by Baranov, Ritzema Bos, Rörig and Kühn given at the end of the next subheading. Probably the broods more and more overlap as the season advances.

## TIMES OF APPEARANCE OF FLIES.

*First Brood:* March (Wilhelm, 1891, Germany) to early June (Zetterstedt, Lappland and Baranov, 1912, Moscow). Widhalm (*vide* Kulagin, 1913, Russia) gives earliest appearance 28th March but more usually 14th April. The period of maximum emergence in England would appear to be from middle of April to middle of May.

*Second Brood:* Early in June (Wilhelm, 1891, Germany) to end of July (Dobrovliansky, 1913, Russia); according to Kulagin, 1913 (Russia), after the first summer rain in June. The period of maximum emergence in England would appear to be during July. Dobrovliansky (1913) wrote as follows concerning this brood: barley sown 21. v., first larvae observed 5. vi., pupae 15. vi., flies 6. vii.-2. viii. Petherbridge (*in litt.* 1918) states that he found swarms of the fly in an oat field on July 21st, 1912.

*Third Brood:* August (middle of August in many places in Russia) to October (Krassiltchik and Vitkovsky, 1913, Bessarabia; Ritzema Bos, 1891, Holland), middle of October (Stormer and Kleine, 1911), but Widhalm (*vide* Kulagin, 1913, Russia) gives the last appearance as usually end of October, sometimes as late as Nov. 14th. The period of maximum emergence in England would appear to be August and September, but in the case of wheat sown after rye-grass or Italian rye-grass the crop has been known to be attacked even when sown as late as November or early December (Petherbridge, November, 1917), apparently indicating the possibility of a migration of the larvae from the ploughed-in rye-grass to the young wheat plants (*vide* Fryer and Petherbridge, 1917). Dobrovliansky (1913) gave the following sample of the life history of this brood: Oats sown 11. vii., larvae 23. vii., pupae 6. viii., flies 12. ix.

Baranov (1912) found all stages (eggs to imago) on summer sown grain on June 27th. Ritzema Bos (1891) stated that both pupae and flies are to be found during nearly all the spring and summer, Rörig (1893) that the insect may be found in all stages at one and the same time on any occasion between spring and autumn, and Roebuck (*in litt.* 1918) that he had no difficulty in finding larvae, pupae, and imagines from the end of April until September. Rörig (1893) recorded the breeding out of flies in December and January in a warm room. Kühn (1893) collected infected plants on December 16th and kept them in a room when flies appeared in abundance at the end of January: other infected plants collected on January 26th produced flies in abundance at the end of February. Jügner (1901) gave an account of a similar experiment;

flies hatching out in January in a warm room were found to copulate and when given fresh young plants, laid eggs which hatched in a few days.

#### EGGS.

In the autumn and spring the eggs are laid on the leaves of the young plants (preferably on the underside), or on the stem close to the ground. Kurdjumov (1913) said at the level of the soil. Krassiltchik (1912?) in Bessarabia found no eggs on the leaves but all on the young stems. Baranov (1912, Moscow) on the other hand found them mostly upon the upper side of the leaf near the stalk, or (1914) on both sides of the leaves, sometimes on the stalk near tillering knot. In the summer the eggs may be laid on the sheaths enclosing the ears, on the panicles of oats, the young corn of oats and barley, or on wild grasses. A female may lay from 20 (Lindeman, *vide* Kulagin, 1913) to 30 (Rörig, 1893) or according to Wahl (1914) 70 eggs; and the eggs take from three to seven days to hatch (three to four days, Wilhelm, 1891; three to seven days, Rörig, 1893; four days spring, seven days autumn, Baranov, 1914). According to Dobrovliansky (1915) the maximum number of eggs laid by a female in one day is six, and while in moist air and a high temperature the eggs may hatch in three days, dry air will kill them.

#### LARVAE.

The young larva of the autumn and spring broods makes its way into the young stem and eats the tender central leaves and shoot, ultimately killing the shoot which in the meanwhile may produce side shoots. According to Krassiltchik and Vitkovsky (1913) the newly hatched larva may mine the leaf upon which it was laid very extensively before working its way into the stem. Several writers have noted that a larva can migrate from one shoot to another. Normally only one larva is present in each shoot, but as many as ten larvae have been found in a single plant. The summer larvae live in the summit of the stem, feeding upon the hidden ears or panicles, on the young corn in the ear or panicle, or in the stems of grasses. The spring and summer larvae may feed for 14-15 days (Baranov, 1912), three weeks (Ritzema Bos, 1891), three to four weeks (Kulagin, 1913), or five weeks (Rörig, 1893), while the majority of writers are agreed that the autumn larvae normally winter in that state and do not pupate until the early spring. Baranov (1912) gave the proportion of larvae to pupae found in the winter as 100 to 10-15. Dobrovliansky (1913) found in the Government of Kiev that on

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August 26th 10 per cent. of the young plants sprouting from fallen grain were infested with larvae; and that on September 5th 20-26 per cent. of winter wheat plants were infested.

### PUPAE.

The spring and autumn larvae leave the centre of the stem and pupate under the sheath of the outer leaves. Baranov (1912) says near roots, sometimes 1"-2" in the earth. Roebuck (*in litt.* 1918) states that on oats he has invariably found the pupa of the spring brood under the sheath and between the first node and 1½ inches above; in wheat however the distribution was not so even—at first, second, or even third node from ground and anywhere from the ligule to the node. The summer larvae pupate among the leaves surrounding the hidden ear or panicle, or in the grain itself or between the grain and the husk. The pupa stage may last 8-14 days<sup>1</sup> (8-10 days Taschenberg, 1879; 10-12 days Schesterikov, 1910, and Baranov, 1912; average 14 days Lindeman, *vide* Kulagin, 1913), the length of time being governed by the amount of moisture, the dryer the conditions the longer the period (Dobrovliansky, 1915). Experiments made by Krassiltchik and Vitkovsky (1913) proved that flies were capable of getting through 7"-9" of rammed wet earth upon emergence from pupae buried at that depth.

### IMAGO.

According to Kulagin (1913) Kurdjumov in Russia found that the male lives a very short time, often dying the same day; a female lived for two weeks in captivity, and he estimated its life when free at about a month, but Kurdjumov (1913) himself stated that he found the length of the life of the adult to be two to three months (under exceptionally favourable circumstances five months), and Dobrovliansky (1915) gave the length of the life of the male in captivity as about a month, while four females lived 74, 55, 45 and 63 days respectively, and the period during which they oviposited was 24-36 days. Most writers refer to the short hopping flight of the insect.

The appearance in immense numbers of the flies from grains threshed at harvest has been several times recorded.

"From oats threshed in the field and stored in bulk in loft" (England, Westwood, 1881).

<sup>1</sup> Compare also Dobrovliansky's sample life histories of second and third broods given under the subheading "Times of appearance of Flies."

“Oats drilled April 1st on late folded land, threshed in August and found very light in weight (32 lbs. per bushel). Innumerable flies swarmed a few days later in granary where corn was stored” (England, Theobald, 1906).

“Large numbers of flies bred from store of threshed oats at Poltava” (Russia, Vassiliev, 1908).

“In swarms in an outbuilding this autumn (1881), in the lofts of which newly threshed barley had been stored” (Meade *in litt.* 1881, Ormerod, Report for 1881).

“Found in great numbers in a loft in Dorsetshire where barley had been stored” (Fitch, *Proc. Ent. Soc. Lond.* 1881).

“A number of these little flies were sent to me some years ago by the Rev. O. Pickard-Cambridge, which he had found in a granary in Dorsetshire in which (I think he said) barley had been stored” (Meade, *Ent. M. Mag.* 1899, p. 103). It is possible that these three last references refer to one and the same case.

#### SYNONYMS AND VARIETIES.

The original description of *Oscinis frit* was made from specimens bred from the ears of barley. *Musca hordei* Bjerk. was bred from rye and subsequently considered by Bjerkander himself to be a synonym of *frit*. *Musca avenae* Bjerk. was bred from the stems and panicles of oats. *Oscinis vastator* Curtis from young wheat plants sent to Curtis towards the end of June. *Oscinis granarius* Curtis was bred from a grain of wheat. Of these *granarius* was distinguished by Curtis by having the tibiae black with only the tip of the intermediate tibiae (front pair missing in type specimen) yellowish, *O. vastator* by having the base as well as the tip of the four anterior tibiae ferruginous. Specimens bred from oats threshed early and stored in a loft were described by Westwood as having the legs uniformly black, and these he considered to be identical with *avenae* Bjerk. and *atricilla* Zett. *Oscinis pusilla* Mg. has been recorded as living in cereal crops, but the *O. pusilla* of Wilhelm which he called the “Oat-fly” and which attacked the oats in the panicles in its summer generation, and was described by him as having the tibiae of only the front legs a little paler, the others dark as the femora, is certainly not the same species as Meigen’s. True *O. pusilla* Mg. has the four anterior tibiae entirely yellowish.

Very little information is available as to whether different varieties are responsible for the attack on different plants or different parts of the same plant; the variety *pusilla*, however, has been noted by different

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writers on the Continent as attacking only rye in the winter generation and only the panicles of oats in the summer generation, whereas these generations of *frit* are recorded as not being so particular as to the object attacked.

### PARASITES.

*Sigalphus caudatus* (Curtis, 1860); *Pteromalus puparum*, *P. micans*, and *Sigalphus caudatus* (Rörig, 1893); *Rhoptomeris wildhami* Kour. and *Trichomanus cristatus* Forst. (Baranov, 1912); *Polysextus oscinidis* Kurd. sp. n. (Mokrzecki, 1913); *Mersius intermedius* and *Semiotellus nigripes* Lindm. (Wilhelm, 1891); *Miris dolobratius* and *Pteromalus micans* (Schesterikov, 1910); Coccinellidae destroy the larvae (Wilhelm, 1891, Rörig, 1893 and Schesterikov, 1910), and an unclassified entomophagous fungus kills considerable numbers (Schesterikov, 1910).

Dobrovliansky (1913) found that in barley sown on May 21st in the Government of Kiev, 21 per cent. of the pupae of *frit* were parasitised, and on oats sown July 11th 16 per cent. of the pupae were parasitised.

### RESISTANCE TO ATTACK OF DIFFERENT VARIETIES OF CORN.

Very indefinite conclusions have been arrived at on this point. Kulagin (1913, Russia) recorded "Triumph" oats and naked barleys as suffering most. Rörig (1893, Germany) said that experiments apparently showed that "Triumph" and other "bearded oats" (*Fahnenhafer*) were less attacked. Aurivillius (1892, Sweden) came to the conclusion that "six-rowed" barleys were much more liable to attack than "two-rowed" barleys. McDougall (1912) found that in Scotland "Hamilton" and "Potato" oats were least damaged, followed by "Sandy," "Wide-Awake" and "Abundance," while "Tartar King," "Beseler" and "Banner" were very badly attacked; this would appear to support the view that those oats that tiller freely are better able to stand against attacks of frit-fly than those that do not.

In the Report on the breaking up of grass land in 1916-17, published by the Board of Agriculture in 1917 as *Miscellaneous Publications*, No. 19, a case is recorded from Yorkshire where two varieties, "Bountiful" and "Beseler's Prolific," were sown in April on a ten acre field which had been broken up in February. "Bountiful" provided an excellent crop of 7 qrs. per acre, but "Beseler's Prolific" suffered greatly from frit-fly and was a much lighter crop.

Ritzema Bos (1894) recorded some observations on a number of varieties in Holland in which he found that "Longfellow," "White Canadian," "Black Canadian" and "Early Blossom" exhibited considerable powers of resistance.

## CONDITIONS FAVOURABLE TO AN ATTACK.

It is the universal opinion that *late sown* spring crops are most affected, and the evidence of many cases submitted to the Board of Agriculture strongly supports this opinion. The date of the commencement of the dangerous period is probably dependent upon weather conditions and would therefore be best indicated by association with some natural phenomena also governed by the same conditions. Past experience has tended to show that spring corn sown before the end of March is usually not attacked; occasionally it may be safe to sow up to the middle of April on a good tilth, but after that date an attack is very probable in *frit*-infested districts. Professor M'Cracken of the Royal Agricultural College, Cirencester, writing to Miss Ormerod in 1889 (Ormerod, Report for 1889), stated that "Black Tartarian Oats sown on March 29th enjoyed almost complete immunity from attack; in another field sown on April 29th, over 70 % of the first stems were destroyed"; while in the *Annual Report of the Intelligence Division*, Part II, published by the Board of Agriculture in 1911, it was stated that crops sown early in March have been known to escape when others sown late in March were infested. In a Report on the breaking up of Grass Land in England and Wales in the Harvest Year 1916-17, published by the Board of Agriculture and Fisheries as *Miscellaneous Publications*, No. 19, in 1917, it is stated that "Frit flies are most troublesome in the case of crops sown in mid-season. Oats sown before March 15th and after April 15th may escape when crops sown between these dates may be destroyed." No authority for the statement that oats sown after April 15th may escape can be traced, while this statement is certainly in opposition to the expressed views of all economic entomologists in this country. Reports of bad frit-fly attacks on crops "after grass" were frequently received in 1917, and it is worthy of note that in Canada grasslands ploughed late in autumn or in spring are stated to be attacked the worst (Criddle, 1916).

Enquiries instituted by the Board of Agriculture in 1909-10 and published in Part II of the *Annual Report of the Intelligence Division* in 1911 appeared to show that late sown oats following roots fed by sheep, when the fields were only once ploughed and not much cultivated, were most attacked. Ormerod (Report for 1881) noted attacks on wheat on land fallowed the previous year, no attacks where land ploughed first time in autumn. Fitch (1881) stated that wheat after a whole summer's fallow was almost invariably attacked. It must be remembered that in some of these cases of attacks on wheat the real cause of the damage may

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have been *Hylemyia coarctata*, the damage by this insect and by *Oscinia frit* often being confused (*vide* Wahl, 1914 and Dafert and Kornauth, 1914). It has been noted that on a field of wheat after Italian rye-grass and clover, where it was ploughed in July, bastard fallowed, and drilled on October 3rd, there was no *frit* attack; while another part of the same field where the grass and clover crop was fed off by sheep, ploughed on October 1st and drilled on October 3rd, 10 per cent. of the wheat plants were attacked (Petherbridge, November, 1917). On the Continent, in addition to late sown spring crops on newly broken land, spring corn planted next to winter rye is almost always attacked, the attack spreading from the rye in parallel lines or concentric circles (Cohn, 1869).

### POSSIBILITY OF INFECTION FROM INFESTED SEEDS.

Those larvae attacking the grain of oats in the panicles, often pupate within the husk of the oat and remain in the corn after it is threshed; the flies normally emerge during August and September and several records of the occurrence of swarms on oats threshed early in August have been noted (*vide* under "Imago"). In order to account for infection from the seed it would appear necessary for there to be either (1) deferred emergence on the part of some of the flies from pupae in the grain, or (2) oviposition on the corn by the females of the emerging flies, with the larvae hatching out after the corn is planted. Neither of these suppositions appears very probable, but attention has been called to this possible source of infection by Miss Ormerod in 1889, by the author of an article in the *Journal of the Board of Agriculture* for September, 1901, and by Kulagin (1913) in Russia; while quite recently (1917) in England observations have been made in districts where *frit-fly* is very prevalent that when seed from districts where oats do not suffer to the same extent from the fly has been used, the crops in some cases have not been seriously attacked, and that where seed has been dressed with corvusine, seedolin, or sulphate of copper, the crops have been fairly free from attack (Bland, July, 1917). Moreover, in an experiment in which seed from a badly attacked field was sown under a fine mesh muslin frame which seemed to be impervious to the flies, an examination of half the plants at the end of June brought to light two *frit* larvae (Roebuck, Shropshire, 1917 *in litt.*).

### REMEDIES.

Spring sowings should be as early as possible, and the early growth stimulated in order that the young plants may be as forward as possible at the time of appearance of the first brood of flies, for then the small

weak side shoots only will be attacked. The best time for this sowing probably varies according to the season, but crops sown in March (the earlier the better) usually enjoy immunity from attack. It must be remembered, however, that early sowing on a bad tilth or too early sowing, with damage from frost, may result in a more backward plant than somewhat later sowing. Sulphate of ammonia and sodium nitrate appear to be two of the best top dressings for young oats, and in regard to these it has been specially noted in the Oxford district (Bland, July, 1917) that sodium nitrate, applied as soon as the oats are through, gave better results in a dry season than sulphate of ammonia applied when oats were drilled.

Vassiliev (1914) has recorded some of the results of experiments made in 1911 in the Government of Petrograd on the effect of manure on the yield of *frit* infested oats in a table as follows:

Manures	Percentage of plants attacked		Percentage of plants not producing normal grain		Percentage of plants killed		Yield per dessiatine (=2.7 acres)	
	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2
	Unmanured ... ..	45	41	48	49	22	20	115
Superphosphate ... ..	33	35	32	29	11	10	125	77
Superphosphate and Potash ... ..	40	52	26	46	10	24	142	66
Sodium nitrate and superphosphate ... ..	32	39	17	15	5	6	158	96
Sodium nitrate, superphosphate and potash	40	43	11	24	4	10	156	112

The important facts may be shortly summarised as follows:

Percentage of infested plants on all plots ... ..	40
Percentage of plants completely killed on unmanured plots ... ..	21
Percentage of plants killed on plots manured with superphosphate at rate of about 267 lbs. per acre and sodium nitrate 80 lbs. per acre ... ..	5½
Percentage of plants on unmanured plots not producing normal grain ... ..	48½
On plots manured with superphosphate and sodium nitrate as above the percentage of plants not producing normal grain reduced to ... ..	16
The addition of potash at rate of 80 lbs. per acre to above manures, in one case reduced the percentage of plants not producing normal grain to ... ..	11
Increase in yield 37 % in one case, 65 % in another.	

He found that oats damaged by *frit* when manured with sodium nitrate tillered well, producing new shoots which ripened at the normal time, and came to the conclusion that damage caused by anything up to 40 per cent. of *frit* infestation could be reduced to practically nil if proper manures were used under suitable conditions.

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Spring sowing should be avoided, when possible, on or near fields which were attacked in the previous year. With regard to the seed, early varieties, and such as are best suited to the soil and locality, should be chosen.

In 1917 in the *frit*-infested county of Oxfordshire it was found that the best time to roll the fields sown with spring oats was immediately after the seed had been drilled, or at least before the young plants were through the ground; oats rolled later, probably owing to the check in their growth, were more severely attacked (Bland, July, 1917).

Rörig (1893) recommended that a forage crop should not be sown with oats or barley on a field that had been affected, but this advice was directed to continental farmers. It would appear that grass layers or newly cultivated grass or waste-land should be ploughed early in the summer and bastard fallowed before planting with winter wheat (Petherbridge, November, 1917). It should be remembered that on a field which has been attacked and the crop harvested, the grasses and young plants growing from the shelled-out corn are probably badly infested; these should therefore be ploughed up early.

Kulagin (1913) mentioned an experiment recorded by Lindeman (Russia) in which a field was sown with rye on August 10th next to a badly infested crop of oats; in the ordinary course the complete destruction of the rye would have been certain, but on August 13th (before the rye had sprouted) the oat field was ploughed up, with a result far exceeding expectations, there being no subsequent damage to the rye. Fields should be kept clean of grass, and the destruction of grass borders round fields, and grass edgings to field roads has been recommended.

### OBSERVATIONS.

This summary must not be accepted as complete, as many observations may have been overlooked, and the publications in which some are recorded have been inaccessible: also it naturally contains many conflicting and probably often inaccurate statements, and impracticable advice, but it should prove of some value to those who are working, or about to work, at the *frit*-fly problem.

There are still very many points in the bionomics of the *frit*-fly requiring elucidation, and a very large amount of experimental work to be done, before the efficient control of this pest can be assured: moreover, research and experimental work undertaken in (say) Russia cannot be relied upon as giving correct data for England. The climatic conditions and the agricultural methods differ so much in different countries, that

it is quite possible the life history of the fly will be found to be more or less modified; for the same reasons, experimental work in controlling the pest may be found successful in one country, but fail in another.

It is remarkable that no definite experiments, beyond those of Krassiltchik and Vitkovsky mentioned under "Pupae," appear to have been made as to how far the fly can be controlled by being buried under the ground in its earlier stages, especially as to whether the larva can complete its feeding and pupate after the affected plant has been ploughed in.

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## ON THE TRANSPORT OF HERRING SPAWN TO THE SOUTHERN HEMISPHERE.

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Two unsuccessful attempts have been made to transport the ova of the herring to New Zealand. The first was, I believe, made in the eighties.

As a preliminary to a second attempt certain experiments were made at this laboratory, and in 1913 Mr Anderton, of the Marine Fish Hatchery, Portobello, Dunedin, conveyed some spawn along with small turbot, and adult crabs and lobsters, which were secured for him through the very efficient assistance of the staff of the Plymouth Biological Laboratory. Mr Anderton's labours resulted in 191 turbot, 43 crabs, and 41 lobsters being landed alive in New Zealand—an achievement reflecting the greatest credit upon him. The late Mr H. C. Dannevig had previously transported a number of plaice alive to Australia.

The herring ova survived till the steamer reached Cape Town. The water supply was on more than one occasion dirty with rust, and other sediment. The ova became coated with this matter, and although the plates were cleaned more than once, the eggs all died off.

The method adopted for the conveyance of the spawn, which is adhesive, was to cause the eggs to adhere to glass plates. The plates were put into a frame which slowly revolved, submerged in water. A current of water flowed through a series of boxes in each of which a frame carrying four glass plates rotated.

During incubation the current flowing over the eggs must be strong. It is not very easy to cool down a large quantity of water continuously, and the arrangement of rotating the plates was adopted in order to change the water in contact with the eggs. Mr Anderton reported that this apparatus worked well. New water was being steadily added, and none of the water was used a second time. This was possible because Mr Anderton had his tanks in a cold storage compartment, and brine-cooled coils reduced the temperature of the water which was supplied from an overhead tank.

Where a cold storage room is not available, or where the expense involved in its use is considered greater than should be incurred in a preliminary experiment, the cooling may have to be done with ice, and to reduce the quantity of water to be cooled to its smallest limit would be an advantage. Such an end might be secured if the cooled water were recirculated.

For the voyage to New Zealand it was necessary to prolong the period of incubation to 50 days. To retard hatching for that time, it was necessary to keep the ova at a temperature of about 35° F.

The Provincial Cape Government has had under contemplation the possibility of introducing the herring into South African waters. How far it may be possible to acclimatise the herring there is not to be solved *a priori*. In such matters an ounce of practice is better than a bushel of theory. The only answer to be trusted is that furnished by experiment. And if the experiment can be carried out without an undue expenditure it is well worth doing.

In order that the ova reach Cape Town unhatched they require to be exposed to water of a temperature of from 39° to 46° F. This is the range of temperature ordinarily exhibited by the water of this laboratory in March. During the voyage the sea-water may have to be cooled down from a temperature of 86° F.

So far no method has been devised of incubating the ova except in a current of water. I have been able to keep the eggs of the herring alive in stagnant sea-water, a third of which was renewed daily. Some survived for 20 days at a low temperature; the majority was dead by the end of that period; all died without hatching. Similarly some of the ova which were kept in dead moss wet with sea-water, remained alive for 19 days, but they also died, without hatching. It is quite possible that these methods might be successfully developed. That would simplify the problem very much.

It is possible to keep certain marine animals alive in sea-water that is unchanged during a considerable period, all that is necessary being to drive air into the water. The excretory products do not then apparently seriously pollute the water. Where there are dead eggs present, the air current is not sufficient to keep the water in an innocuous condition. The water must be changed; to what extent is a matter for experiment. In the case of artificially spawned eggs it is probably impossible to avoid having some eggs die during incubation, and the dead eggs cannot be readily removed from among the living herring spawn.

Among the eggs of the herring which were incubated at this labora-

tory, the death-rate was often large; in some cases all the eggs of a batch succumbed without hatching. There are various factors which one can suppose will or may injuriously affect the ova, and it is necessary to eliminate them as far as possible.

So far as the water was concerned the only precaution which was taken was against mud, etc. in suspension: the water was filtered through sand. Since ova develop in the water, it was considered that a suitable environment for the eggs depended simply on the quantity of water supplied. When however it is desirable to reduce the quantity of water employed, its quality, in respect to the quantities of dissolved gases and of matters in solution, as well as the bacterial content, demands attention. Mr Anderton considered that the water of the tropics when cooled down was short of oxygen. Therefore a means of adding to the air content would be necessary. The quality of the air which is bubbled through is important<sup>1</sup>. There is further in this connection a certain risk that may follow from the supersaturation of the water with gases. Some fishes have suffered through such a condition. Gas-bells may form in the tissue and cause death. I have observed a gas-bell inside the dead egg of plaice which had been in water into which air had been pumped in great quantity. But the bells did not occur in all the dead eggs: they appeared to be an exception.

There is, in certain places, an important difference in quality between the shore-water and off-shore water. Cunningham<sup>2</sup> reported that the water from the shore at Plymouth, although constantly supplied in a pure condition to the eggs in the circulation apparatus, was rapidly fatal; while in the water from the open sea, although perfectly still and unchanged, the ova lived.

In the herring eggs which were incubated in water cooled below the temperature prevailing, viz. 39°–46° F., crystals were often found<sup>3</sup>. The crystals were rectangular, sometimes ending in an oblique tapering point. They may be fine needle-like, or fairly thick bars. They have been observed on the inside of the zona, between the layers of the zona, attached to the yolk or embryo; in two instances they were noticed inside the gut of the living embryo.

The cooled water was restricted in amount, and it was cooled in galvanized iron pipes. I consider that these crystals resulted from

<sup>1</sup> Cf. Shelford and Allee, *Journ. Exper. Zoology*, Philadelphia, xiv, 1913.

<sup>2</sup> *Journ. Mar. Biol. Assoc.* 1889–90.

<sup>3</sup> Cf. Williamson, H. C., "The retardation of the Development of the Ova of the Herring," *Fisheries Scotland Sci. Investig.* 1910, II (1911).

deficient aeration, but I have also thought that they were in some way due to the galvanized metal. They did not however appear in all the eggs of a plate: they occurred in both living and dead eggs. They were observed in certain of the eggs of a plate which was rotated. In one instance the crystals appeared in the egg within 36 hours after fertilization:

The layer of eggs was, towards the end of the period of incubation, often attacked by a fungus. The mould grew in water of 37° to 43° F. Whether it was the cause of the death of the eggs, or whether it grew there in consequence of the death of the ova I was unable to decide. It probably was instrumental in killing some of the eggs. Diatoms have also grown on ova exposed to strong light; it is better therefore that the eggs be screened.

Mr Anderton used tanks of wood, coated with asphaltum. I now think that earthenware vessels would be preferable for the spawn.

How far sterilized water would be an advantage is uncertain. Stone<sup>1</sup> preferred for his successful transport of fishes and lobsters across the American continent, sea-water which had stood for two or three weeks covered and perfectly still, to sea-water that had been boiled. "At the end of the three weeks the microscopic creatures will be found at the bottom of the tanks, in the form of a deposit of slime. The water above will be perfectly sweet and clear, and it will remain so indefinitely."

I think however that there is reason to doubt that the environment is the sole cause of the death of the ova. It seems to me that the eggs differ in vitality. It is noticeable that about 48 hours after spawning, the eggs on the plates very often look well: with very few exceptions they are fertilized. One might infer then that all that was necessary, was to provide a suitable environment, in order that all may eventually hatch. The eggs however gradually die off: a certain proportion survives and hatches. Any difference of environment of the ovum due to its particular position on the plate, or the fact that two or three other eggs crowd it closely, cannot surely, except in a few cases, account for its death. The eggs of fishes are known to exhibit very great vitality. Both pelagic and demersal eggs are recorded as having been frozen and still they hatched out, after thawing.

In the case of artificially spawned eggs one may argue that the ova, on being pressed out of the fish, may receive slight mechanical injury, which does not inhibit fertilization, but only permits development up to a certain point.

<sup>1</sup> Stone. *Report U.S. Fish Commission*, 1879 (1882).

There is the question of how much milt the ova require. The most common method of spawning salmon eggs is to bathe them in the milt, water being added after a short time. Jousset de Bellesme states that "the robustness of an organism would depend in great measure on the number of fecundating elements which entered the egg." There would however appear to be a danger from water which was excessively laden with milt. I have observed a white deposit of milt in the interstices of the eggs, and that would no doubt prove to be a source of danger through its decay.

The spawn on glass plates is easily handled; but when the eggs have been attached to gravel satisfactory results have also been obtained. Such spawn is conveniently incubated in a box having a sieve bottom. The water finds issue through the bottom after passing among the gravel. If the box is now and then lifted and then pressed down into the water an effective change of water is secured.

There is a reasonable expectation that naturally spawned herring ova could be dredged during February, or March, at Ballantrae Bank, Firth of Clyde, and it seems likely that such spawn would stand transport better than the artificially spawned ova. The spawn secured in this way would probably not be newly deposited, still development might be thereafter retarded sufficiently for the object in view.

Some herring ova, after incubation at from 37° to 40° F. for 19 days, had embryos in an advanced stage. The eggs were then treated with water of 33.8° to 37° F. The first larva appeared on the 30th day, and hatching proceeded for the next 12 days. Eggs left at the original temperature hatched in from 23 to 36 days. In another case the spawn began to hatch on the 20th day; the temperature of the water had been 38° to 44.5° F. Thereafter the temperature was lowered, and the larvae hatched out daily till the 41st day. All the eggs in a batch do not hatch out simultaneously; there have occurred, during the experiments, intervals of 5 to 21 days between the appearance of the first larva and the last to hatch.

There is another alternative method of obtaining the spawn; that is to arrange, if possible, that the herrings spawn in confinement. Ewart<sup>1</sup> described the spawning of herrings in Rothesay Aquarium.

<sup>1</sup> Ewart, C., "Natural History of the Herring." Plates. *2nd Ann. Report Fisheries Board for Scotland*, 1883, p. 61.

THE LARVAL AND PUPAL STAGES OF  
*SCATOPSE NOTATA*, L.

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(With Plate X and 7 Text-figures.)

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I. INTRODUCTION AND HISTORICAL REMARKS.

THE material used in this investigation was obtained at Holmes Chapel, Cheshire, at the end of October 1917; a small number of fully grown larvae were found in the decaying remains of a wasp's nest, the latter apparently having been destroyed some time previously. The remains consisted of parts of the nest and of the wasps, with organic matter of other kinds, fallen leaves, etc.

The larvae obtained were kept in the laboratory, and pupated soon afterwards, remaining in the pupal state about fourteen days, but the exact period was not noticed. Bouché(1) gives this period as eight to fourteen days.

I have to thank Mr C. G. Lamb, M.A. of Cambridge, for his kindness in confirming my identification of the adult, and Dr A. D. Imms, who suggested this investigation to me in the first instance, and who has assisted me in many ways throughout its course.

De Geer (1776) has given a short description of the life history of this species under the name of *Tipula latrinarum*. Bouché (1834) also has given an account of it as *Scathopse noir* Geoffr., which is probably

the present species. Perris (1847) has also given an account of this species under the name of *Scathopse punctata* Meig. None of these observers however give detailed descriptions or figures, and their accounts are not entirely free from inaccuracies. Sharp(s) has drawn attention to the fact that while Bouché considered that the larva possesses nine pairs of spiracles, Dufour and Perris considered it to be amphipneustic.

## 2. THE LARVA

The larva when fully grown is about 7 mm. long and 1 mm. broad at its widest part, and its thickness is rather less than its width. It is clearly divided into two regions, (i) the *Head*, and (ii) the *Body*.

The *Head* is about .48 mm. long, and .43 mm. in width, and is invested by a brown chitinous capsule which is considerably darker and stronger than the covering of the body. The anterior part of the head is rather darker than the posterior part and bears a few short setae, some of which occur in groups. There is no indication of eyes.

The antennae are small but conspicuous, and consist of a basal portion which bears several processes at its apex, one of which may be a much reduced second joint (Text-fig. 5).

The labrum is somewhat triangular in vertical section, the apex projecting between the mandibles. The ventral side of the labrum bears many setae of several types and also chitinous processes, possibly of a sensory nature (Text-fig. 3).

The mandibles (Text-fig. 1) are strong and bear six teeth. Of these teeth five are in a row and are directed in such a manner that in the natural position they project ventrally and slightly inwards, while the sixth tooth is separate and projects dorsally, towards the other five. The maxillae (Text-fig. 2) consist of a basal portion which bears a stout undifferentiated lobe, upon which are a number of setae and chitinous processes. A single jointed maxillary palp is present and bears on its ventral surface an annular depression within which are a number of short projections. On the apex of the palp are a few processes and setae. The labium is composed of a flat dorsal plate, which is supported below by two small sclerites, of which one is anterior to the other. These two parts project beneath the head, and bear a large number of setae (Text-fig. 4).

The *Body* is nearly cylindrical, but it is rather flattened dorso-ventrally, while its diameter decreases from about the middle towards both ends (Plate X, fig. 1). It consists of twelve segments and is curved longitudinally, the ventral surface being almost straight and the dorsal

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surface convex. It is a dirty white in colour, but this colour is obscured during life by particles of soil, etc. which adhere to it and give it a much darker appearance. During life the form of the larvae, in particular of the posterior end, was very much obscured by adherent particles.

The larva bears nine pairs of spiracles, which are situated a pair on each segment, on the first and the fourth to eleventh segments inclusive. The spiracles are brown in colour and are situated laterally. They are placed rather nearer the anterior than the posterior border of the segments except for the pair on the eleventh segment. These latter spiracles are considerably larger, and are situated in a more dorsal position on the posterior margin of the segment. All the spiracles project considerably from the body, the amount of the projection being more than twice the diameter of the spiracle. The last pair, however, projects to a much greater extent than the previous pairs, each spiracle being about as long as the twelfth segment.

The spiracles on the eleventh segment bear near their apices a number of fine setae projecting downwards towards the body. The other spiracles are rather spatulate in shape, those on the first segment being slightly larger than the others.

The structure of the posterior spiracles is very similar to that of the spiracles of *Bibio* larvae, in that the opening is within a funnel which is supported internally by a system of trabeculae (Text-fig. 7).

The segments of the body bear a large number of setae, which vary in length on the different regions. The first ten segments each bears on the dorsal surface a transverse row of numerous setae, placed near the posterior border. In front of these bands of setae are five short broad longitudinal rows, of which the central one is median in position with two rows on either side of it. On segments four to ten the outermost of the longitudinal rows of setae are inclined inwards anteriorly, and become confluent or nearly confluent with the adjacent row of setae.

The eleventh segment bears dorsally a single median transverse row of setae, this row being continued backwards, at the sides, to the posterior margin of the segment.

The twelfth segment, which is much smaller than any of the preceding segments, bears a pair of large reddish-brown processes at its posterior end. These processes are about equal in length to the segment and bear a number of long setae, which are spread out in a fan-like manner. (Plate X, fig. 4.)

The anterior part of the ventral surface of the first segment projects slightly, and is covered with small setae. Ventrally, the fourth to tenth

segments bear two transverse rows of setae, with a number of small groups of setae. The first three segments are without the two transverse rows, but bear instead a pair of groups of setae. These, especially on the second and third segments, are rather horse-shoe shaped, with the opening anteriorly.

The eleventh segment bears, on its ventral surface, a transverse row of setae, near its posterior margin. Placed in front of these setae is a second but incomplete transverse row.

The twelfth segment is provided ventrally with a number of large setae surrounding the anus, with a smaller row on each side.

Between all the segments, both dorsally and ventrally, are a number of short spines. On the first three segments they are arranged in groups of from three to five in a short row (Plate X, fig. 8), while on the remaining segments they are separate and not grouped together (Plate X, fig. 7).

On the first two segments the dorsal transverse row of setae is composed, on all the larvae I have been able to examine, of short blunt processes, which in size and colour resemble the basal part of the largest and longest of the other setae. In some cases the tops of these processes were flat, as if the upper part had been broken off, but some of them were rather conical in shape.

### 3. THE PUPA.

The pupa (Plate X, figs. 2 and 3) is formed within the larval skin, which is persistent and remains entire except for a longitudinal slit exposing the back of the thorax of the pupa. It foreshadows, therefore, the puparium of the higher Diptera.

The pupa does not completely fill the larval skin, an empty space being left within the skin at both ends. The abdominal spiracles of the pupa project through the larval skin laterally, and are closer together than those of the larva. The thoracic spiracles are exposed by the splitting of the anterior dorsal part of the larval skin. The larval skin thus affords some slight protection to the pupa: this protection must, however, be very slight as the skin is easily torn.

The pupa, when completely removed from the larval skin, is of a uniform reddish-brown colour and is about 4 mm. long, 1.2 mm. broad across the thorax and 1.3 mm. broad across the widest part of the abdomen, which is slightly flattened.

There are six pairs of abdominal spiracles. These project laterally to the extent of about .11 mm. and are situated on the anterior part of

the second to seventh segments. Each spiracle bears a number of minute openings at its apex.

There is also a pair of prothoracic spiracles, which are dorsal in position. Each arises from an enlarged base and is a considerably branched structure, with a length of about .24 mm. At the apex of each of the branches are a number of minute openings.

On the ventral surface of the thorax the sheaths of the legs, wings and antennae are visible, but they are much more closely attached to the body than is the case with the pupa of *Bibio* (6). The head is adpressed to the prothorax, and the antennal sheaths curve outwards and backwards, extending to the base of the wing sheath of the same side.

The leg sheaths lie side by side, those of the first and second pairs meeting in the middle and, along with the wing sheaths, cover the underside of the meso- and metathorax. The sheaths of the third pair of legs are almost entirely covered by the wing sheaths, only their extreme apices being exposed. The leg and wing sheaths extend nearly to the posterior margin of the first abdominal segment (Plate X, fig. 3).

The parts of the sheaths of the appendages which are directed outwards, are composed of a tough cuticle similar to that covering the greater part of the body. Those portions of the sheaths which are closely adpressed to the body, consist of a delicate colourless membrane. A similar delicate membrane invests those portions of the body which lie beneath the sheaths of the appendages.

Dorsally the thorax bears a slight longitudinal ridge extending from the hind margin of the mesothorax to the anterior extremity of the pupa. This ridge is exposed by the slitting of the larval skin, and along this ridge the pupal cuticle divides for the emergence of the imago.

On all the abdominal segments, both dorsally and ventrally, are a number of small oval depressions, which are slightly paler in colour than the other parts. The pupa is covered with minute blunt processes, which are usually circular in shape. These structures, however, are absent from the oval depressions just mentioned, from the intersegmental parts of the abdomen and from the spiracles and their bases.

#### 4. GENERAL REMARKS ON THE MORPHOLOGY AND AFFINITIES OF THE LARVA.

It has been already mentioned that both Dufour and Perris considered the *Scatopse* larvae, which they described, to be amphipneustic. Bouché, on the other hand, stated that the larva carried nine pairs of spiracles, which is the correct number. Dufour mentioned that the

larva bore a pair of brown projections on each segment of the abdomen which, however, he did not consider to be spiracles, although they are almost certainly the structures which have now been found to be undoubted spiracles.

Dufour also considered that the larva had no mandibles, although they are distinctly present. As they are somewhat difficult to separate from the maxillae, this may account for Dufour's failure to distinguish between the mandibles and the maxillae.

In previous accounts of larvae of this genus, it is stated that the body is composed of eleven segments. The eleventh segment is described as being large, and divided dorsally into two distinct regions, the anterior region bearing the pair of large spiracles, and the posterior region bearing the posterior processes.

After a careful examination of this apparent eleventh segment, it appears to me to be distinctly composed of two segments, both regions being actually complete segments. The division between these segments is not very marked dorsally, but there is a slight transverse depression just posterior to the spiracles, which bears a few small setae similar to those borne between the other segments. Ventrally the division between the eleventh and twelfth segments is more clearly marked.

The posterior processes appear to have a somewhat similar structure to that of the spiracles, and they may be a modified pair of spiracles. It seems more probable, however, that they have been formed by the modification of some structure similar to the protrusible conical structures which are found in the larva of *Bibio Johannis*(6). In another species of *Bibio* larva, of which it is hoped to give an account at a later date, these structures are more strongly developed than in *B. Johannis*. They distinctly suggest that some structures, more or less similar to them, may have developed into the processes of the *Scatopse* larva.

The larva of *Scatopse* agrees with that of *Bibio* in possessing twelve trunk segments, in the projecting spiracles, and the fact that the hindmost pair is greatly enlarged and the anterior pair slightly enlarged. This larva further agrees with that of *Bibio* in the absence of eyes.

It differs, however, from that of *Bibio* in the fact that the hindmost pair of spiracles is carried on the eleventh and not the twelfth segment and are much drawn out to form conspicuous elongate processes. Other important differences are seen in the absence of the characteristic cuticular processes so well displayed in *Bibio*, in the single jointed maxillary palpi, in the pair of fan-like caudal processes to the twelfth segment, and in the pointed and more triangular head.

The pupa of *Scatopse* differs from that of *Bibio* in being broader and less tapering towards the anal extremity, in the presence of branched prothoracic spiracles, in the prominently projecting abdominal spiracles, and the total absence of the cephalic and caudal processes. A further difference is afforded by persistence of the larval cuticle to form a covering for the pupa.

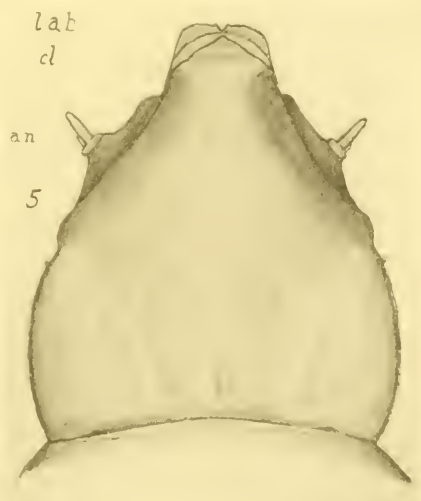
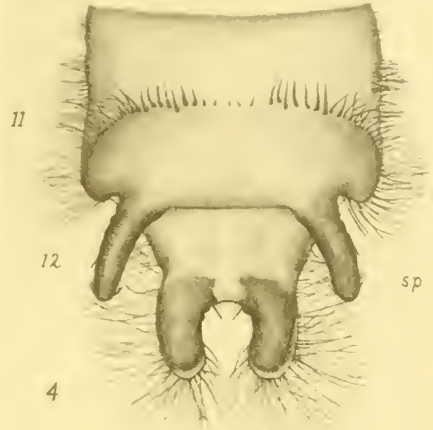
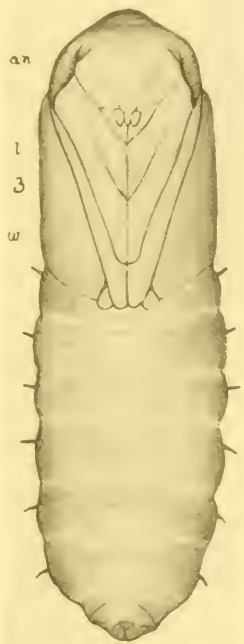
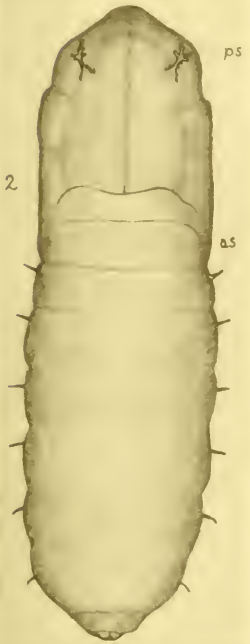
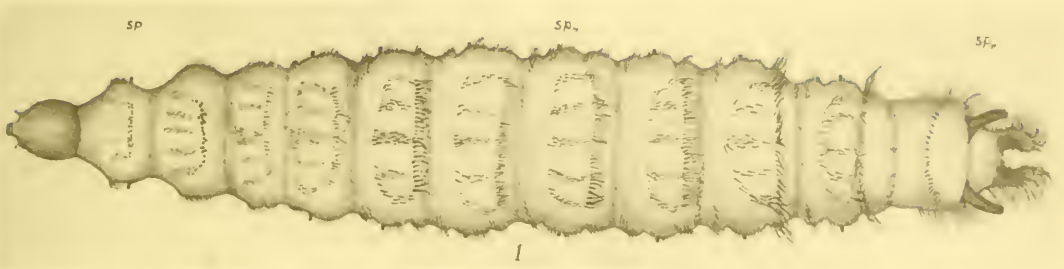
Until the larvae and pupae of other genera of Bibionidae have been fully studied it is scarcely possible, in our present state of knowledge, to judge whether these differences are of a sufficiently fundamental nature to lend support to the view of certain systematists who elevate the Scatopsinae to family rank. So far as my observations go, however, they do afford some justification for that conclusion.

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- (8) SHARP, D. (1909). *Cambridge Natural History*, Vol. VI. Insects, Part II, p. 476.

#### DESCRIPTION OF PLATE.

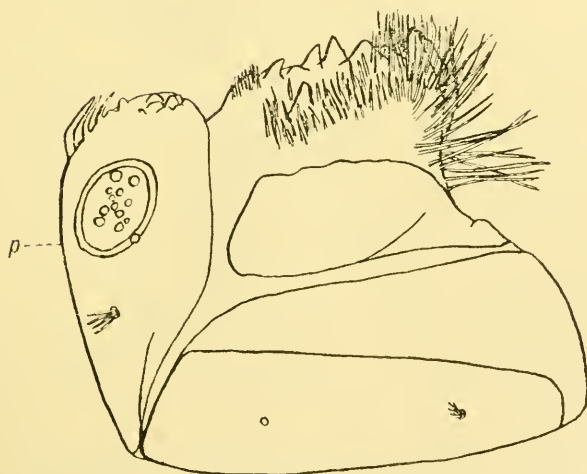
- Fig. 1. Fully grown larva of *Scatopse notata*. *sp*, spiracle of first segment; *sp*, spiracle of seventh segment; *sp*, spiracle of eleventh segment. × 20.
- Fig. 2. Pupa of *Scatopse notata*, dorsal aspect. *ps*, prothoracic spiracle; *as*, first abdominal spiracle. × 20.
- Fig. 3. Pupa of *Scatopse notata*, ventral aspect. *an*, right antenna case; *l*, leg cases; *w*, right wing case. × 20.
- Fig. 4. Posterior end of larva, dorsal aspect. 11, eleventh segment; 12, twelfth segment; *sp*, spiracle of eleventh segment. × 52.
- Fig. 5. Head of larva, from above. *an*, left antenna; *lab*, labrum; *cl*, clypeus. × 115.
- Fig. 6. Typical seta. × 625.
- Fig. 7. Small setae of the type found on segments one and two. × 625.
- Fig. 8. Small setae of the type found on other segments. × 625.



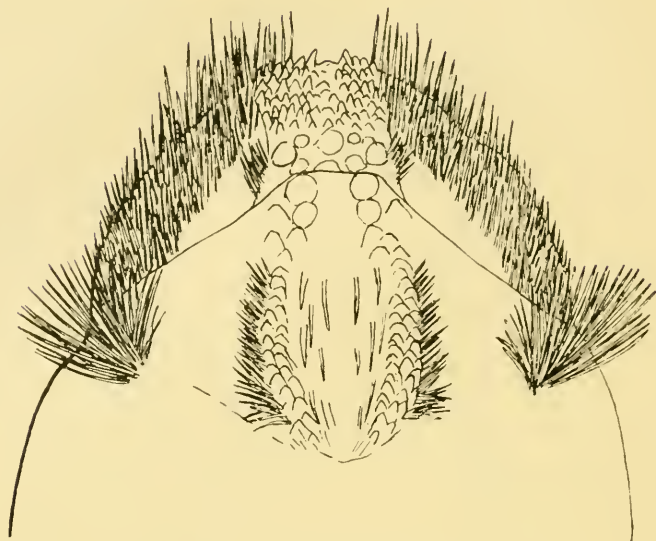




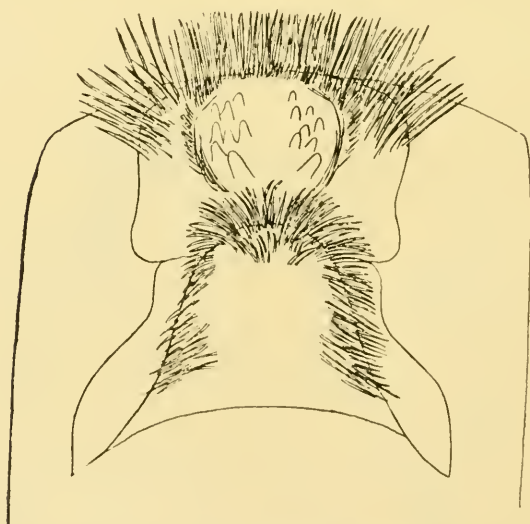
Text-fig. 1. Right mandible, from the right side.  $\times 625$ .



Text-fig. 2. Right maxilla from ventral side. *p*, maxillary palp.  $\times 625$ .



Text-fig. 3. Labrum, ventral view.  $\times 625$ .



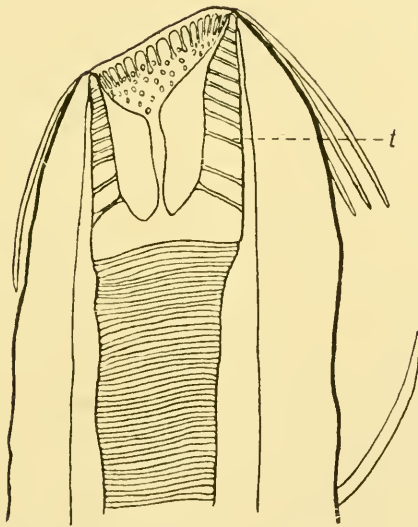
Text-fig. 4. Labium, ventral view.  $\times 625$ .



Text-fig. 5. Right antenna.  $\times 750$ .



Text-fig. 6. Left prothoracic spiracle of pupa.  $\times 250$ .



Text-fig. 7. Left posterior spiracle of larva, optical section. *t*, tracheolae.  $\times 600$ .

PHYSIOLOGICAL PRE-DETERMINATION: THE  
INFLUENCE OF THE PHYSIOLOGICAL CONDI-  
TION OF THE SEED UPON THE COURSE OF  
SUBSEQUENT GROWTH AND UPON THE YIELD.

II. REVIEW OF LITERATURE. CHAPTER I.

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INTRODUCTION.

IT may not always be fully realised to what a degree the developmental capacity of plants is pre-determined by the action of environmental conditions during the earliest stages of their life-histories. During the course of germination and in the seedling stage, or even earlier during the sojourn of the seed upon the parent and in the dormant period, the "potentialities" of plants may be affected by actions which only subsequently produce visible results. These results appear during the later stages of development, without reference to the conditions then existing. In this way adverse conditions in the later stages of development may not suppress a vigour of growth which has been pre-determined under favourable conditions during the ripening of the seed in

<sup>1</sup> *I.e.* the capacity of the resulting plant for growth and yield

the previous year; or favourable conditions during summer may fail to increase the yield owing to adverse conditions which have previously operated during the period of germination. It is such effects, namely those which are to be traced to the environmental conditions which have operated in the past stage of the plant's life, that we may term effects of physiological pre-determination in order to mark their distinction from those which are due to hereditary causes.

The present authors are engaged upon experimental work dealing with the effect of various conditions acting upon seeds during their maturation, dormancy, and germination in pre-determining the course of subsequent development and size of yield. Some preliminary results have been communicated in a previous paper (Part I of this series<sup>(4)</sup>); the present communication is a critical review of the literature bearing directly or indirectly on the problem.

It is interesting to note how exclusively attention has hitherto been concentrated upon the isolated question of germination in the enormous mass of literature dealing with the seed. In only a relatively small number of cases has experimental work with seeds included observations upon the subsequent course of development, nevertheless, the present review indicates clearly the wideness of the field and the possibility of obtaining important results if suitable experimental work on a sufficiently large scale be carried out both in the field and in the laboratory.

The most obvious categories under which we may deal with the conditions affecting the "potentiality" of the seed, meaning by this the capacity of the resulting plant for growth and yield, are as follows:

- I. Parental conditions,
- II. Harvesting conditions,
- III. Conditions during, or immediately preceding, germination, or in the early stages of the seedling.

## CHAPTER I

### PARENTAL CONDITIONS AFFECTING THE "POTENTIALITY" OF THE SEED.

#### A. SOIL, LOCALITY, AND CLIMATE.

In considering cases which come under this category there is always the difficulty of excluding the possible operation of hereditary factors such as may make themselves obvious in the course of growth and development as differences between forms of the same species, but do not concern the question of physiological pre-determination.

That the environmental conditions of the parent plant and the position of the seeds on the parent plant affect the capacity of the seeds and produce obvious results in the course of their subsequent development has often been stated, but so far as we have been able to discern amongst the literature, no decisive investigation has been carried out on this subject. A number of indications are to be found, however, which make it clear that the question is one which would repay critical examination.

As is well known, traditions, of which we need not quote examples in detail, are common among farmers and seedsmen to the effect that the seed obtained from certain localities can be relied upon to produce a vigorous crop under normal conditions. Turning to experimental results, an interesting paper was read in 1904 before the Botanical Club of Washington by W. W. Tracy (70). He speaks first of leguminous plants. After stating that "Seedsmen commonly believe that, in the case of peas, the character of the soil has a marked influence over the character of the plant, and that this influence extends to and is carried by the seed, but that such soil influence is decidedly cumulative in its effects," he goes on to describe an actual experiment of his own, as follows: "In the case of garden beans, the tendency of rich, moist, heavy soil is to produce thick, fleshy pods slow to mature, while that of warm sandy land is to the production of flatter, less fleshy and quicker maturing pods. I can best illustrate this by experience. Some ten years ago I sent each of two growers living within a mile of each other, seed of 'Valentine' bean of precisely the same stock grown the previous year in the same field, which was a rich clay loam. One of these, whom I will call C., planted on rather heavy, rich soil, the other, S., on a light warm, but rich sandy one. The next season C. received seed grown by S. and S. seed grown by C., while a third man, M., some five miles away, on rich loam soil, received equal parts of both. When I visited the fields I noticed that in C.'s field, which I supposed was planted wholly with seed grown by S., there were ten rows which differed from the rest and were such as I would expect if seed from C. was planted, and I tried to account for them by extra manure, etc., but I learned that as there was not quite enough of the seed from S. sent him, he had filled out with some of his own, and I had detected the exact row where the seed was used. I then visited M. on loam soil, and while I could tell that one part of the field was planted with C. stock and the other with S., I could not detect the line between them."

De Vries (71) has emphasised as a result of his many years of experi-

mental experience the conclusion that external influences exert their effect on the development of organs during their youth, that is to say, during the so-called susceptible period. He finds that in many cases the most susceptible stage seems to be that of the young embryo in the ripening seed. It is in this stage that external conditions exercise a powerful pre-determining effect upon the whole subsequent course of the development of seed plants. He was led to enunciate two principles which we may quote fully in view of their importance.

1. "*The younger a plant is, the greater is the influence of external conditions on its variability, that is, on the place which its various characters will occupy in the curves of variability of the whole culture or race.*"

2. "*In connection with this principle the nutrition of the seed on the mother plant has, in many cases at any rate, a greater effect upon variability than nutrition during germination and vegetative life itself.*"

In an experiment with *Oenothera Lamarckiana*, after showing that the lengths of the fruits fall on a Quetelet-Galton frequency curve of variation and that a strong correlation exists between thickness of stem (taken as a criterion of vigorous development) and the mean fruit-length of the plant. De Vries shows that the effect of manuring the plant in increasing the mean fruit-length is not confined to one generation. He gave his plants similar manurial treatment for three generations, and his results are brought together in the following table:

Mean value for length of fruit:

After 1st year without selection	= 25.2 mm.
After 2nd year combined with positive selection	= 33.4 mm.
After 2nd year combined with negative selection	= 29.9 mm.
After 3 generations without selection	= 38.5 mm.

It is thus seen that the effect of high nutrition continued through a number of generations without selection proved itself superior to the most stringent selection, and even when combined with negative selection it improved the mean. The effect of manuring the parent plant was not confined to one generation. Under favourable nutritional conditions the parent plants produced embryos which were well-nourished during the "susceptible" period of seed-formation and the physiological condition of the seed thus produced pre-determined to a considerable degree the development of the plant produced after germination. It will be seen that this result is essentially the same as that obtained by Tracy. It shows, further, that the operation of high nutrition of the seeds is capable of accumulation through two or more generations, and the same is true of low or defective nutrition.

Harris<sup>(30 & 31)</sup> in a very elaborate statistical investigation has experimented in the opposite direction by submitting a race of beans (*Phaseolus vulgaris*) to recurrent starvation conditions for three generations in order to determine whether any accumulated effect was transmitted through the seed when the race was finally returned to normal conditions. His "starvation" conditions were obtained by growing the plants in fields in which the soil barely sustained the given species.

He arrived at the conclusion that statistical constants showed an unmistakable, though slight, influence resulting from the treatment of the ancestors upon the race when returned to normal conditions. He records this influence as mainly shown by a decrease in the number of pods per plant and in the number of ovules per pod, but by no modification in average seed-weight. The direct effect of the environment was of the same nature, but far more pronounced.

Gain<sup>(23)</sup> discussing the results of Raulin<sup>(60)</sup> concludes that a change in the chemical nature of the soil is favourable. Plants grown in different soils from generation to generation produce a larger average weight of seed than plants grown from generation to generation in the same kind of soil<sup>1</sup>.

The results obtained by Raulin appear to be in contradiction to those of most other workers and to general experience with regard to cereals. Thus according to Hieks and Dabney<sup>(41)</sup>, although a marked difference in crop is frequently noted when seed is transferred to a different type of soil from that in which it was grown, this difference is often in the negative direction. They state that (*l.c.* p. 308) "Experiments in growing oats have shown that certain varieties raised on a light soil were the most productive if sown on a similar soil, while the same varieties of seed, if grown on heavy soil, showed a preference for heavy soil."

With regard to the grasses, according to Tracy's (*l.c.*) experience, the character of the soil exercises little influence upon the character of the seed; climatic conditions acting upon the parent plant, however, have a marked effect upon the "potentiality" of the seed produced.

<sup>1</sup> "Il y a un maximum et un minimum d'influence correspondant à une certaine succession des divers sols (humus, sable, argile, calcaire).

Les *maxima* répondent, pour le Blé, aux changements suivants: graines cultivées dans l'humus, doivent venir de l'argile; celles destinées au sable doivent venir du calcaire; celles pour argile, du sable; celles pour calcaire, du sable.

Les *minima* répondent aux changements: graines cultivées dans l'humus, venant du calcaire ou de l'humus; en sable, venant de l'humus ou du sable; en argile, venant de l'humus ou de l'argile; en calcaire, venant du calcaire ou de l'humus."

“People who use large quantities of sweet corn are positive in their belief that seed produced in the eastern states gives better product than that grown at the west.”

In a later communication by the same author (71), p. 15) he says: “If a field of sweet corn is planted with two lots of seed of the same variety, one eastern and the other western grown, and ears as uniform as possible as to maturity and quality are gathered from the two parts of the field, processed, and canned in the same way, experts can with a fair degree of certainty decide which lot of seed the corn in different cans was grown from, and they will generally declare that the corn from eastern-grown seed is the better.” Tracy’s observations on the influence of climatic conditions upon Sweet Corn are confirmed by Duggar (17), who states that it is now recognised that Sweet Corn grown from the same seed from points north and south in the United States produces seed which when again sown side by side shows marked differences in that the seed from the north will produce plants that will mature earlier<sup>1</sup>.

The best data on this question are due to T. Lyon (52). A variety of wheat was grown for several years in different localities, and finally in adjacent plots. The differences in date of ripening and in yield then observed are marked as is seen in the following table:

TABLE I.

*Modification induced in Wheat by its Environment.*

			Kansas Seed	Nebraska Seed	Iowa Seed	Ohio Seed
Date of sowing	...	...	Sept. 9th	Sept. 9th	Sept. 9th	Sept. 9th
Lodged	...	...	None	None	Badly	Badly
Rust	...	...	Very little	Very little	Much	Much
Date of ripening	...	...	June 25th	June 27th	July 2nd	July 3rd
Yield of grain per acre	...		29.1 bushels	27.5 bushels	22.3 bushels	23.1 bushels
Weight of grain per bushel			64.2 lb.	62.2 lb.	56.9 lb.	58.9 lb.

The influence of the climatic environment of the parent plant upon the properties of the seed produced finds many illustrations in recent scientific works dealing with the question of seed germination alone, and has come to be regarded as a matter worthy of notice. For example,

<sup>1</sup> Quite recently Boerker (3) has contrasted seeds produced by *Pinus ponderosa* growing in the Rocky Mountains with the seeds produced by this tree growing near the Pacific coast. The seeds of the former are smaller and have a different capacity for germination. This botanist noted somewhat similar differences between the seeds of *Pseudotsuga taxifolia* from the Rocky Mountain and the Pacific coast regions respectively.

Kinzel(45) in his monograph on the influence of light upon seed germination emphasises the importance of the local origin of the seeds of *Poa pratensis* with regard to their light-sensitiveness in germination. His numerous experiments with seeds of *Poa pratensis* from different regions show that every degree of light-sensitiveness may exist independently of after-ripening, which occurs during storage. Seeds from plants of the same original stock growing in different regions, when tested, showed various degrees of light-sensitiveness in their germination. In one case Kinzel (*l.c.*) with *Poa pratensis* was able to show that, even in the same locality, different climatic conditions during maturation exert a marked effect upon the light-sensitiveness of the resulting seeds. Seeds from the crop matured in bright sunny weather at Munich in 1906 showed themselves extraordinarily sensitive to the deleterious effect of blue light; on the other hand, the seed-crop from the same original stock of seed matured in dull rainy weather at Munich the following year showed scarcely any sensitiveness to the harmful effects of these rays.

Ottenwalder(58), working on the effect of light on germination of seeds of *Epilobium hirsutum* and other plants, found that the age and origin of the seeds modified his results considerably.

The environmental conditions which obtain during the maturation of the seed are undoubtedly of great importance (cf. Von Lochow(48)). Excessive moisture may hinder the gradual ripening processes and thus affect the conditions under which food-reserves are stored in the seed, and such effects may become evident in the plants produced from these seeds. Duggar (*l.c.*) mentions these possibilities, but critical work on the subject seems to be non-existent.

It is possible that the effects of soil and climate resolve themselves into a question of the degree of maturity reached by the seed at the time of harvesting.

#### B. SIZE OF SEED AS AN INDEX OF PARENTAL CONDITIONS AFFECTING "POTENTIALITY."

Under this first category of parental conditions and their effect upon the capacity of the seed for producing plants of greater or less vigour, we deal next with the influence of the size of the seed upon the resulting plant. This question has received more attention by both practical and scientific workers than the less obvious, but equally important, factors alluded to above.

It is obvious that any sample of seed can be graded according to

size; this is a common practice in seed selection, water-culture experiments, etc., and in scientific work generally. The main conclusion to be drawn from the available evidence, to which we shall allude immediately, concerning the selection and use of seed of different size, both in the case of forest-trees and in the case of herbaceous plants of economic importance, is distinctly in favour of the general conclusion that large seed produces a more vigorous crop and larger yield, although important contradictions to this statement have been published.

In view of its importance in practice it is essential in considering this question to analyse the conditions which affect the size of the seed. The latter may depend either upon the environmental conditions of the parent plant, or upon the position of the flower on the inflorescence and of the inflorescence on the plant, or upon a hereditary factor.

In experimental work planned to determine differences in crop production arising from the selection of seeds of different size there has usually been no distinction drawn between the various causes influencing the size of the seed. This failure has introduced some confusion into the interpretation of the results which have hitherto been obtained in research work on this subject. If we are dealing with a hereditary factor for large seed, the average weight of seed in the crop, but not necessarily the total weight of the crop (cf. Waldron<sup>(75)</sup>), would probably be pre-determined by heredity, and the question with which we are dealing, namely, a question of physiological pre-determination, would not come in.

(a) *Determined by Climatic and Edaphic Factors acting upon the Parent Plant.*

When the size of the seed is altered by climatic or edaphic factors acting through the parent plant, any resulting increase or decrease in yield from the seed thus altered can only be a matter of physiological pre-determination.

The literature bearing on this question is very scanty. The effect of various light-intensities upon seed-formation and the size of seeds has been subjected to investigation by Combes<sup>(11)</sup>. He tested the germination capacity of the seeds of different sizes which he obtained by differential treatments of the parent plants. His plants were grown for the whole period of their existence under five intensities of light obtained by glass screens of various thicknesses which gave  $\frac{1}{9}$ ,  $\frac{1}{3}$ ,  $\frac{1}{2}$ ,  $\frac{3}{4}$ , and 1 of the total insolation as determined by Wiesner's method.

The following table gives both the air-dry weight and the absolute dry-weight of 1000 seeds ripened in each case.

TABLE II.

Light-intensity ...	$\frac{1}{9}$	$\frac{1}{3}$	$\frac{1}{2}$	$\frac{3}{4}$	1
<i>Cannabis sativa</i> ...	{ 20.2* 176	{ 22.1† 199	{ 20.4 187	{ 17.8 161	{ 16.5 146
<i>Saponaria officinalis</i> ...	{ — —	{ — —	{ 1.87 162	{ 1.83 157	{ 1.59 135
<i>Sinapis arvensis</i> ...	{ — —	{ — —	{ — —	{ 2.19 199	{ 1.58 141
<i>Amaranthus retroflexus</i>	{ — —	{ .348 303	{ .443 376	{ .447 380	{ .422 352
<i>Chenopodium album</i> ...	{ — —	{ .752 630	{ .696 594	{ .680 578	{ .671 570

\* Calculated from three achenes, all that were produced from 1000 plants.

† Calculated from 600 achenes.

It is seen that the largest average seed-weight is never obtained in full light, but with *Cannabis sativa* in  $\frac{1}{3}$  light, with *Saponaria officinalis* in  $\frac{1}{2}$  light, with *Sinapis arvensis* in  $\frac{3}{4}$  light, with *Amaranthus retroflexus* in  $\frac{3}{4}$  light, and with *Chenopodium album* in  $\frac{1}{3}$  light.

This somewhat striking result shows that the largest seeds are produced under conditions of light-intensity which are only just sufficient to allow the production of fruit at all, *i.e.* with the minimum light intensity. The case of *Cannabis sativa* illustrates this point very clearly; the maximum average weight of single achenes was obtained in  $\frac{1}{3}$  light, as stated above; in  $\frac{1}{9}$  light only two out of 1000 plants produced achenes, to the number of three in all. The average weight of these, however, falls only very little short of the average weight of those obtained in large numbers with  $\frac{1}{3}$  light<sup>1</sup>. The seeds from Combes' harvest were tested for germination; in result it was found that the highest percentages of germination were obtained with seeds developed under light-intensities which were most favourable for the production of large seeds, in other words, the heaviest seeds gave the highest percentages of germination<sup>2</sup>.

It is to be expected that many other environmental conditions acting through the parent plant would greatly affect the size of the seed

<sup>1</sup> The number of fruits per individual plant and the number of seeds per fruit diminish from the full light to  $1/9$  light.

<sup>2</sup> Similar results have been obtained for twelve different species of economic and garden plants by Lubimenko (50), who, however, only submitted fruits during their development to different light-intensities.

Under this heading attention must be drawn to the observations of Boerker (2) mentioned above (p. 117, footnote).

produced, but we have been able to trace few critical published results bearing upon this point.

The results of investigations by J. L. Jensen<sup>(42)</sup> indicate that the average grain-weight of cereals is clearly related to climatic conditions. In brief, the average grain-weight decreases as the continental character of the country becomes more marked and, *vice versa*, it increases with an insular or coast climate, and in connection with such climate it also increases with rising temperature. In the following table the average weight in grams of 10,000 grains is given for wheat, barley, oats, and rye respectively from each country investigated:

TABLE II a.

*Grain-weights according to climatic conditions.*

Group	Countries	Average weight in grams of 10,000 grains.					Average	Ratio
		Wheat	Barley	Oats	Rye			
1	Russia ... ..	244	333	245	178	250	100	
2	U.S.A. ... ..	346	347	253	194	285	114	
3	Germany ... ..	353	399	302	231	321	128	
4	Denmark, Norway, Sweden ...	354	410	322	244	332	133	
5	Great Britain, Holland, Belgium...	405	440	311	266	355	142	
6	Italy, Spain, France ... ..	468	465	329	295	389	156	
Average for continental climates...		314	360	267	201	—	—	
Average for insular and coast climates ...		409	438	321	268	—	—	

Such records as the following, however, occur. Raulin<sup>(60)</sup> grew varieties of wheat at Lyons and in the Ardennes for comparison. The crop ripening at Lyons was planted the following year in the Ardennes, and *vice versa*, for several years. The conclusion drawn was that "les poids de 100 grains paraissent tendre à Lyon et dans les Ardennes d'année en année, vers des limites différentes: inférieure à Lyon (Pierre-Bénite), supérieure dans les Ardennes."

The interesting indications provided by Combes' work that environmental conditions which result in a weak or a slow development of the parent plant may be correlated with the production of larger seeds though fewer in number, find confirmation in a series of statistical studies by Waldron<sup>(75)</sup> and Harris<sup>(39)</sup>. Waldron (*l.c.*) found in the case of oats a strong correlation between short culms, short heads and small number of grains on the one hand, and heavy-seededness on the other. On the basis of some data of Lyon's he worked out for wheat a similar, but less marked, negative correlation between the number of grains per head and

size of the grains. Harris (*l.c.*) found in the case of *Phaseolus vulgaris* that the weight of the seeds increased in relation to the percentage of ovules which failed to develop.

Von Lochow (48), working with rye plants of the same origin, showed that the average grain-weight was higher for the plants with spikes incompletely filled with grains than for those with spikes completely filled with grains, the proportions being 39 : 32.5; but that the total yield of grain was considerably in favour of the latter, the proportions in this case being 72.5 : 90. As a result of his experience Von Lochow made the interesting observation that heavier seed of unknown ancestry might be inferior to smaller seed of the same origin.

Owen (59), as a result of five seasons' work with beans, found that by limiting the yield of the plant to one pod the weight of the seed was greatly increased, so that the question still to be answered is whether it is not the number of seeds developing that controls their average size even in such experiments as those of Combes quoted above.

(b) *Determined by the Position of the Seed in the Fruit, of the Fruit on the Inflorescence, and of the Inflorescence on the Plant.*

Where the size of the seed is obviously mainly controlled by its position on the parent plant, the presumption is that differences obtained by the use of seeds of different size are to be accounted for by physiological pre-determination.

Several recent authors have worked out on a large scale correlations between seed-size and the position of the seed in the fruit and on the inflorescence, and of the inflorescence on the plant. Halsted and Owen (28) found that the heaviest seeds of Scarlet Runner beans occur in the three-seeded pods and in the middle position in these pods; two-seeded pods and seeds from the basal position give the smallest average weight, nevertheless seeds from the two-seeded pods show the greatest average germination percentage and the greatest average weight of seedling per plant<sup>1</sup>. This result points to a correlation between vigorous growth and seeds of *small size*, which would appear to be one of physiological pre-determination, but unfortunately these experiments were not carried far enough to enable one to decide this point with certainty.

<sup>1</sup> Cummings (12) observed that in beans 49 per cent. of the small seed were found to occur in the basal end, while 18 per cent. occurred in the middle of the pod. In the case of garden peas the small seeds were almost always found at the ends of the pods, with one end as prolific as the other.

Halsted<sup>(26 & 27)</sup> shows that with Soy Beans the size of the seed is controlled by the number of seeds in the pod and by their position in the pod. The basal seeds and the seeds in one-seeded pods are the heaviest, but these produce the poorest plants. According to Halsted the seeds which occur in the middle position in the pod give the most vigorous plants.

Working with *Phaseolus vulgaris* J. A. Harris<sup>(36, 37, & 39)</sup> found that a correlation existed between the number of seeds in a pod and the seed-weight, and that the seed-weight is influenced by the position of the seed in the pod. In an earlier study with the same species Harris<sup>(29)</sup> found that seeds of *medium weight* are more capable of developing into fertile plants than those produced from the larger or smaller seeds of which the weight exceeds or falls below the average. With regard to germination, however, this observer<sup>(30)</sup> states that the larger the seed the longer it takes to germinate.

The same author<sup>(32)</sup>, working with *Staphylea*, obtained indecisive results.

In the sugar beet two to five or more fruits are associated to form a so-called "clump." In this "clump" the upper flower produces the largest seed, the lateral seeds are markedly smaller. Briem<sup>(5)</sup> has conducted a series of experiments to determine what effect the difference in seed-size has upon the subsequent plant and its yield. He sowed the individual seeds of a "clump" separately and compared the resulting plants with one another throughout the whole course of their development. The largest seed produced the largest seedling, the finest beet, and lastly, the most fertile seed-parent. The figures for the relative weights of five seedlings of a "clump" in one case were 100, 74, 67, 51 and 46 respectively. The full-grown beets derived from a single "clump" weighed 1156, 859, 574, 344, and 310 grams and furnished respectively 241, 167, 202, 239, and 104 grams of seed at the end of their second year. Townsend and Rittue<sup>(69)</sup> found that sugar-beet plants produced from "single-germ" seeds, which appear to be strictly localised on the parent plant, not only gave a higher (about 30 %) percentage of germination, but were more vigorous and possessed greater vitality than those produced from the so-called "multiple-germ" seeds.

In a classical experiment many years ago Nobbe<sup>(57)</sup> showed in the case of wheat and barley that variation in the size of the grains on the ear is correlated with their position on the ear. A random distribution, such as would occur if genetic factors were concerned, does not occur. The largest grains occur in the middle-length of the ear. In the same

experiments it was shown that the most vigorous plants are the outcome of the largest seeds.

In view of what follows with regard to the large amount of experimental work that has been carried out with cereals with the object of improving the yield obtained by the selection of large seed, and in view of the emphasis which has been laid for the most part in this work on the assumption that the authors were dealing with genetic factors in their selection, the importance of Nobbe's results justifies the quotation of his table in full:

TABLE III.

No. of 3-seeded spikelet (from base of ear upwards)	BARLEY		WHEAT	
	Air-dry weight in milligrams of the 3 seeds of spikelet (after removal of the awn)	Total root-length in millimetres of seedlings produced from the 3 seeds after 5 days in a germinator	Air-dry weight in milligrams of the 3 seeds of spikelet	Total root-length in millimetres of seedlings produced from the 3 seeds after 5 days in a germinator
1	0 mg.	0 mm.	0 mg.	0 mm.
2	1.5	0	0.5	0
3	2.5	0	0.8	0
4	55.5	144	17.7	48
5	67.5	121	22.5	40
6	79.5	102	26.5	34
7	90.5	90	30.2	30
8	72.5	90	24.2	30
9	92.5	123	30.8	41
10	103.5	532	34.5	177
11	95.5	294	31.8	98
12	97.5	464	32.5	132
13	95.5	273	31.8	125
14	97.5	299	32.5	100
15	92.0	311	30.7	104
16	92.5	335	30.8	112
17	86.5	367	28.8	155
18	87.0	397	29.0	91
19	81.5	140	27.2	47
20	81.5	129	27.2	43
21	74.5	190	24.8	63
22	74.5	118	24.8	39
23	66.5	273	22.2	91
24	47.5	216	15.8	72
25	26.5	96	8.8	32
26	27.0	63	9.0	21
27	32.5	139	10.8	46
Average	71.5 mg.	221.5 mm.	23.3 mg.	77.5 mm.

The above results are summarised in the following table:

TABLE IV.

No. of spikelet (from base of ear upwards)	No. of seeds	BARLEY		WHEAT	
		Total air-dry weight in milligrams of seeds	Total root-length in millimetres after 5 days in germinator	Total air-dry weight in milligrams of seeds	Total root-length in millimetres after 5 days in germinator
Spikelets 1- 9	27	426 mg.	670 mm.	153 mg.	223 mm.
„ 10-18	27	828	3281	282	1094
„ 19-27	27	512	1364	191	454

It is unfortunate that Nobbe's experiments were not carried further to determine whether the plants which he obtained from his larger seed would continue to show throughout their development a superiority over those obtained from the smaller seed and would finally produce a larger yield. This point, however, has since been investigated by Bolley and by Richardson and Green. Bolley (1) in the course of a series of experiments extending over four years to test the difference in yield when plump grains of large size and plump grains of small size were selected for seed, found that "perfect grains of large size and greatest weight produce better plants than perfect grains of small size and light weight, even when the grains come from the same head."

Richardson and Green (2) carefully analysed a large number of heads of wheat and found the heaviest grains in the middle of the ear. They found, however, a complication due to the fact that the median grain of each spikelet tended to suffer in its development with the result that the median grains were almost always lesser in weight and, if they happened to germinate, gave rise to inferior plants.

The following table gives their results in comparing both percentage of germination and yield for the heavier grains from the central region of the ear with that for the lighter grains from the tip and base of the ear together with the *median* ones from the central region.

TABLE V.

*Comparison of Yield of Produce from median\* grains together with the light grains at either extremity of the head with that from heavy grains.*

Group	Treatment	Number of grains taken	Average weight of seed	Percentage unproductive	Average weight of ears produced per plant
1	All <i>median</i> grains and grains under 35 milligrams	38	27.9 mg.	16 %	1.81 gms.
2	Grains over 35 milligrams	80	43.5 mg.	4 %	2.86 gms.

\* *I.e.* the seed which occupies the median position in the spikelet.

Other investigators who have dealt with the effect on the size of seed of their position on the parent plant in the case of cereals and whose results confirm those of Nobbe may be mentioned. Von Rümker<sup>(63)</sup><sup>1</sup> in the case of wheat showed that the heaviest grains on the inflorescence occur on the lower half of the spike while Fruwirth<sup>(21)</sup> showed that the heaviest grains of Barley, Rye, Wheat, Spelt, and Maize, are situated at the middle or somewhat below the middle of the ear (cf. also Wenholz<sup>(80)</sup>). Bruyning<sup>(6)</sup> found that the lower grains of the lateral ears are the best in the case of oats<sup>2</sup>.

Halsted<sup>(26)</sup> has recently shown that seeds of corn taken from the middle of the ear produce more vigorous plants than those taken from the base, whilst those from the base are better again than those from the tip of the ear. Walls<sup>(77)</sup> in 1905 found that a strong relationship existed between the size of the germ and the vigour of the resulting plant and that this vigour continued throughout its life-history. He also found that the plants from the grains with the largest germs were better able to withstand drought.

(c) *Experiments in which the Factors controlling the Size of the Seed are undetermined.*

A large number of experiments have been conducted chiefly with cereals to determine the difference in yield obtained when selected large and selected small seed are used for comparison. The balance of evidence is in favour of the conclusion that more vigorous plants and better yields are obtained by the use of heavy seed. The chief difficulties to be encountered in interpreting these results from the point of view of their significance as evidence of physiological pre-determination lie first in the possibility of hereditary factors for seed-size being concerned, and secondly in the fact that in field experiments on the basis of the data given it is not possible to compare yield *per plant*.

In the case of cereals the presumption has usually been that the experimenter is concerned with a hereditary factor, but, as we have already indicated, the fact that the size of the seed appears to be almost entirely controlled by its relative position on the ear militates strongly at the outset against this view. Further, in most experiments continued over several years with continuous selection of large and of small

<sup>1</sup> In contrast to Waldron, von Rümker found in the case of wheat that the average seed-weight increases with the size of the spike.

<sup>2</sup> As long ago as 1830 Giron de Buzareingues<sup>(9)</sup> stated that in the hemp the largest seeds occur in the middle region of the inflorescence and give rise to the largest plants.

grain, the great divergence in yield is almost always observed only in the first year (see Desprez(15), Lyon(51), also Soule and Vanatter(67)), whereas if a hereditary factor for seed-size is concerned, it should take many years to segregate it by selection since it would be in any case almost completely masked by the effect of position upon the seed-size.

Waldron's (*l.c.*) statistical results with oats indicated that, if any hereditary factor were involved in the selection of large grain, the size of the individual grain might be increased, but the total yield would probably be decreased. For in all populations examined, he found a strong correlation between large-seededness and weak development, *i.e.* small size of plant combined with small yield in number of grains. As in nearly all experiments with cereals an increased yield has been observed following the use of large grain, but in very few cases has any increase in the average size of the grain been noted, the obvious presumption is, therefore, that increased yield is due in the main to physiological, and not to hereditary pre-determination. Waldron concluded that if plants from larger grains produce a better yield, then they must do so by virtue of the increased vigour of the embryo and the increased amount of food-material available.

When the crop is a leaf crop, the correlation between large-seededness and yield may in all probability be safely put down to physiological pre-determination.

The second difficulty that is encountered when considering the results of many large-scale field experiments is that we cannot definitely decide how far they are due, not to differences in the vigour and yield of individual plants, but to differences in number of plants.

In many experiments the sowing has been carried out at the bushel-acre rates and no determination has been made of the relative number of grains per bushel, so that the real rate of sowing with regard to number of grains per given area is not the same with the large and small seed respectively, but is in favour of the latter.

In the second place a difference in germination capacity between light and heavy seed will introduce an unknown error from this point of view. A. Müller(55), who experimented with oats, wheat, and rye, found, for example, that the heavier grains gave a higher percentage of germination and produced larger seedlings than the lighter grains. The light seeds of oats gave 68 per cent. germinations in eleven days whereas the heavy seeds gave 92 per cent. germinations in the same interval (see also Grenfell(25), Boerker(3), Shamel(65), Lehmann(47), Vandevelde(72), Webber and Boykin(78), Eisenmenger(20), and Hicks and Dabney(41)).

The question of probable error in agricultural experiments is also important<sup>1</sup>. Thus Soule and Vanatter (67) working with wheat carried out an experiment for three years with continuous selection and found an average difference in yield at the end of three years between large and small grains of 5.18 bushels per acre in favour of the large grains, but when the experiment was continued on different plots in the two following years the divergence in yield was no more than 0.32 bushels per acre in favour of the large grain.

In quoting results of various workers with regard to the better yield obtained by the use of large seed we will confine ourselves as far as possible to those in which equal numbers of light and heavy seeds have been sown.

The following are some of the results obtained by C. A. Zavitz (82) (Table VI). He selected seeds of three grades, viz. large, medium-sized, and small. For grade I none but well-developed grains of large size were selected; for grade II the grains selected were of uniform character, plump, and of medium size; while for grade III none but sound, plump, and apparently good seeds of small size were used. In the selection of large plump grain  $\frac{1}{2}$  lb of each class was carefully weighed and counted and a corresponding number was then taken of the medium-sized and of the small plump grains. The different selections were sown upon plots of similar size.

TABLE VI.

Crop	Number of years of tests	Yield of grain per acre from		
		Grade I Large seed	Grade II Medium-sized seed	Grade III Small seed
Oats ... ..	7	62.0 bushels	54.1 bushels	46.6 bushels
Barley ... ..	6	53.8	—	50.4
Spring wheat	8	21.7	—	18.0
Winter wheat	6	46.9	—	40.4

Zavitz (82) continued these experiments for several years, each year selecting his seed from a common stock of grain sown in the Ontario Experimental Station Farm in the manner described above. The averages of the results thus obtained are tabulated below.

Zavitz believed that in selecting heavy seed and obtaining from it a bigger yield he was dealing with a hereditary factor, either for vigour or for size of seed. In an experiment with oats continued for 13 years with continuous selection he (83) selected his seed for size, plumpness,

<sup>1</sup> "The Interpretation of the Results of Agricultural Experiments." *Suppl. to Journ. Board of Agric.*, London, Nov. 1911.

TABLE VII.

Kind of grain	Number of years test was repeated	Selections	Weight of grain per measured bushel	Average yield per acre (from 5-8 years)	
				Tons of straw	Bushels of grain (by weight)
Barley ...	6 years	Large plump seed	49.5 lbs.	1.5	53.8
		Small plump seed	48.8	1.5	50.4
Spring wheat	8	Large plump seed	59.1	1.4	21.7
	8	Small plump seed	58.3	1.3	18.0
Winter wheat	5	Large plump seed	59.5	2.4	42.4
	5	Small plump seed	59.3	2.0	34.8
Oats ... ..	7	Large seed	33.2	1.9	62.0
	7	Medium-sized seed	32.2	1.8	54.1
	7	Small seed	31.8	1.8	46.6

and dark colour on the one hand, and for light weight and light colour on the other. Equal numbers of seeds of the heavy and light samples were used for the yield tests. We may quote his final results obtained in the thirteenth year. "The large plump seed produced 65.5 bushels, the light seed 44.7 bushels per acre." In this year the average size of the seed from the crop produced by the large plump seed was greater than that from the crop produced by the light seed. In the first case it required 1149 seed-grains to weigh 1 oz. and in the second case 2066.

In this experiment it will be seen that Zavitz, in contrast to most other workers, records a marked increase in average size of grains as well as an increase in total yield. If plants from large grains are more vigorous and produce a larger yield as a result of physiological pre-determination an increase in the average size of the grains yielded would also probably occur<sup>1</sup>, but in these results of Zavitz's it seems more probable that hereditary factors are concerned. We have to note the large number of years over which the experiment was continued and which would allow time for the slow separation of a possible hereditary factor for large-seededness. As has been pointed out, selection for seed-size would have little effect in one generation owing to the fact that seed-size as an hereditary character would be almost entirely masked by the influence upon size of the position of the seed upon the parent plant, so that in a first separation of large and of small seeds the sample of large seed would probably only contain relatively very few more seeds large by heredity than the sample of small seed. In the second place his selection was not

<sup>1</sup> Desprez (15) with wheat found that the use of large seed gave a crop with grains larger than those grown from small seed. In Lyon's (51) work this was also noted.

confined to size of seed, but was also made on the basis of colour-differences such as are known to be often associated with hereditary factors.

We may turn now to an author who has conducted careful experiments with wheat in which equal numbers of small and of large grains were sown and in which the percentage of plants that grew was determined. Grenfell<sup>(25)</sup> describes his selection as between plump and shrivelled grains. These were sown in alternate rows, 150 grains to a row. He notes in the first place that the plants from the plump grains soon began to get a start of the others and kept ahead all through. The percentage of plants that grew from the plump grains was also in excess of that from the shrivelled. The following table gives his results from which it appears that the average yield per acre from plump seed-grain is 9.8 bushels as opposed to 7.5 bushels from shrivelled seed-grain.

TABLE VIII.

Variety of seed	Kind of seed	Percentage of plants that grew	Number of heads	Tillering power	Average yield in bushels per acre
Steinwedel	Plump	96.0	179	1.24	10.9
"	Shrivelled	89.3	174	1.29	9.9
Purple Straw	"	89.3	153	1.14	6.1
"	Plump	90.0	200	1.49	10.0
"	Shrivelled	76.0	140	1.16	6.9
"	Plump	92.0	161	1.23	8.4
"	Shrivelled	98.0	155	1.34	7.2
Plump-kernel averages ...		92.7	180	1.32	9.8
Shrivelled-kernel averages		88.5	155	1.23	7.5

From the point of view of physiological pre-determination the sort of difficulty involved in interpreting his results and the results of many other authors who have worked on the same lines with cereals, is clear: obviously the number of plants that grew and the amount of tillering per plant, which combined give the number of heads per seed sown, greatly affect the results<sup>1</sup>.

From Grenfell's figures, however, we are able to work out the relative yield *per head* and the relative yield *per plant* from plump and shrivelled seed respectively.

<sup>1</sup> Driesdorf (*Zeitsch. f. d. Prov. Sachsen*, 1868) observes that in April winter wheat from large seed-grain showed greater tillering and a deeper green colour than that produced from small seed-grain.

TABLE IX.

Relative yield per head		Relative yield per plant	
Plump grains	Shrivelled grains	Plump grains	Shrivelled grains
50	57	113	111
61	46	111	68
52	40	91	91
—	49	—	73
Average = 54.3	Average = 48	Average = 105	Average = 86

The figures indicate, not only that the yield per plant from heavy seed is greater (about 20 per cent.), but also that the yield per head is greater independently of the tillering, which, if anything, is also greater in the plants from plump seeds.

Edler (18 & 19) carried out experiments with seeds weighing 50.9 and 33.9 gms. per 1000 respectively. In one test the same number of grains of the heavy and of the light seed were sown. It was found that the heavy seed produced the heavier plants, having a larger number of productive stems and producing heavier and a larger number of grains than plants from the light seed.

Before leaving the case of cereals a brief reference must be made to various other authors whose results, although they cannot be critically interpreted from the point of view of physiological pre-determination, make it clear that from the practical point of view the balance of evidence, as we have said before, is in favour of the use of large seed<sup>1</sup>.

Author	Description of experiments	Average yield of seed-grain
Sauborne et al. (64) ...	4 years' continuous selection of large and shrivelled grain of wheat	7.47 bushels per acre in favour of the <i>heavy</i> grain
Latta (46) ... ..	3 years' discontinuous selection of heavy and light wheat grains separated by a fanning mill	2.5 bushels per acre in favour of the <i>heavy</i> grain
Georgeson et al. (24) ...	3 years' discontinuous selection of light and heavy wheat grain	1.88 bushels per acre in favour of the <i>heavy</i> grain
Desprez (15) ... ..	3 years' continuous selection of large and small grain of five varieties of wheat	761 kilograms per hectare in favour of the <i>large</i> grain
Dehérain et Dupout (13)	Experiment extending over a single year with large and small grain of five varieties of wheat	150 kilograms per hectare in favour of the <i>large</i> seed
Hickman (40) ... ..	9 years' continuous selection of large and small grain of wheat	0.25 bushel per acre in favour of the <i>small</i> grain

<sup>1</sup> Many other workers have obtained similar results; for example, Cobb (10), Bolley (4), Lyon (51), Blanchard (2), and Richardson (61) with wheat; Dietrich (16), Buckmann (7), Sorauer (66), and Welton and Gearhart (79) with oats; Lubanski (49) with winter wheat, barley, and oats; and Von Lochow (48) with rye.

Author	Description of experiments	Average yield of seed-grain
Voeleker (73) ... ..	Woburn pot-culture experiments with wheat and barley (1900-4). (The Hill's experiments)	Yield very slightly in favour of the <i>small</i> grain
Nielsen (56) ... ..	Experiments with rye extending over 10 years	
	I. Using equal numbers of large and small grains	I. Very slightly in favour of the <i>large</i> grains
	II. Using equal weights of large and small grains	II. No marked difference in yield

In conclusion we may quote the results of Hicks and Dabney (41) with cereals, which show clearly the effect of seed-weight upon vigour, although the experiments are not carried further than the seedling stage. They found similar results with Vetch, Sweet Pea, and Radish.

TABLE X.

*Experiments with Heavy and Light Seeds.*

Name and variety	Number of seeds in each lot	Weight of seeds* in grams	Number germinated	Number of plants weighed in each lot	Number of days of experiment	Weight of seedlings in grams
Kaffir Corn (red)	100	{ A. 3.298 B. 1.741 }	{ A. 90 B. 49 }	47	39	{ A. 22.0 B. 13.0 }
Rye (University of Minnesota, No. 2)	50	{ A. 1.105 B. 0.745 }	{ A. 45 B. 45 }	45	23	{ A. 34.5 B. 20.0 }
Oats (White Wonder)	50	{ A. 1.298 B. 0.805 }	{ A. 50 B. 49 }	49	23	{ A. 37.2 B. 25.0 }
Barley (Salzer's)	50	{ A. 2.522 B. 2.146 C. 1.496 D. 0.957 }	Not recorded	Equal number of each lot	19	{ A. 39.5 B. 34.5 C. 29.0 D. 23.0 }

\* A, heavy seed; B, lighter than A; C, lighter than B; D, lighter than C.

Leaving cereals upon which most of the work dealing with differences in yield resulting from the use of large and small seed has been carried out, a few results may be quoted which show that the same fact, namely, that more vigorous plants giving a bigger yield of leaf- and seed-crop result from large seeds than from small, holds generally good in the case of plants belonging to other families.

As early as 1869 a very complete series of results was obtained by Lehmann (47) for peas. He showed that the capacity for germination was greater in the case of the large seeds, but that, independently of the percentage of germination, the yield per 100 plants from heavy seed greatly exceeded that from the same number of plants from light seed.

TABLE XI.

Kind of seed used	Weight of 100 seeds	Number of seeds used	Number of plants obtained from 528 seeds	
Peas (small seed) ... ..	160 gms.	528	423	
Peas (medium-sized seed) ... ..	221	528	478	
Peas (large seed) ... ..	273	528	480	
Yield from 100 mature plants				
Kind of seed used	Yield from 100 mature plants			
	Seeds	Pods	Stalks	Total weight in gms.
Peas (small seed) ... ..	236 gms.	66 gms.	475 gms.	777 gms.
Peas (medium-sized seed) ... ..	313	75	550	938
Peas (large seed) ... ..	378	91	660	1129

He further showed that a better yield was obtained from a given weight of heavy seeds than from the same weight of light seeds in spite of the fact that nearly twice as many plants were obtained in the latter case, thus emphasising the fact that from the point of view of the agriculturalist it is advantageous to use large seed.

TABLE XII.

*Results obtained from 188 grams of each kind of seed sown in plots 8.5 metres square.*

Kind of seed used	Number of seeds sown	Plants developed	Weight of grain	
			per 8.5 sq. m.	per 100 plants
Peas (small seed) ... ..	780	680	1590 gms.	234 gms.
Peas (medium-sized seed) ... ..	530	505	2224	440
Peas (large seed) ... ..	384	360	2307	640

In view of Lehmann's results reference must be made to Johannsen's (43) work with beans. Taking a mixed sample of seeds of a single variety of *Phaseolus*, he obtained a simple Galton frequency curve for their weights. As a result of sowing the large seeds he found that the plants produced (self-fertilised) showed a shifting of the modal weight in the direction of large-seededness. Similarly, when small seeds were chosen, the modal weight of the crop obtained from them was found to be smaller than that of the original sample. But when the same experiment was repeated with any one family (*i.e.* the crop raised from a single seed), selection did not alter the modal weight.

Johannsen's results might have an application in interpreting those of Lehmann: it is to be noted, however, that in Lehmann's experiment the data do not allow one to determine whether there was any increase or decrease in the average seed-weight. It is also to be noted that he remarks that the plants from the smaller seeds were less well-developed

and less productive than those from the larger seed. His figures for weight of pods and stalks indicate this clearly.

Some recent work by M. Delassus<sup>(14)</sup> strongly favours the inference drawn that Lehmann's results are largely due to physiological pre-determination. Delassus worked with *Vicia Faba*, *Vicia sativa*, *Lupinus albus*, *Cicer arietinum*, and *Zea Mais*. We quote the results he obtained with *Vicia Faba*.

Forty large and 40 small seeds were chosen from the same source and subsequently received exactly similar treatment. The seedlings were grown "en pleine terre"; "dans un sol n'ayant reçu aucune fumure pendant l'année courante de façon à rendre plus sensible encore l'action des réserves de la graine." From the very beginning of germination marked differences were observed and distinct morphological differences manifested themselves throughout the development of the plants produced. In comparison with the plants produced from the sample of large seed those produced from the sample of small seed show a retarded vegetative development which is obvious in the number and dimensions of the leaves and leaflets produced (Table XIII). The root system is also adversely affected in the case of the plants from the small seeds.

TABLE XIII.

*The Influence of Seed-size upon the Development of the Resulting Plant in the case of Vicia Faba.*

	After 1 month's growth		After 2 months' growth		After 3 months' growth	
	Lot I*	Lot II*	Lot I	Lot II	Lot I	Lot II
Growth of plants in millimetres	171 mm.	146 mm.	408 mm.	323 mm.	664 mm.	528 mm.
Number of leaves produced	7.7	6.6	48.7	34.6	96.0	78.0
Number of leaflets produced	19.1	15.1	154.5	112.6	386.0	308.0
Breadth of leaflets	... 48.0 mm.	39.9 mm.	47.0 mm.	40.7 mm.	—	—
Length of leaflets	... 71.9 mm.	59.8 mm.	75.9 mm.	67.1 mm.	—	—
Dry weight of five samples dried at 100° C. for 10 hours	5.577	3.428	9.20	5.58	29.3	20.5

\* Lot I = plants from large seeds; Lot II = plants from small seeds

It is also to be noted that the number of flowers produced is greater in the plants from the large seeds and that these flowers give rise to more numerous and larger fruits than those of the plants from small seed.

Striking anatomical and histological differences also become evident. Thus, a greater development of xylem and phloem elements and especially of stereome (*i.e.* sclerenchyma and collenchyma) occurs in the case of the plants produced from large seed.

This work of Delassus exactly confirms the results of detailed experiments reported by Hicks and Dabney (41) in 1896, who compared large and small seeds of Soy Beans and Garden Peas respectively. The seeds were planted in pure sand in a greenhouse, equal amounts of a culture solution which contained all the elements necessary to plant growth being

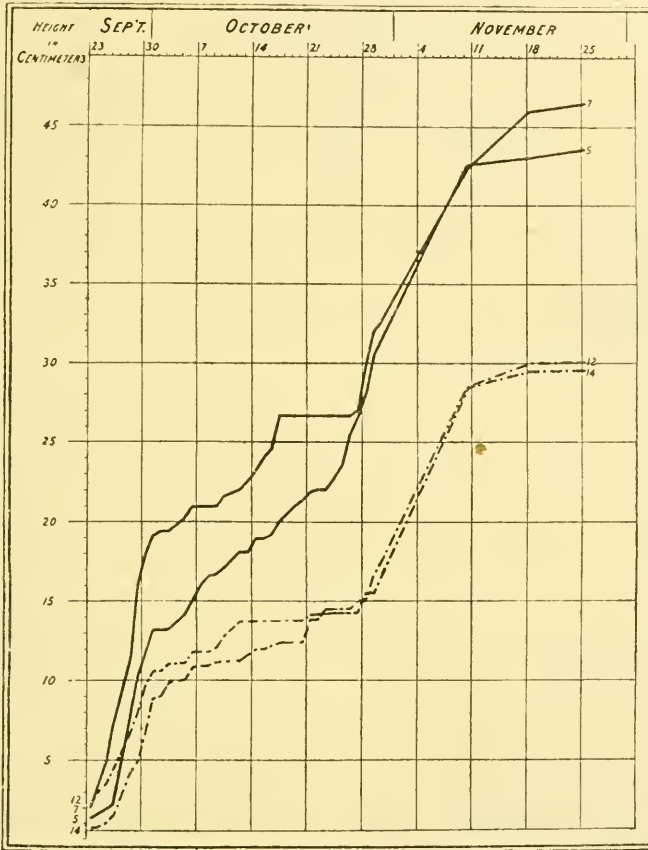


Fig. 1. Curves showing development of Soy Beans from heavy and light seed respectively. The upper curves represent plants from heavy and the lower those from light seed. (After Hicks and Dabney.)

given to the plants, which were kept from first to last under identically similar conditions so far as possible. In result they found that the large seed produced plants which gained continually upon those from the small seed and finally gave larger and more vigorous plants and a better yield as is shown by the curves represented in Figs. 1 and 2.

In the case of the peas a further important advantage is gained by the selection of large seed, namely, increased earliness (see Fig. 2).

Burgerstein (8) has very thoroughly worked out the case for *Phaseolus vulgaris*, var.; the following table summarises his results:

TABLE XV.  
*Yield from Small Seeds compared with the Yield from Large Seeds taken as 100\*.*

Kind of seed used	Number of seed-bearing pods	Number of harvested seeds	Weight of harvested seed in mg.	Relation of average weight	
				A. of the harvested seed Large : Small	B. of the seed sown Large : Small
1. Flageolet ...	99	82	76	100 : 93	100 : 50
2. Niger ...	72	70	58	100 : 84	100 : 46
3. Non plus ultra ...	96	98	96	100 : 98	100 : 59
4. Osborn ...	96	99	91	100 : 92	100 : 56
5. Spargel ...	92	96	86	100 : 89	100 : 57
6. Wiener Zweig ...	88	72	68	100 : 95	100 : 78

\* The plants produced from the small seeds ripened by the 16th of August, those produced from the large seeds by the 22nd of August.

From the above table it is seen that the bean plants produced from very small seeds gave rise to seeds which were only slightly smaller than those which under similar conditions were produced by plants from very large seeds. Statistical work by Harris (31, 35, & 38) has since confirmed Burgerstein's results. Harris found that in the case of *Phaseolus vulgaris* the number of pods and also the number of ovules and seeds per pod were greater in plants produced from the larger seeds.

With many other crops conclusions similar to those of Lehmann have been reached<sup>1</sup>, for instance, Lyon and Hitchcock (53) with alfalfa, Walker (76) with beet, Shamel (65) with tobacco, Webber and Boykin (78) with several varieties of cotton, and Sprecher (68) with *Hevea brasiliensis*, but the results recorded by Fruwirth in 1917 are worth recording in more detail. Fruwirth (22) carried out investigations with lucerne and sainfoin for five years. His work proceeded from the earlier investigations of Wollny (81), who showed that for a given area and equal numbers of plants heavy seeds of fodder maize and red clover were superior to the light seeds. Fruwirth's work is excellent in that he eliminated spacing as a factor disturbing the yield results. Three lines of experiment were followed, viz.:

(i) comparison of single plants:

<sup>1</sup> Arthur (1), Zavitz (84), and Cummings (12) give data which clearly show a distinct advantage in the use of large and heavy seed in the case of several different classes of farm crops.

- (ii) seed-bed experiments, using equal numbers of plants and also equal weights of seed, the results from which were compared;
- (iii) field experiments for comparing yields from heavy and light seed respectively, using equal numbers of plants per given area.

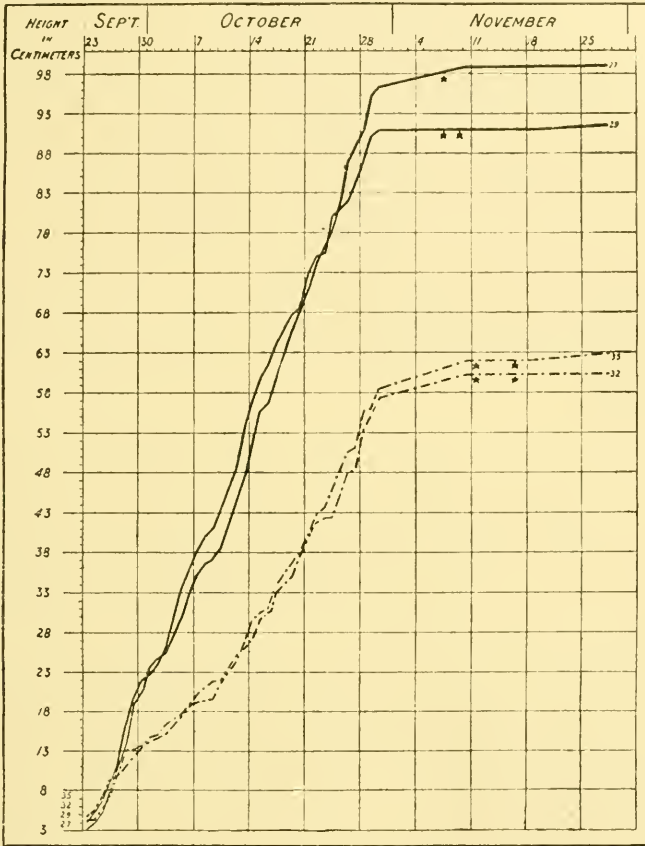


Fig. 2. Curves showing development of Extra Early Alaska Peas from heavy and light seed respectively. The upper curves represent plants from heavy seed and the lower curves plants from light seed. The stars indicate when the pods were ready for the table. (After Hicks and Dabney.)

From each line of investigation similar results followed. For equal numbers of plants per given area the heavier seeds gave rise to plants of greater productivity than that of the plants produced from the lighter seeds. He also found that the superiority of the heavier seed became more marked the larger the ground space ("Standraum") allowed for each plant. The superiority of the plants from the heavier seeds

decreased with the increasing age of the plants, and the author concluded that the result depended upon the larger quantity of reserve materials in the heavier seeds. In the case of perennial plants the original advantage of the heavier seed is gradually lost.

#### C. CONCLUSION.

The general conclusion to be drawn from this review of the literature is that the effect of parental conditions upon the seed in determining its subsequent course of development may be considerable.

The environmental conditions operating upon the seed whilst on the parent plant may be divided into two classes, viz.:

(1) The environment of the seed itself, in other words, its position on the parent plant. The effect of the position of the seed upon the parent plant is most clearly reflected in the size of the seed and is independent of external conditions. The balance of evidence is in favour of the conclusion that larger seeds give rise to more vigorous plants and a better yield.

(2) The environment of the parent. Here again differences in the size of the seed are the only effects which are visible in the seed itself, but there is evidence that environmental conditions which affect the parent may also markedly influence the subsequent course of development of the seeds produced. So that effects which become visible in one generation may have to be traced back to the external conditions which operated in a previous generation.

The question of the pre-determining effect of parental conditions is much complicated by the ever-present possibility of hereditary factors being concerned, and in most cases the facts have so far been almost entirely considered from the point of view of heredity alone. In the following sections, in which we shall deal with the pre-determining effect of the conditions operating during harvesting, dormancy (storage), and germination respectively, the difficulty of interpreting the results will not be complicated by the intrusion of the question of heredity.

*(To be continued.)*

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## A LIST OF COCCIDAE AFFECTING VARIOUS GENERA OF PLANTS.

BY E. ERNEST GREEN, F.E.S., F.Z.S.

*(Continued from Vol. IV, page 239)*

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| <p>LABURNUM (Leguminosae).<br/>PHENACOCCLUS aceris.<br/>LECANIUM corni.<br/>CHIONASPIS salicis.<br/>LEPIDOSAPHES ulmi.<br/>LACTUCA (Compositae) 'Lettuce.'<br/>ORTHEZIA insignis.<br/>LAGERSTROEMIA (Lythraceae).<br/>ERIOCOCCUS lagerstroemiae.<br/>LAMIUM (Labiatae).<br/>ASTEROLECANIUM fimbriatum.<br/>LANDOLPHIA (Apocynaceae).<br/>TACHARDIA albizziae.<br/>ISCHNASPIS filiformis.<br/>LANTANA (Verbenaceae).<br/>ORTHEZIA insignis.<br/>PSEUDOCOCCUS longispinus.<br/>CEROPUTO yuccae.<br/>ASTEROLECANIUM pustulans-seychel-<br/>larum.<br/>PULVINARIA antigoni.<br/>HEMICHIONASPIS minor.<br/>ASPIDIOTUS cydoniae.<br/>LAPAGERIA (Liliaceae).<br/>ASPIDIOTUS hederac.<br/>LAPOANA (Compositae).<br/>GUERINIELLA serratulac.<br/>LARREA (Zygophyllaceae).<br/>ICERYA rileyi, rileyi-larreae.<br/>GYMNOCOCCUS lahillei.<br/>TACHARDIA larreae.<br/>ERIOCOCCUS larreae.<br/>ERIUM irishi, steeli.<br/>LECANODIASPIS americana.<br/>LECANIUM elegans.</p> | <p>CEROPLASTES irregularis.<br/>ASPIDIOTUS larreae.<br/>PROTARGIONIA larreae.<br/>LASIANTHUS (Rubiaceae).<br/>LEPIDOSAPIES lasianthi.<br/>LATANIA (Palmaeae).<br/>PSEUDOCOCCUS nipae.<br/>DIASPIS bromeliae.<br/>ASPIDIOTUS lataniae, dictyospermi.<br/>ISCHNASPIS filiformis.<br/>LATHYRUS (Leguminosae).<br/>ORTHEZIA urticae.<br/>LAURUS (Lauraceae).<br/>ICERYA braziliensis, purchasi.<br/>PSEUDOCOCCUS indieus, laurinus, ci-<br/>trophilus, longispinus.<br/>LECANIUM brunfelsiae, tessellatum,<br/>hesperidum, hesperidum-lauri, ce-<br/>rasi, inflatum, elongatum, oleae.<br/>PARALECANIUM geometrieum.<br/>PULVINARIA plana, floecifera.<br/>PROTOPULVINARIA pyriformis.<br/>PLATINGLISIA noacki.<br/>GASCARDIA madagascariensis.<br/>ASPIDIOTUS cyanophylli, camelliae,<br/>fieus, hederac, lauretorum, britan-<br/>nieus, laurina, dictyospermi.<br/>CRYPTASPIDIOTUS aonidioides.<br/>XANTHOPHTHALMA coneinum.<br/>AONIDIA lauri.<br/>LEPIDOSAPHES nigra.<br/>LAVANDULA (Labiatae) 'Lavender.'<br/>PSEUDOCOCCUS lavandulae, citri.<br/>LAVATERA (Malvaceae).<br/>LECANIUM oleae.</p> |
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- LAWSONIA (Lythraceae).  
 WALKERIANA cinerea.  
 LECANIUM nigrum.
- LEDUM (Ericaceae).  
 PSEUDOCOCCUS ledi.
- LEONTODON (Compositae) 'Dandelion.'
- ORTHEZIA urticae.
- LEPIDIDENIA (Lauraceae).  
 LECANIUM expansum.
- LEPIDIDIUM (Cruciferae).  
 MACROCEROCOCCUS superbus.
- LEPIDOSPERMA (Cyperaceae).  
 ASPIDIOTUS cladii.
- LEPTILOX (Compositae).  
 LECANIUM hemisphaericum.
- LEPTOCARPUS (Restiaceae).  
 ODONASPIS leptocarpi.
- LEPTOSPERMUM (Myrtaceae).  
 ICERYA koebelei.  
 COELOSTOMIDIA wairoensis.  
 SPHAEROCOCCUS leptospermi, pirogallis, rugosus.  
 ASTEROLECANIUM epacridis, fimbriatum, stypheliae.  
 ERIOCOCCUS leptospermi.  
 RIPERSIA leptospermi.  
 TACHARDIA melaleuca.  
 CTENOCHITON flavus.  
 INGLISIA leptospermi, ornata.  
 CHIONASPIS eugeniae, angustata.  
 POLIASPIS exocarpi.  
 FIORINIA fioriniae.  
 ASPIDIOTUS cladii.  
 LEPIDOSAPHES intermedia, leptospermi.
- LESPEDEZA (Leguminosae).  
 ICERYA genistae.
- LEUCADENDRON (Proteaceae).  
 PSEUDOCOCCUS trichiliae.  
 ASPIDIOTUS camelliae.
- LEUCOPOGON (Epacridaceae).  
 ASTEROLECANIUM epacridis.  
 POLIASPIS media.
- LIBOCEDRUS (Coniferae).  
 ASPIDIOTUS chlomi.
- LICHENS.  
 PHENACOCCUS kuwanae.
- LIGUSTICUM (Umbelliferae).  
 RIPERSIA halophila.
- LIGUSTRUM (Oleaceae) 'Privet.'
- ASTEROLECANIUM fimbriatum.  
 ERICERUS pela.  
 LECANIUM hemisphaericum.  
 CHIONASPIS salicis.  
 LEUCASPIS japonica.  
 ASPIDIOTUS africanus, dietyospermi, hederac, perniciosus, ficus.  
 LEPIDOSAPHES ulmi.
- LILIACEAE, sundry.  
 PSEUDOCOCCUS liliaceum, simplex.
- LIMNANTHEMUM (Gentianaceae).  
 LECANIUM limnanthemi.
- LIMONIA (Rutaceae).  
 ASPIDIOTUS orientalis.  
 LEUCASPIS limoniae.
- LIQUIDAMBAR (Hamamelidaceae).  
 ASPIDIOTUS juglansregiae-pruni.  
 CRYPTOPHYLLASPIS liquidambaris.
- LIRIODENDRON (Magnoliaceae) 'Tulip tree.'  
 ICERYA brasiliensis.  
 PHENACOCCUS aceris.  
 LECANIUM liriodendri, tulipiferae.  
 CHIONASPIS salicis-nigrae.  
 ASPIDIOTUS piccus.
- LITHOSPERMUM (Boraginaceae).  
 ASTEROLECANIUM fimbriatum.
- LITSEA (Lauraceae).  
 WALKERIANA floriger.  
 ASTEROLECANIUM litseae.  
 LECANIUM litseae, acutissimum, expansum, mangiferae, tessellatum.  
 CHIONASPIS litseae, pallida.  
 LEPIDOSAPHES maideni, retrusus.
- LIVISTONIA (Palmaeae).  
 ICERYA aegyptiaca.  
 PELVINARIA psidii.  
 FIORINIA pellucida.  
 ASPIDIOTUS britannicus, rapax, ficus, spinosus.
- LODOICEA (Palmaeae).  
 GYMNASPIS grandis.
- LONICERA (Caprifoliaceae).  
 ORTHEZIA insignis.  
 PSEUDOCOCCUS longispinus.  
 PHENACOCCUS aceris.  
 LECANIUM vini, corni, hesperidum.  
 PROTOPULVINARIA pyriformis.  
 ASPIDIOTUS perniciosus, palmae, hederac.
- LEPIDOSAPHES ulmi.

- LORANTHUS (Loranthaceae).  
 POROCOCCUS pergandei, tinctorius.  
 ERIODES rimulae.  
 LECANIUM hemisphaericum, viride,  
 nigrum.  
 PULVINARIA betulae.  
 PROTOPULVINARIA longivalvata.  
 TECTOPULVINARIA loranthi.  
 INGLISIA foraminifer.  
 DIASPIS phoradendri, visci, loranthi,  
 pentagona-rubra, barberi, parva.  
 CHIONASPIS fodiens, vitis, salicis,  
 nilgirica, varicosa.  
 HEMICHIONASPIS mussoendae.  
 FIORINIA rubrolineata.  
 ASPIDIOTUS destructor, transparentis,  
 pothi, fuscus, fodiens.  
 HYBRIDASPIS producta.  
 AONIDIA loranthi, obscura.  
 LEPIDOSAPHES kamerunensis.
- LOTUS (Leguminosae).  
 ASTEROLECANIUM fimbriatum.  
 MACROCEROCOCCUS superbus.  
 PSEUDOCOCCUS longispinus.
- LUZULA (Gramineae).  
 NEWSTEADIA floccosa.  
 ERIOPELTIS festucae.  
 LUZULASPIS luzulae.
- LYCASTE (Orchidaceae).  
 PULVINARIA floccifera.
- LYCIUM (Solanaceae).  
 TACHARDIA lycii.  
 LECANIUM hesperidum.  
 PULVINARIA argentina.  
 LICHTENSIA lycii.  
 CEROPLASTES jamaicensis.  
 LEPIDOSAPHES ulmi.
- LYCOPERSICUM (Solanaceae) 'Tomato.'  
 ORTHEZIA insignis.  
 PSEUDOCOCCUS solani, virgatus, maritimus.  
 PHENACOCCLUS solani.  
 CHIONASPIS solani.
- LYONIA (Ericaceae).  
 CHIONASPIS salicis.
- MACARANGA (Euphorbiaceae).  
 LECANIUM formicarii.  
 CHIONASPIS pellicida.
- MACHILUS (Lauraceae).  
 FIORINIA phantasma.
- PARLATORIA proteus.  
 LEPIDOSAPHES machili.
- MACLURA (Moraceae) 'Osage Orange.'  
 LECANIUM aurantiacum, maclurarum,  
 robiniae.  
 PULVINARIA machurae.  
 ASPIDIOTUS aneylus, perniciosus.
- MACROLOBIUM (Leguminosae).  
 DIASPIS hamata.  
 CHIONASPIS bussii.  
 LEPIDOSAPHES meridionalis.
- MACROZAMIA (Cycadaceae).  
 PSEUDOCOCCUS macrozamiaae.  
 PARALECANIUM frenchi-macrozamiaae.  
 ASPIDIOTUS hederaceae.  
 PARLATORIA proteus.
- MAGNOLIA (Magnoliaceae).  
 PSEUDOCOCCUS maritimus.  
 LECANIUM turgidum, magnoliarum,  
 tulipiferae, oleae, nigrofasciatum.  
 CEROPLASTES rubens.  
 LEUCASPIS japonica.  
 PSEUDOPARLATORIA parlatorioides.  
 ASPIDIOTUS hederaceae, perscarum, perseaee, dietyospermi.  
 LEPIDOSAPHES gloveri.  
 ISCHNASPIS filiformis.
- MALLOTUS (Euphorbiaceae).  
 CHIONASPIS malloti.
- MALVA (Malvaceae).  
 PSEUDOCOCCUS capensis.  
 PHENACOCCLUS solani.
- MALVACEAE, miscellaneous.  
 PSEUDOCOCCUS capensis.  
 PHENACOCCLUS gossypii, iceryoides.  
 PULVINARIA cestri, tuberculatus.  
 INGLISIA malvacearum.
- MALVASTRUM (Malvaceae).  
 ERIOCOCCUS tinsleyi.
- MALVAVISCUS (Malvaceae).  
 CEROPLASTES dugesii.  
 ASPIDIOTUS tesscratus.
- MAMMEA (Guttiferae).  
 PULVINARIA mammeae.  
 DIASPIS pentagona.  
 HOWARDIA biclavata.  
 ASPIDIOTUS lucumae, destructor, perssonatus.
- MAMMILLARIA (Cactaceae).  
 PSEUDOCOCCUS mammillariae.  
 RHIZOECUS targionii.

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- MANGIFERA (Anacardiaceae) 'Mango.'  
 MONOPHLEBUS *stebbingi-mangiferae*, octocaudata.  
 LLAVEIA *axin*.  
 ICERYA *scychellarum*, minor.  
 ASTEROLECANIUM *pustulans*.  
 PSEUDOCOCCUS *longispinus*, obtusus, *marchali*, *virgatus*.  
 PHENACOCOCCUS *mangiferae*, *iceryoides*, *ballardi*.  
 LECANIUM *acuminatum*, *mangiferae*, *psidii*, *adersi*, *acutissimum*, *punctuliferum*, *diversipes*, *discrepans*.  
 PULVINARIA *psidii*, *ficus*.  
 CEROPLASTES *ceriferus*, *floridensis*, *rubens*, *aetiniformis*.  
 VINSONIA *stellifera*.  
 DIASPIS *rosae*, *cinnamomi-mangiferae*, *tubercularis*, *pentagona*, *barberi*.  
 CHIONASPIS *dilatata*, *natalensis*, *vitis*, *hedyotidis*.  
 HEMICHIONASPIS *aspidistrae*.  
 LEUCASPIS *indica*.  
 ASPIDIOTUS *destructor*, *trilobitiformis-darutyi*, *dietyospermi*, *personatus*, *greeni*, *rossi*, *biformis*, *aurantii*.  
 PSEUDISCHNASPIS *linearis*.  
 PARLATORIA *calianthina*.  
 MANIHOT (Euphorbiaceae) 'Tapioca,' 'Ceara Rubber,' etc.  
 LLAVEIA *primitiva*.  
 STIGMACOCCUS *zimmermanni*.  
 LECANODIASPIS *manihotis*.  
 LECANIUM *nigrum*.  
 PSEUDOCOCCUS *virgatus*.  
 DIASPIS *pentagona*.  
 HEMICHIONASPIS *aspidistrae*.  
 FIORINIA *floriniae*.  
 ASPIDIOTUS *cyanophylli*, *destructor*.  
 LEPIDOSAPHES *dispar*.  
 MARANTA (Zingiberaceae).  
 LECANIUM *hesperidum*, *nigrum*.  
 ASPIDIOTUS *ficus*.  
 MARISCUS (Cyperaceae).  
 CHIONASPIS *paolii*.  
 MARKHAMIA (Bignoniaceae).  
 STICTOCOCCUS *dimorphus*.  
 LECANIUM *somereni*.  
 PULVINARIA *psidii*.  
 MATAYBA (Sapindaceae).  
 ASPIDIOTUS *tesseractus*.  
 MATRICARIA (Compositae).  
 ORTHEZIA *urticae*.  
 MAYTENUS (Celastraceae).  
 LECANIUM *mayteni*, *obscurum*.  
 CEROPLASTES *albolineatus*, *communis*, *formicarius*, *rotundus*, *sanguineus*.  
 MEDICAGO (Leguminosae).  
 GUERINIELLA *serratulae*.  
 ASTEROLECANIUM *fimbriatum*.  
 MELALEUCA (Myrtaceae).  
 TESSAROBOLUS *guerinii*.  
 ASCELIS *melaleucac*.  
 SPHAEROCOCCUS *acaciae-melaleucac*, *ferrugineus*, *morrisoni*, *tepperi*, *pulchellus*.  
 TACHARDIA *melaleucac*.  
 LECANODIASPIS *melaleucac*.  
 ERIOCOCCUS *imperfectus*.  
 LECANIUM *melaleucac*, *hemisphaericum*.  
 CEROPLASTES *ceriferus*.  
 CEROPLASTODES *melaleucac*.  
 CTENOCHITON *cellulosus*.  
 CHIONASPIS *eugeniae*.  
 FIORINIA *expansa*.  
 ASPIDIOTUS *casuarinae*, *fodiens*, *unilobis*, *dietyospermi*, *delicatulus*, *tuberculatus*.  
 LEPIDOSAPHES *melaleucac*, *nivea*, *spinosa*, *crassa*, *incisor*.  
 MELAMPYRUM (Scrophulariaceae).  
 ORTHEZIA *urticae*.  
 MARGARODES *polonicus*.  
 MELASTOMA (Melastomaceae).  
 ASPIDIOTUS *transparentis*.  
 MELIA (Meliaceae).  
 LECANIUM *nigrofasciatum*, *nigrum*, *hemisphaericum*.  
 PULVINARIA *maxima*.  
 DIASPIS *erawi-fulleri*.  
 HEMICHIONASPIS *minor*.  
 ASPIDIOTUS *hederae*, *orientalis*.  
 MELICOPA (Rutaceae).  
 ERIOCHITON *spinus*.  
 MELICYTUS (Violaceae).  
 CHIONASPIS *dysoxyli*.  
 MELITTIS (Labiatae).  
 ORTHEZIA *urticae*.

- MELOCHIA (Sterculiaceae).  
 PSEUDOCOCCUS corymbatus.
- MEMECYLON (Melastomaceae).  
 LECANIUM bicruciatum, caudatum,  
 fusiforme, hemisphaericum.  
 AONIDIA crenulata.
- MENISPERMUM (Menispermaceae).  
 LECANIUM cecconi, corni, persicae.
- MESEMBRYANTHEMUM (Aizoaceae).  
 PSEUDOCOCCUS capensis.  
 PULVINARIA mesembryanthemi.  
 PARAFARMARIA bipartita.  
 ASPIDIOTUS lounsburyi, hederac.
- MESPILUS (Rosaceae) 'Medlar,' etc.  
 PHENACOCCLUS mespili, aceris.  
 LECANIUM bituberculatum, corni,  
 coryli.  
 PULVINARIA carpini, betulae.  
 CEROPLASTES rusci.  
 EPIDIASPIS leperei.  
 ASPIDIOTUS hederac, ostreaeformis,  
 piri.  
 PARLATORIA oleae.  
 LEPIDOSAPHES ulmi.
- MESUA (Guttiferae).  
 AMORPHOCOCCUS mesuac.  
 AONIDIA mesuac, ferreae, perplexa.  
 ASPIDIOTUS cuculus.  
 PARLATORIA mesuac.  
 GYMNASPIS spinomarginata.  
 LEPIDOSAPHES ambigua.
- METROSIDEROS (Myrtaceae).  
 ERIOCOCCUS pallidus.  
 LECANIUM hesperidum.  
 LECANOCHITON metrosideri, minor.  
 ASPIDIOTUS dictyospermi.  
 LEPIDOSAPHES metrosideri.
- METROXYLON (Palmaceae) 'Sago  
 Palm.'  
 LECANIUM hemisphaericum.
- MICHELIA (Magnoliaceae).  
 LECANIUM punetuliferum.  
 ASPIDIOTUS maskelli, camelliae.  
 PARLATORIA champaca.
- MICONIA (Melastomaceae).  
 PULVINARIA depressa.  
 CEROPLASTES purpureus.
- MICROGLOSSA (Compositae).  
 HOWARDIA biclavis.
- MICROGYNE (Compositae).  
 DIASPIS pugionifera.
- ASPIDIOTUS replicatus.
- MICROLOBIUM (Leguminosae).  
 LECANIUM quinquepori.
- MICROMERIA (Labiatae).  
 LECANIUM hesperidum.  
 CHIONASPIS canariensis, berlesii.
- MILIUM (Gramineae).  
 ANTONINA purpurea.  
 ACLERDA subterranea.
- MILIUSA (Anonaceae).  
 AONIDIA targionopsis.
- MIMOSA (Leguminosae).  
 LOPHOCOCCUS mirabilis.  
 PALAEOCOCCUS hempeli.  
 ICERYA littoralis-mimosae.  
 CRYPTOKERMES brasiliensis.  
 LECANODIASPIS mimosae.  
 PSEUDOCOCCUS longispinus.  
 TACHARDIA albida, fulgens, lacea,  
 LECANIUM hesperidum. [mexicana.  
 LICITENSIA mimosae, parvula.  
 CEROPLASTES confluent, egharum,  
 mimosae.  
 CEROPLASTODES dugesii.  
 SCHIZOCHLAMIDIA mexicana.  
 DIASPIS pentagona.  
 ASPIDIOTUS mimosae, phenax, denti-  
 LEPIDOSAPHES mimosarum. [lobis.
- MIMULUS (Scrophulariaceae).  
 CEROPUTO yuceae.
- MIMUSOPS (Sapotaceae).  
 LECANIUM expansum, scutatum.  
 ASPIDIOTUS malleolus, trilobitiformis,  
 dictyospermi.  
 AONIDIA spinosissima.
- MISCANTHUS (Gramineae).  
 RIPERSIA japonica, agasawarensis.  
 LEPIDOSAPHES arii.
- MISCHOCARPUS (Sapindaceae).  
 CHIONASPIS mischocarpi.
- MOESA (Myrsineae).  
 LECANIUM tessellatum.  
 HEMICHIONASPIS mussoendae.  
 ASPIDIOTUS transparent.  
 LEPIDOSAPHES cocculi.
- MOLINIA (Gramineae).  
 PSEUDOCOCCUS perrisi.
- MONANTHERA (Crassulaceae).  
 CHIONASPIS berlesii.
- MONARDELLA (Labiatae).  
 PHENACOCCLUS stachyos.

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- MONODORA (Anonaceae).  
 ICERYA seychellarum.  
 LECANIUM longulum.
- MONOTOCA (EPACRIDACEAE).  
 TACHARDIA decorella.
- MONSTERA (Araceae).  
 LECANIUM longulum, melaleucæ.  
 ISCHNASPIS filiformis.
- MORINDA (Rubiaceae).  
 PULVINARIA psidii.  
 CHIONASPIS thoracica.  
 ASPIDIOTUS orientalis.
- MORINGA (Moringaceae).  
 HOWARDIA biclavata.
- MORUS (Moraceae) 'Mulberry.'  
 MONOPHLEBUS octocaudatus.  
 GUERINIELLA serratulæ.  
 ICERYA longisetosa, purchasi.  
 ASTEROLECANIUM pustulans.  
 PSEUDOCOCCUS bromeliæ, comstocki,  
 citri, filamentosus, virgatus, longi-  
 spinus, longicornis.  
 STRICTOCOCCUS dimorphus, diversiseta.  
 LECANIUM hesperidum, mori, ribis,  
 websteri, nishigaharæ, oleæ, som-  
 mereni, nigrofasciatum, corni, per-  
 siciæ.  
 PULVINARIA innumerabilis, kuwacola,  
 maxima, cupaniæ, psidii.  
 TAKAHASHIA japonica.  
 CEROPLASTES rusei, ceriferus, solidus.  
 INGLISIA bivalvata.  
 DIASPIS pentagona.  
 ASPIDIOTUS aurantii, mori, longi-  
 spinus, lataniæ, hederæ, per-  
 niciosus.
- MOSESSES.  
 ORTHEZIA cataphracta.  
 NEWSTEADIA floeosa.  
 ORTHEZIOLA vejtdovskyi.  
 PSEUDOCOCCUS sphagni.  
 RIPERSIA globata.
- MUEHLENBECKIA (Polygonaceae).  
 COELOSTOMIDIA zealandica.  
 LECANIUM hesperidum.  
 PULVINARIA psidii.  
 ERIOCHITON spinosus.  
 INGLISIA foraminifera, fossilis.  
 CEROPLASTES sinensis.  
 ASPIDIOTUS dictyospermi, lataniæ,  
 hederæ, cyanophylli.
- MURALTIA (Polygalaceae).  
 PSEUDOCOCCUS muraltiæ.
- MURRAYA (Rutaceae).  
 PHENACOCCUS iceryoides.  
 LECANIUM discrepans.  
 ASPIDIOTUS trilobitiformis-darutyi,  
 quadriclavatus.  
 FLORINIA rubrolineata.  
 LEPIDOSAPHES citricola.
- MUSA (Musaceae).  
 ICERYA montserratensis.  
 PSEUDOCOCCUS citri, longispinus, bro-  
 meliæ, nipæ.  
 CEROPUTO yuccæ.  
 LECANIUM signiferum, hesperidum,  
 hemisphaericum, discrepans.  
 PROTOPULVINARIA pyriformis.  
 HEMICHIONASPIS minor.  
 ASPIDIOTUS destructor, palmar, ficus,  
 personatus, orientalis, exesus,  
 lataniæ, cyanophylli, scutiformis,  
 hederæ, articulatus, cydoniæ.
- MUSSOENDA (Rubiaceae).  
 LECANIUM nigrum.  
 HEMICHIONASPIS mussoendæ.
- MYOPORUM (Myoporaceae).  
 ERIOCOCCUS pallidus, eucalypti.  
 PSEUDOCOCCUS stolatus.  
 LECANIUM hemisphaericum.  
 PULVINARIA dodonacæ, greeni.  
 CTENOCHITON testudo.  
 ASPIDIOTUS camelliæ, myopori.  
 LEUCASPIS myopori.
- MYRCEUGENIA (Myrtaceae).  
 LEPIDOSAPHES diaspidiformis.
- MYRCIA (Myrtaceae).  
 PSEUDISCHNASPIS linearis.
- MYRCIARIA (Myrtaceae).  
 CEPULINIA jaboticabæ.
- MYRICA (Myricaceae).  
 TACHARDIA decorella.  
 PHENACOCCUS aceris.  
 LECANIUM longulum, capræ.  
 CEROPLASTES ceriferus, myricæ.  
 ASPIDIOTUS duplex.  
 LEPIDOSAPHES ulmi.
- MYRISTICA (Myristicaceae) 'Nutmeg.'  
 LECANODIASPIS malaboda.  
 LECANIUM mangiferæ, incisum,  
 psidii.  
 PARALECANIUM expansum, expan-

- MYRISTICA (Myristicaceae)—*cont.*  
 sum-metallicum, expansum-quad-  
 ratum.  
 VINSONIA stellifera.  
 DIASPIS myristicae.  
 CHIONASPIS dilatata.  
 ASPIDIOTUS destructor, samoana.  
 AONIDIA javanensis.  
 ISCHNASPIS filiformis.  
 MYRSINE (Myrsinaceae).  
 ASPIDIOTUS hederæ, lauretorum.  
 MYRTACEAE, miscellaneous.  
 APIOCOCCUS asperatus, globosus, gre-  
 garius, singularis.  
 TECTOCOCCUS ovatus.  
 SPHAEROCOCCUS socialis.  
 PSEUDOCOCCUS grandis.  
 ERIOCOCCUS perplexus.  
 TACHARDIA parva.  
 LECANIUM discoides, glanulosa, reti-  
 culata, inflatum.  
 PULVINARIA grandis, psidii.  
 CEROPLASTES jancirensis, simplex,  
 speciosus, variegatus.  
 PLATINGLISIA noacki.  
 DIASPIS australis.  
 DIASPIDISTIS multilobis.  
 ASPIDIOTUS trilobitiformis.  
 MYRTUS (Myrtaceae).  
 CEROPLASTES cirripediformis, flori-  
 densis, rusci.  
 LECANIUM nitens, hesperidum, oleae,  
 myrti.  
 PULVINARIA psidii.  
 FILIPPIA oleae.  
 DIASPIS rosae.  
 CHIONASPIS myrthi.  
 PSEUDOPARLATORIA serrulata.  
 ASPIDIOTUS ficus, dietyospermi, rapax.  
 PARLATORIA myrtus, proteus, pro-  
 teus-virescens.  
 LEPIDOSAPHES myrthi.  
 NAPOLEONA (Lecithydaceae).  
 STICTOCOCCUS sjostedti.  
 NARDUS (Gramineae).  
 RIPERSIA subterranæa.  
 LUZULASPIS luzulæ.  
 NECTANDRA (Lauraceae).  
 ASPIDIOTUS tesseratus, cydoniæ.  
 PSEUDOPARLATORIA noacki.  
 NEGUNDO (Aceraceae).  
 PULVINARIA immuerabilis.  
 NEOLITSEA (Lauraceae).  
 FIORINIA plantasma.  
 NEPHELIUM (Sapindaceae).  
 TACHARDIA albizzia.  
 LECANIUM acutissimum, nigrum.  
 PULVINARIA psidii.  
 DIASPIS euphoricæ.  
 FIORINIA nephelii, hirsuta.  
 ASPIDIOTUS trilobitiformis.  
 NEPHRODIUM (Filices).  
 PSEUDOCOCCUS longispinus.  
 LEPIDOSAPHES desmidioides.  
 NEPHROLEPIS (Filices).  
 LECANIUM mori, hesperidum.  
 NERIUM (Apocynaceae) 'Oleander.'  
 ASTEROLECANIUM pustulans.  
 PSEUDOCOCCUS burnerae, citri, vir-  
 gatus.  
 LECANIUM hesperidum, hemisphaeri-  
 cum, oleae, nigrofasciatum, per-  
 sicæ.  
 CEROPLASTES nerii, floridensis, town-  
 sendi, percrassus.  
 DIASPIS pentagona.  
 CHIONASPIS nerii.  
 HEMICHIONASPIS minor.  
 ASPIDIOTUS hederæ, ficus, rossi,  
 trilobitiformis, dietyospermi, cy-  
 doniæ.  
 AONIDIA distinctissima.  
 PARLATORIA pergandci, oleae, calian-  
 thina.  
 NICOTIANA (Solanaceae) 'Tobacco.'  
 PSEUDOCOCCUS nicotianæ.  
 LECANIUM nicotianæ.  
 PULVINARIA floceifera.  
 NIPA (Palmaceae).  
 PSEUDOCOCCUS nipa.  
 NITRARIA (Zygophyllaceae).  
 ASPIDIOTUS nitrariæ.  
 NOTHOFAGUS (Corylaceae).  
 FAGISUGA triloba.  
 NOTHOPANAX (Araliaceae).  
 LEUCASPIS gigas.  
 NOTHOPEGIA (Anacardiaceae).  
 LECANIUM bicruciatum.  
 ASPIDIOTUS rossi, trilobitiformis.  
 PARLATORIA blanchardi, aonidiformis.  
 GYMNASPIS bullata.

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- NUYTSIA (Loranthaceae).  
   PULVINARIA maskelli-nuytsiae.  
 NYSSA (Cornaceae).  
   CHIONASPIS nyssae, sylvatica.  
  
 OCHNA (Ochnaceae).  
   LECANIUM tessellatum.  
   HOWARDIA biclavata.  
 OCIMUM (Labiatae).  
   CEROPLASTODES cajani.  
 OCOTEA (Lauraceae).  
   ASPIDIOTUS lauretorum, laurinus.  
   FIORINIA pellucida.  
 ODINA (Mangiferae).  
   PHENACOCCLUS iceryoides.  
   FIORINIA odinae.  
 ODONTOGLOSSUM (Orchidaceae).  
   ASPIDIOTUS odontoglossi.  
 OLEA (Oleaceae) 'Olive.'  
   GUERINIELLA serratulatae.  
   ICERYA purchasi.  
   POLLINIA pollini.  
   PSEUDOCOCCLUS citri.  
   PHENACOCCLUS oleae, eleabius, farn-  
     neriana.  
   LECANIUM nigrofasciatum, oleae, hes-  
     peridum.  
   LICHTENSIA eatoni.  
   FILIPPIA oleae, chrysophyllae.  
   EUPHILIPPIA olivina.  
   DIASPIS bromeliae, oleae.  
   EPIDIASPIS leperei.  
   CHIONASPIS nerii, olivina, ceratoniae.  
   LEUCASPIS epidaurica, riceae.  
   ASPIDIOTUS hederac, osmanthi, ca-  
     melliae, aurantii, duplex, rossi,  
     oppugnatus, opimus, articulatus,  
     tafrenus, britannicus, dictyo-  
     spermi, lenticularis.  
   PARLATORIA affinis, calianthina, oleae.  
   LEPIDOSAPHES flava, beckii-oleae,  
     gloveri, pinnaeformis.  
 OLEARIA (Compositae).  
   CRYPTORHIZOCOCCLUS oleariae.  
   ERIOCHITON hispidus.  
   ASPIDIOTUS hederac.  
 ONAGRA (Onagraceae).  
   LECANIUM corni.  
 ONCIDIUM (Orchidaceae).  
   ASTEROLECANIUM aureum, epidendri.  
   PULVINARIA camelicola, floccifera.  
   PSEUDOPARLATORIA parlatorioides.  
 ONCOBA (Bixaceae).  
   LEUCASPIS cockerelli.  
 ONOBRYCHIS (Leguminosae).  
   ORTHEZIA urticae.  
 ONONIS (Leguminosae).  
   DIASPIS pentagona.  
   ASPIDIOTUS hederac.  
 OPHIOPOGON (Haemodoraceae).  
   ASTEROLECANIUM aureum.  
   PARLATORIA proteus.  
 OPHIORRHIZA (Rubiaceae).  
   LECANIUM ophiorrhizae.  
   PULVINARIA tessellata.  
 OPHRYOSPORUS (Compositae).  
   ASPIDIOTUS argentinus.  
 OPUNTIA (Cactaceae) 'Prickly Pear.'  
   GUERINIELLA seratulatae.  
   DACTYLOPIUS cacti, confusus, con-  
     fusus-newsteadii, tomentosus, ca-  
     pensis, argentinus, ceylonicus.  
   PSEUDOCOCCLUS obscurus.  
   DIASPIS echinocacti.  
 ORCHIDACEAE 'Orchids.'  
   CONCHASPIS angraci.  
   ASTEROLECANIUM aureum, epidendri.  
   LECANIODIASPIS dendrobii.  
   LECANIUM acuminatum, anthurii,  
     hemisphaericum, pseudohesperi-  
     dum, tessellatum.  
   DIASPIS boisduvallii, cattleyae, ali-  
     enus.  
   HEMICHIONASPIS aspidistrae, minor.  
   FIORINIA fioriniac.  
   LEUCASPIS stricta.  
   PSEUDOPARLATORIA parlatorioides.  
   ASPIDIOTUS cyanophylli, hederac,  
     biformis, dictyospermi, odonto-  
     glossi, biformis-cattleyae, por-  
     toricensis, aurantii, perseae, rossi,  
     transpareus.  
   PARLATORIA proteus, pergandei, pseud-  
     aspidiotus.  
   LEPIDOSAPHES pinnaeformis, cocculi,  
     vandae, tuberculata.  
 OREODAPHNE (Lauraceae).  
   ASPIDIOTUS lauretorum.  
 OREODOXA (Palmaeae).  
   ASPIDIOTUS oreodoxae.  
 ORIXA (Celastraceae).  
   DIASPIS pentagona-rubra.

- ORMOSIA (Leguminosae).  
   CEROPLASTES vuilleti.  
 OROBANCHA (Orobanchaceae).  
   PSEUDOCOCCUS longisetosus.  
 ORYZA (Gramineae) 'Rice.'  
   RIPERSIA oryzae.  
   CHIONASPIS decurvata.  
 OSBECKIA (Melastomaceae).  
   ASPIDIOTUS orientalis, camelliae,  
     transparentis.  
 OSMANTHUS (Oleaceae).  
   PHENACOCCLUS suwakoensis.  
   DIASPIS pentagona-auranticolor.  
   CHIONASPIS citri.  
   ASPIDIOTUS britannicus, hederac.  
   LEPIDOSAPHES uniloba.  
 OSTODES (Euphorbiaceae).  
   AONIDIA cornigera.  
   FIORINIA theae.  
 OSTRYA (Betulaceae).  
   PHENACOCCLUS aceris.  
   LECANIUM quercitronis, ribis, web-  
     steri.  
   PULVINARIA betulae.  
   ASPIDIOTUS osborni, ostreaeformis.  
 OSYRIS (Santalaceae).  
   ASTEROLECANIUM fimbriatum.  
   LECANIUM oleae, persicae.  
   ASPIDIOTUS hederac, eecoonii, trabuti.  
 OUGEINIA (Leguminosae).  
   TACHARDIA laca.  
 OXALIS (Geraniaceae).  
   PSEUDOCOCCUS eapensis.  
 OXYLOBIUM (Leguminosae).  
   POLIASPIS exocarpi.  
 OXYTENANTHERA (Gramineae).  
   ASTEROLECANIUM ceriferum-promi-  
     nens.  
 PACHIRA (Malvaceae).  
   LECANIUM chelonioides.  
 PADUS (Rosaceae).  
   LECANIUM nigrofasciatum.  
 POEONIA (Ranunculaceae).  
   PSEUDOCOCCUS citri.  
   CHIONASPIS salicis.  
   LEUCASPIS japonica.  
   ASPIDIOTUS peoniae.  
 PALMACEAE 'Palms.'  
   ICERYA montserratensis, seychel-  
     larum.  
   HALIMOCOCCUS lampas, borassi.  
   PHOENICOCCOCCUS marlatti.  
   ASTEROLECANIUM palmae, urichi,  
     spectabile.  
   PSEUDOCOCCUS arceae, nipae, cocotis,  
     pseudonipae, virgatus, citri, longi-  
     spinus.  
   RIPERSIA palmarum.  
   LECANIUM tessellatum, acutissimum,  
     longulum, minimum, palmae, he-  
     misphaericum, oleae, hesperidum.  
   CEROPLASTES actiniformis, rubens.  
   VINSONIA stellifera.  
   DIASPIS boisduvallii, boisduvallii-  
     coccois, pentagona.  
   CHIONASPIS citri, cockerelli, eugeniae,  
     substriata, unilateralis, dentilobis,  
     dilatata, inday, pseudonivea.  
   HEMICHIONASPIS aspidistrac, minor,  
     marehali.  
   PINNASPIS buxi.  
   POLIASPIS eyeadis.  
   LEUCASPIS cockerelli.  
   FIORINIA fioriniae, kewensis, macro-  
     procta, pellucida.  
   ASPIDIOTUS cyanophylli, lataniae, de-  
     structor, similimus, ficus, rossi,  
     dictyospermi, personatus, spino-  
     sus, chamaeropsis, cydoniae, au-  
     rantii, perseae, oceanica, ostreae-  
     formis, oreodoxae, pseudospino-  
     sus, cocotiphagus, clacidis, prop-  
     simus, articulatus, orientalis, cory-  
     phae, palmae, fissidens-constricta,  
     hederac, rapax, mauritanus, pan-  
     goensis.  
   COMSTOCKIELLA sabalis, sabalis-mexi-  
     cana.  
   GYMNASPIS grandis.  
   PARLATORIA blanchardi, proteus,  
     ziziphus, greeni, mangiferae.  
   LEPIDOSAPHES gloveri, megregori,  
     unicolor.  
   ISCHNASPIS filiformis.  
 PANAX (Araliaceae).  
   PSEUDOCOCCUS glaucus.  
   CTENOCHITON flavus, fuscus, per-  
     foratus, viridis.  
   FIORINIA minima.  
 PANCRATIUM (Amaryllidaceae).  
   PSEUDOCOCCUS simplex.

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- PANDANUS (Pandanaeae) 'Screw-pines.'  
 PSEUDOCOCCUS pandani, longispinus.  
 TYLOCOCCUS giffardi.  
 LECANIUM pseudexpansum.  
 CEROPLASTES actiniformis.  
 CHIONASPIS dilatata, pseudaspidistrae.  
 HEMICHIONASPIS aspidistrae.  
 PINNASPIS buxi.  
 ASPIDIOTUS pandani, dictyospermi, aurantii, ficus.  
 POROCYMNASPIS rufa, angulata.  
 ISCHNASPIS filiformis.  
 LEPIDOSAPHES greeni.  
 PANICUM (Gramineae).  
 LECANIUM hemisphaericum.  
 DIASPIS uncinati.  
 ASPIDIOTUS marlatti, panici, saechari.  
 PARIETARIA (Urticaceae).  
 PSEUDOCOCCUS parietariae.  
 ORTHEZIA urticae.  
 PARNARIUM (Chrysobalanaceae).  
 ASPIDIOTUS fissidens.  
 PARITIMUM (Malvaceae).  
 DIASPIS pentagona.  
 PARKINSONIA (Leguminosae).  
 INGLISIA chelonioides.  
 ASPIDIOTUS parkinsoniae.  
 PARSONSIA (Apocynaceae).  
 HEMICHIONASPIS minor.  
 PARTHENIUM (Compositae).  
 LECANIODIASPIS yuceae.  
 TACHARDIA cornuta.  
 PASANIA (Fagaceae).  
 ASTEROLECANIUM pasaniae, tokyonis.  
 PSEUDOCOCCUS quereicola.  
 ASPIDIOTUS densiflorae.  
 PASSIFLORA (Passifloraceae).  
 PSEUDOCOCCUS burnerae, longispinus.  
 LECANIUM caudatum. (maritimus).  
 PULVINARIA jacksoni.  
 ASPIDIOTUS hederac, trilobitiformis.  
 PATERSONIA (Iridaceae).  
 LECANIUM patersoniae.  
 PAULOWNIA (Scrophulariaceae).  
 DIASPIS pentagona.  
 PAVETTA (Rubiaceae).  
 LECANIUM caudatum.  
 'PEACH' (Amygdalus persica).  
 ASTROLECANIUM pustulans.  
 PSEUDOCOCCUS capensis.  
 PHENACOCOCCUS aceris.  
 LECANIUM armeniacum, canadense, cerasifex, cockerelli, persicae, pruinosum, prunastris, rugosum, hemisphaericum, persimile, nigrofasciatum, hesperidum.  
 PULVINARIA amygdali.  
 CEROPLASTES rusci.  
 DIASPIS lepèrii, pentagona, squamosa.  
 EPIDIASPIS piricola.  
 PSEUDOPARLATORIA parlatorioides.  
 CHIONASPIS furfura.  
 ASPIDIOTUS ancyclus, forbesi, juglansregiae, ostreaeformis, lataniae, perniciosus, cyanophylli.  
 PARLATORIA calianthina.  
 PEDDIEA (Thymeliaceae).  
 ASPIDIOTUS trilobitiformis.  
 PELARGONIUM (Geraniaceae).  
 ICERYA purchasi.  
 ASTEROLECANIUM fimbriatum.  
 PSEUDOCOCCUS capensis.  
 PULVINARIA psidii.  
 DIASPIS pentagona.  
 HEMICHIONASPIS minor.  
 PELLAEA (Filices).  
 CHIONASPIS dubia.  
 PENTACME (Dipteroearpaeae).  
 TACHARDIA lacca.  
 PERGULARIA (Aselepiadaceae).  
 LECANIUM caudatum.  
 PERSEA (Lauraceae) 'Avocado Pear.'  
 ICERYA montserratensis, seychellarum.  
 PSEUDOCOCCUS citri, longispinus, nipae.  
 CEROPLASTES cistudiformis, floridensis, rubens.  
 LECANIUM hemisphaericum.  
 PROTOPULVINARIA pyriformis.  
 DIASPIS pentagona.  
 PINNASPIS rhombica.  
 FLORINIA floriniae.  
 ASPIDIOTUS persearum, persicae, scutiformis, destructor, hederac, dictyospermi, lauretorum, subsimilis, personatus, palmae, maskelli.  
 PSEUDOPARLATORIA parlatorioides, ostratea.  
 LEPIDOSAPHES longula, mimosarum.

- PERSONIA (Proteaceae).  
   CHIONASPIS eugeniae.  
 PETROPHILA (Proteaceae).  
   ASTEROLECANIUM petrophilae.  
   PARLATORIA petrophilae.  
 PETROPHYTES (Crassulaceae).  
   CHIONASPIS berlesii.  
 PHAGNALON (Compositae).  
   ASTEROLECANIUM fimbriatum.  
 PHAJUS (Orchidaceae).  
   PULVINARIA floccifera.  
 PHALERIA (Thymeliaceae).  
   TACHARDIA aurantiaca.  
 PHASEOLUS (Leguminosae) 'Garden  
   Beans,' etc.  
   PSEUDOCOCCUS virgatus.  
   PULVINARIA antigoni.  
   DIASPIS pentagona.  
   ASPIDIOTUS articulatus.  
 PHILADELPHUS (Saxifragaceae).  
   LECANIUM corni.  
 PHILLYREA (Oleaceae).  
   LECANIUM oleae.  
   LICHTENSIA catoni.  
   FILIPPIA oleae.  
   ASPIDIOTUS hederæ.  
   LEPIDOSAPHES conchiformis.  
 PHILODENDRON (Araceae).  
   PSEUDOCOCCUS nipae.  
   LECANIUM insolens.  
   PULVINARIA idesia.  
   PINNASPIS buxi.  
 PHLEUM (Gramineae).  
   PSEUDOCOCCUS elongatus.  
   PHENACOCCLUS graminis.  
 PHLOMIS (Labiatae).  
   ORTHEZIA urticae.  
 PHLOX (Polemoniaceae).  
   LECANIUM hesperidum.  
 PHOEBE (Lauraceae).  
   ASPIDIOTUS barbusano.  
 PHOENIX (Palmaeae) 'Date Palms.'  
   ICERYA aegyptiaca.  
   PHOENICOCCLUS marlatti.  
   SPHAEROCOCCUS draperi, marlatti.  
   PSEUDOCOCCUS nipae.  
   LECANIUM hesperidum, tessellatum,  
     oleae, expansum.  
 PHORADENDRON (Loranthaceae).  
   PSEUDOCOCCUS phoradendri.  
   LECANIUM phoradendri, nigrofascia-  
     tum.  
 PHORMIUM (Liliaceae) 'New Zealand  
   Flax.'  
   COELOSTOMIDIA wairoensis.  
   PSEUDOCOCCUS calceolariae.  
   LEUCASPIS stricta.  
   POLIASPIS media.  
   FIORINIA fioriniae.  
   ASPIDIOTUS phormii, sphaerioides,  
     dietyospermi, hederæ.  
   LEPIDOSAPHES cordylinidis.  
 PHOTINIA (Rosaceae).  
   PULVINARIA photiniae.  
   ASPIDIOTUS perniciosus-andromelas.  
 PHRAGMITES (Gramineae).  
   ANTONINA phragmitis.  
   ACLERDA bivakoensis.  
 PHYLLANTHUS (Euphorbiaceae).  
   ERIOIDES rimulæ.  
   ASPIDIOTUS taprobanus, phyllanthi,  
     lataniæ.  
   PARLATORIA phyllanthi.  
 PHYLLIREA (Oleaceae).  
   LEPIDOSAPHES destefanii.  
 PHYLLOCLADUS (Coniferae).  
   COELOSTOMIDIA assimilis.  
   ERIOCOCCUS phyllocladi.  
   PERRISIA phyllocladi.  
 PHYLLIDIUM (Leguminosae).  
   CRYPTHEMICHIONASPIS nigra.  
 PHYLOSTACHYS (Gramineae).  
   CHIONASPIS hikosani.  
 PHYMATODES (Filices).  
   LEPIDOSAPHES phymatodidis.  
 PHYTOLACCA (Phytolaccaceae).  
   PSEUDOCOCCUS capensis.  
 PICCONIA (Oleaceae).  
   ASPIDIOTUS lauretorum, hederæ.  
 PICEA (Coniferae).  
   PHENACOCCLUS minimus, piceae.  
   LECANIUM cooleyi, piceae.  
   ASPIDIOTUS abietis.  
   SYNGENASPIS parlatoriae.  
 PICRADENJA (Compositae).  
   PALAEOCOCCUS townsendi.  
 PICRIS (Compositae).  
   GUERINIELLA serratulæ.  
 PILEA (Urticaceae).  
   LECANIUM flaveolum.  
 PIMENTA (Myrtaceae).  
   LLAVEIA primitiva-pimentae.  
 PIMPINELLA (Umbelliferae).  
   ASTEROLECANIUM fimbriatum.

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- PINUS (Coniferae).  
 MONOPHLEBUS burmeisteri, maskelli.  
     fuscipennis, hirtus.  
 GUERINIELLA scratulacae.  
 ICERYA purchasi.  
 PSEUDOCOCCUS caricus, pini, comstocki, maritimus.  
 PHENACOCOCCUS minimus, hystrix.  
 PUTO antennatus, eupressi.  
 PHYSOKERMES coloradensis, insignicola, piceae.  
 LECANIUM genistae, minimum-pinicola, parvicornis, pini.  
 PSEUDOPHILIPPIA quintanecci.  
 CEROPLASTES rubens-minor.  
 DIASPIS visci.  
 CHIONASPIS pinifoliae, austriaca.  
 POLIASPIS pini.  
 LEUCASPIS locwi, pini, pusilla, signoreti, perezi, suleii, corsa, leonardi, affinis, indiae-orientalis, candida.  
 ASPIDIOTUS abietis, coniferarum, glanduliferus, californicus, florentiae, corticis-pini, ehrhorni.  
 AONIDIA pinicola, lauri.  
 PARLATORIA proteus.  
 LEPIDOSAPHES pyriformis, newsteadi, ulmi.
- PIPER (Piperaceae) 'Pepper,' etc.  
 PSEUDOCOCCUS glaucus.  
 LECANIUM piperis, marsupiale, longulum, acutissimum, peradeniyense.  
 PROTOPULVINARIA longivalvata.  
 PLATYLECANIUM eribrigerum.  
 CTENOCHITON piperis.  
 CHIONASPIS varicosa.  
 HEMICHIONASPIS aspidistrae, minor.  
 PINNASPIS siphonodontis.  
 FIORINIA diaspiformis, proboscidea.  
 ASPIDIOTUS capsulatus, destructor.  
 LEPIDOSAPHES piperis, citricola, glomeri.
- PIPTURUS (Urticaceae).  
 NESOCOCCUS pipturi.
- PISONIA (Nyctaginaceae).  
 PULVINARIA pseudotloccifera.
- PISTACIA (Anacardiaceae).  
 LECANIUM oleae.  
 PULVINARIA psidii.  
 FILIPPICIA oleae.
- CEROPLASTES rusci.  
 DIASPIS genuadii, syriaca.  
 LEUCASPIS pistaceae.  
 ASPIDIOTUS aurantii, hederacae.  
 LEPIDOSAPHES pistaceae.
- PITCAIRNIA (Bromeliaceae).  
 DIASPIS boisduvallii.
- PITHECOLOBIUM (Leguminosae).  
 ICERYA montserratensis.  
 TACHARDIA laeae.  
 PSEUDOCOCCUS epronis.  
 CERONEMA koebeleii.  
 CEROPLASTES egbarum.  
 INGLISIA chelonioides.  
 HEMICHIONASPIS minor.  
 ASPIDIOTUS fodiens.
- PITTOSPORUM (Pittosporaceae).  
 ICERYA purchasi.  
 ASTEROLECANIUM fimbriatum.  
 CEROCOCCUS punctiferus.  
 ERIOCOCCUS paradoxus, eucalypti.  
 PSEUDOCOCCUS glaucus, longispinus.  
 LECANIUM notatum, hemisphaericum.  
 PULVINARIA psidii, floccifera.  
 CTENOCHITON perforatus.  
 LEUCASPIS gigas.  
 ASPIDIOTUS subrubescens, junctilobius, aurantii, hederacae, ficus.  
 PARLATORIA pittospori, viridis, proteus.  
 LEPIDOSAPHES pyriformis, subarmatus.
- PITURANTHOS (Umbelliferae).  
 CHIONASPIS bilobis.
- PLAGIANTHUS (Malvaceae).  
 CTENOCHITON depressus.
- PLATANUS (Platanaceae) 'Plane tree.'  
 PHENACOCOCCUS osborni, platani, aceris.  
 LECANIUM nigrofasciatum, corni.  
 ASPIDIOTUS ostreaeformis.
- PLATYLOBIUM (Leguminosae).  
 ASPIDIOTUS hederacae.
- PLECTRONIA (Rubiaceae).  
 LECANIUM luzonicum.  
 HEMILECANIUM recurvatum.
- PLOCAMA (Rubiaceae).  
 CHIONASPIS canariensis, berlesii.
- PLUCHEA (Compositae).  
 PALAEOCOCCUS pluchaeae.  
 LECANIUM hesperidum.  
 PULVINARIA pluchaeae.

- PLUMBAGO** (Plumbaginaceae).  
*ICERYA purchasi*.  
*CEROPLASTES plumbaginis*.
- PLUMERIA** (Apocynaceae).  
*CONCHASPIS newsteadi*.  
*LECANIUM viride*.  
*PULVINARIA psidii*.  
*HOWARDIA bielavis*.
- POA** (Gramineae).  
*MARGARODES hamclii*.  
*PHENACOCOCCUS graminis*.  
*HETEROCOCCUS arenae*.
- PODOCARPUS** (Coniferae).  
*ICERYA seychellarum*.  
*COELOSTOMIDIA compressa, pilosa*.  
*PHENACOLEACHIA zealandica*.  
*ERIOCOCCUS spinifrons*.  
*RHIZOCOCCUS totaræ*.  
*PULVINARIA floceifera*.  
*POLIASPIS pini*.  
*AONIDIA longa*.  
*LEPIDOSAPHES pallida*.
- POINCIANA** (Leguminosae).  
*LECANIUM longulum*.
- POLIANTHES** (Amaryllidaceae).  
*LECANIUM oleæ*.  
*ASPIDIOTUS lataniæ*.
- POLYALTHIA** (Anonaceae).  
*ASPIDIOTUS orientalis*.
- POLYGONUM** (Polygonaceae).  
*MARGARODES polonicus*.  
*CHIONASPIS polygoni*.  
*ASPIDIOTUS hederæ*.
- POLYPODIUM** (Filices).  
*LECANIUM hesperidum*.  
*CHIONASPIS dilatata*.
- POPADERRIS** (Rhamnaceae).  
*LECANIODIASPIS atherospermae*.  
*ASPIDIOTUS subfervens*.  
*LEPIDOSAPHES citricola*.
- POPULUS** (Salicaceae) 'Poplar.'  
*ERIOCOCCUS borealis*.  
*LECANIUM capreae, tiliae, nigro-fasciatum, coryli, corni, ciliatum, zebrinum*.  
*PULVINARIA occidentalis, tremulae, betulæ, vitis*.  
*CEROPLASTES rusci*.  
*DIASPIS pentagona*.  
*CHIONASPIS longiloba, ortholobis, salicis, salicis-nigræ, micropori, africana*.
- LEUCASPIS kermanensis*.  
*FIORINIA africana*.  
*ASPIDIOTUS ostreaciformis, perniciosus, canellia, popularum, transcaspensis*.  
*LEPIDOSAPHES ulmi*.
- 'POTATO' (Solanaceae).  
*PSEUDOCOCCUS affinis, solani*.  
*LECANIUM tolucanum*.
- POTENTILLA** (Rosaceae).  
*ASTEROLECANIUM fimbriatum*.  
*PHENACOCOCCUS comari*.  
*LECANIUM pulchrum*.
- POTHOS** (Araceae).  
*LECANIUM marsupiale*.  
*ASPIDIOTUS pothi*.
- POUZOLZIA** (Urticaceae).  
*CEROPLASTES eceriferus*.
- PRASIMUM** (Labiatae).  
*ASTEROLECANIUM fimbriatum*.
- PRINOS** (Aquifoliaceae).  
*PULVINARIA cockerelli*.  
*LICHTENSIA viburni*.
- PRITCHARDIA** (Palmaceae).  
*LECANIUM hesperidum*.  
*CEROPLASTES rusei*.  
*HEMICHIONASPIS aspidistrae*.  
*LEUCASPIS cockerelli*.  
*ASPIDIOTUS cyanophylli*.  
*ISCHNASPIS filiformis*.
- PROSOPIS** (Leguminosae).  
*PALAEOCOCCUS mexicanus, rosæ*.  
*ICERYA rileyi*.  
*OPISTHOSCELIS prosopidis*.  
*LECANIODIASPIS prosopidis*.  
*ERIOCOCCUS quercus-toumeyii*.  
*PSEUDOCOCCUS prosopidis, virgatus-farinosus*.  
*TACHARDIA fulgens, lacca*.  
*LECANIUM mirabile*.  
*DIASPIS arizonica, townsendi*.  
*ASPIDIOTUS candidulus*.  
*XEROPHILASPIS prosopidis*.
- PROSTANTHERA** (Labiatae).  
*CHIONASPIS eugeniae*.
- PRUNUS** (Rosaceae).  
*CEROCOCCUS koebeleii*.  
*PSEUDOCOCCUS longispinus*.  
*PHENACOCOCCUS aceris*.  
*LECANIUM hoferi, armeniacum, capreae, cerasifex, cockerelli, guignardi, juglandifex, juglandis*.

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- PRUNUS (Rosaceae)—*cont.*  
 persicae, prunastri, prunosum, rugosum, tiliae, variegatum, vini, oleae, padi, kunoensis, nigrofasciatum, coryli, bituberculatum, corni, hemisphaericum, hesperidum.
- PULVINARIA amygdali, mammeae, occidentalis, pruni, psidii, betulae.
- DIASPIS santali, pentagona.
- CHIONASPIS lintneri.
- EPIDIASPIS piricola, lepèrei.
- ASPIDIOTUS forbesi, hederæ, howardi, juglansregiæ, dictyospermi, juglansregiæ-pruni, ostreaeformis, perniciosus, aurantii, alni, pyri.
- PARLATORIA theae, proteus, oleae, calianthina.
- LEPIDOSAPHES ulmi.
- PSEUDOTSUGA (Coniferae).
- PHYSOKERMES taxifoliae.
- ASPIDIOTUS ehrhorni.
- PSIDIUM (Myrtaceae) 'Guava.'
- ICERYA seychellarum, montserratensis, sulphurea.
- PSEUDOCOCCUS longispinus, virgatus, citri, nipae.
- PHENACOCCLUS mangiferae, gossypii-psidiarum.
- LECANIUM nitens, acuminatum, longulum, viride, depressum, nigrum, discoides, hemisphaericum, oleae, psidii, signatum, setigerum.
- PULVINARIA cupaniae, ficus, psidii, africana.
- PROTOPULVINARIA pyriformis.
- CEROPLASTES campinensis, floridensis, grandis, psidii, vinsonii, singularis, destructor, vinsonioides.
- VINSONIA stellifera.
- CARDIOCOCCUS umbonatus.
- CHIONASPIS eugeniæ, megaloba.
- PSEUDOPARLATORIA parlatorioides.
- ASPIDIOTUS ficus, cyanophylli, cydoniæ, rossi, lataniae, aurantii, translucens, camelliae, destructor, transparentis.
- LEPIDOSAPHES pallida.
- PSYCHOTRIA (Rubiaceae).
- LECANIUM hesperidum, piperis, marginatum.
- CEROPLASTES rubens.
- AONIDIA cornigera, spatulata.
- PARLATORIA mytilaspiformis.
- PTELEA (Rutaceae).
- ASPIDIOTUS perniciosus, ulmi.
- PTERIS (Filices).
- ERIOCOCCUS insignis.
- PTEROCARYA (Juglandaceae).
- PHENACOCCLUS aceris.
- PTEROSPERMUM (Sterculiaceae).
- LECANIUM tessellatum.
- PTYCHOSPERMA (Palmaceae).
- CEROPLASTES rubens.
- PUERARIA (Leguminosae).
- DIASPIS pentagona.
- PUNICA (Punicaceae) 'Pomegranate.'
- PSEUDOCOCCUS crotonis.
- LECANIUM oleae.
- CEROPLASTES floridensis, rusci.
- ASPIDIOTUS cydoniæ, orientalis, rossi, cydoniæ-punicae.
- PUTORIA (Rubiaceae).
- ASPIDIOTUS hederæ.
- PYRUS (Rosaceae) 'Pear,' 'Apple,' etc.
- PSEUDOCOCCUS bakeri, capensis.
- PHENACOCCLUS aceris.
- FONSCOLOMBIA fraxini.
- LECANIUM hoferi, armeniacum, capreae, cerasifex, cockerelli, corni, prunosum, pyri, rugosum, tiliae, vini, oleae, glandi, bituberculatum, variegatum, kunoensis, nigrofasciatum, coryli, persicae.
- PULVINARIA innumerabilis, amygdali, occidentalis, betulae.
- CEROPLASTES rubens, rusci.
- DIASPIS pyri, santalis, rosae, squamosa.
- CHIONASPIS furfurus, salicis.
- EPIDIASPIS piricoea, lepèrei.
- LEUCASPIS japonica.
- ASPIDIOTUS ancyclus, forbesi, juglansregiæ, ostreaeformis, pyri, perniciosus, camelliae, aurantii, tenebricosus, fuscus, africanus, pectinatus, ancyclus-latilobis, lataniae.
- PARLATORIA pergandei, proteus, calianthina, chinensis, pyri, oleae.
- LEPIDOSAPHES ulmi, flava-hawaiensis.

PHYSIOLOGICAL PRE-DETERMINATION: THE  
INFLUENCE OF THE PHYSIOLOGICAL CONDI-  
TION OF THE SEED UPON THE COURSE OF  
SUBSEQUENT GROWTH AND UPON THE YIELD.

III. REVIEW OF LITERATURE. CHAPTER II.

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CHAPTER II

INFLUENCE OF THE DEGREE OF MATURITY OF THE SEED  
AT THE TIME OF HARVESTING UPON ITS "POTENTIALITY."

INTRODUCTION.

IN the previous chapter we have reviewed the literature dealing with the effect of parental conditions upon the "potentiality" of the seed, meaning by this not only the capacity of the seed for germination, but also the capacity of the resulting plant for growth and yield. In the present chapter we shall consider the influence of the degree of maturity of the seed at the time of harvesting upon the vigour and yield of the resulting plant.

Different degrees of maturity of the seed are determined (1) by harvesting the seed at a time prior to that of the natural shedding of the

seed, the degree of maturity depending also upon whether the seeds are harvested alone or whether they are harvested along with and allowed to dry in organic connection with the parent plant, and (2) by the weather conditions which obtain during the formation and ripening of the seed.

In dealing with immature seed of cultivated plants we have to distinguish in the first place between the immature seed as it comes from the plant with a relatively high moisture content, and the same seed after drying in air. This distinction is an important one, but the work dealing with the comparison of immature seed as it comes from the parent plant, and the same seed after air-drying has been for the most part confined to the question of capacity for germination.

THE "POTENTIALITY" OF THE SEED AS INFLUENCED BY  
THE TIME OF HARVESTING.

Mazé<sup>(19)</sup> described experiments with maize in which the germination of immature seeds straight from the parent-plant was compared with that of similar immature seed artificially dried.

The results of these experiments showed that the drying of the immature seeds did not affect their capacity for germination, which was 100 per cent. in both cases, but altered the physiological condition of the seeds in such a way that germination could take place quickly and normally. Thus, in the experiment quoted below (Table I) in which immature maize seed in the so-called milky stage was used, the sample previously dried over concentrated  $H_2SO_4$  for 48 hours at  $30^\circ C.$  germinated fully in two days, whereas the sample which was not dried, but set to germinate immediately after removal from the parent plant, showed slow and sporadic germination extending over a period of 30 days.

Similar results were obtained with peas.

TABLE I.

*Lot I* consisted of a single vertical series of 19 grains, which were dried over concentrated  $H_2SO_4$  for 48 hours at  $30^\circ C.$  before sowing.

*Lot II* consisted of a single vertical series of 20 grains (containing 45.6 per cent. moisture) detached from a head of maize. These grains were set to germinate *immediately* after removal from the parent-plant. They were placed one by one in test-tubes containing distilled water and provided with two cotton plugs, one of which supported the seed at the surface of the water whilst the other was used to keep out organisms from the air.

	Percentage of germinations after					
	2 days	7 days	14 days	22 days	28 days	30 days
<i>Lot I</i>	100 %	—	—	—	—	—
<i>Lot II</i>	—	15 %	30 %	55 %	95 %	100 %

Results of the same nature were recorded by Babcock(2) and by Eberhart(8). Babcock found (*l.c.* p. 129) that radish seeds taken from green pods, corn picked whilst the husks were still green, and sweet corn gathered whilst the kernels were still soft and milky failed to germinate when transferred direct from the parent plant to wet filter paper, whereas similar immature seeds after a preliminary exposure to warm dry air for a period of 10 days germinated quickly and completely in the normal way (Table II).

TABLE II.

*Germination of Mature and Immature Seeds.*

Influence of Maturity and Exposure to Air upon Germination.

Variety of seeds	State of maturity	Percentage moisture content	Germination percentage	
			On wet filters	In hydrogen peroxide
Yellow Dent Corn	Ripe, one year old	8.50	100 in 48 hours	100 in 48 hours
Yellow Dent Corn	Ripe, but soft	40.62	0	100 after 14 days
Yellow Dent Corn	Ripe, but soft	54.22	0	100 after 14 days
Stowell's Evergreen } Sweet Corn	In edible condition	74.71	0	—
Radish	From green pods	—	0	—
Radish	From same green pods as above, but after 10 days' drying in air	—	100 in 48 hours	—

Eberhart (*l.c.*) found that whereas a sample of dead-ripe rye germinated immediately upon harvesting, the same grain, harvested in the milk stage, did not germinate until it had been stored for 40 days.

At this point it is interesting to enquire further as to the cause of the dormant condition of the maturing seed, and as to the reason why drying terminates this dormant condition and renders possible immediate germination and growth.

No satisfactory answer to these questions is as yet forthcoming. Mazé(20), however, in a more recent paper ascribed the dormancy of immature maize seeds placed under suitable germinating conditions immediately after gathering to the presence of small quantities of ethyl aldehyde in the cell-sap. He found small, but measurable, quantities of this substance in the freshly gathered green seed, but was unable to detect its presence in the same seed after drying. Mazé (*l.c.*) found also that when immature maize seed was artificially infected with various parasitic and saprophytic fungi (e.g. *Aspergillus*, *Mucor*, *Botrytis*, *Sclerotinia*, etc.) germination quickly ensued as compared with non-

infected control seed. Heads of maize picked before maturity were placed in a damp atmosphere under bell jars at the laboratory temperature. After an interval of 15 days it was found that the seeds, which had germinated, corresponded with the infected areas on the head as indicated by the presence of fungal mycelium. Mazé suggested that these organisms in some way destroyed the aldehyde, since the seeds which had germinated after inoculation were found to contain no aldehyde, whereas in a control head which was not inoculated a concentration of roughly  $\frac{1}{50,000}$  aldehyde was found in the cell-sap (cf. also Mazé(18)).

Lastly, Mazé rules out direct oxidation processes as being responsible for the effect produced by desiccation. He dried some immature maize seeds in a vacuum and others in an atmosphere of  $\text{CO}_2$  and found that in both cases the effect produced was similar to that produced by drying the seeds in air.

Babcock(2), however, believes that the characteristic effect of drying in rendering immature seeds capable of immediate germination is to be traced to an increase in direct "respiration," since the same effect can be produced without drying by treating the seeds with hydrogen peroxide. He suggests that the change brought about in the seed by increased respiration is the liberation of diastatic enzymes, which, according to Babcock, are normally absent from immature seeds.

His experimental data are meagre. There seems to be no criterion to distinguish cause from effect.

In a recent communication (Kidd(15)) it has been shown that the testa may play an important rôle with regard to the germination of immature or unripe seeds. In the case of *Brassica alba* and *Pisum sativum* it was found that the removal of the testa not only accelerated germination in the same way as drying, but also increased the germination percentage of unripe seeds as is shown in the following Table III. It is clear that the rest-period observed when attempts are made to germinate green immature seeds may be largely attributed to the presence of the living testa which, in the author's opinion, functions by limiting gaseous exchange to the embryo<sup>1</sup>.

Although the point has not been fully investigated, the results so far obtained tend to show that there is no inherent rest-period in the developing embryo itself. Recent observations of Duggar(6) may be mentioned in this connection.

<sup>1</sup> The testa dies during the process of drying and its character as a membrane is thereby completely changed.

TABLE III.

*Brassica alba.*

*Lot I* consisted of 10 immature seeds.

*Lot II* consisted of 10 bare embryos from similar seeds.

*Set on damp sand.*

	Number of germinations after					
	2 days	4 days	6 days	7 days	12 days	18 days
<i>Lot I</i>	0	0	0	0	1	2*
<i>Lot II</i>	0	0	5	10†	—	—

\* The remaining 8 ungerminated seeds finally died.

† Healthy plants.

*Pisum sativum.*

- A { *Lot I* consisted of 20 immature seeds.  
       *Lot II* „ 20 bare embryos from similar seeds.
- B { *Lot I* „ 20 less immature seeds.  
       *Lot II* „ 20 bare embryos from similar seeds.
- C { *Lot I* „ 20 seeds picked 10 days later.  
       *Lot II* „ 20 bare embryos from similar seeds.

*Set on damp earth and covered with a damp cloth.*

	Number of germinations after		
	5 days	10 days	11 days
A { <i>Lot I</i>	0	1 (19 dead)	—
<i>Lot II</i>	20	20 (18 vigorous plants)	—
B { <i>Lot I</i>	0	0 (all dead)	—
<i>Lot II</i>	20	20 (vigorous plants)	—
C { <i>Lot I</i>	—	—	10 (10 dead)
<i>Lot II</i>	—	—	20 (vigorous plants)

Duggar (*l.c.* pp. 387-8) states that “so far as ability to grow is concerned, no very narrow restrictions may be placed upon the stage of development of the seed, provided adequate and suitable nourishment can be given the young embryo. In a series of experiments recently carried out by the writer, whereby the young embryos were transferred from the developing seeds to sterile nutrient solutions, the results confirm the view that embryos thus treated are able to maintain themselves and sometimes able to develop mature plants.”

The question now arises as to whether there is any difference in final yield from immature seeds as compared with that from fully ripe seeds. We have at the outset to distinguish between:

A. Immature seeds not dried (*i.e.* sown immediately after harvesting) as compared with fully ripe seeds.

B. Immature seeds separated from the parent stalk immediately after harvesting and then dried as compared with fully ripe seeds.

• C. Immature seeds dried on the haulm after harvesting as compared with fully ripe seeds.

With regard to A no data have been found. In the case of B the question arises as to the effect of storage of the dry seed upon its potentiality. The general conclusion to be drawn from the experiments of numerous workers is clearly that immature seeds deteriorate much more rapidly than mature seeds when stored dry under similar conditions. For example, Hellriegel(12), working with rye, found the following percentages of germination after a period of dry storage of seeds harvested at different stages of maturity:

TABLE IV.

Stage of ripeness at which the seeds were harvested	Percentage germination
Contents of kernel watery	4.5
Milk stage	5.0
Dough stage	9.5
Yellow ripe stage	36.0
Dry ripe stage	84.0

And Nobbe(21), working with red clover, obtained the following results with ripe and unripe seeds respectively after 4 years' (*i.e.* 1870-1874) dry storage.

TABLE V.

A. Red Clover harvested in 1874 and tested in Dec. 1874.  
 B. „ „ „ 1870 „ „ Dec. 1874.

100 seeds were used in each experiment.

Kind of seed used	Percentage of germination after 13 days
A. Fresh seeds { Ripe	88
{ Unripe	48
B. 4-year-old { Ripe	58
{ Unripe	6

Nobbe obtained similar results with other seeds, for example, *Brassica Rapa* var. *biennis*.

The experience of the Copenhagen Seed Testing Station as reported by the Director(4) leads to the same general conclusion, namely, that ripe seeds retain their germinating capacity longer than seeds which are less ripe.

The complication introduced by the harmful secondary effect of dry storage upon immature seeds must have entered into such experiments as those carried out by Lucanus. Lucanus(17) conducted a very elaborate series of experiments with rye, harvesting his seed at five different stages of maturity and dividing each harvest into four divisions, viz.:

Seeds immediately removed from the head (Section I of Table VI).

Seeds dried in the ear (Section II of Table VI).

Seeds dried in the ear on the stalk (Section III of Table VI).

Seeds dried in organic connection with the entire plant, the roots of which were placed in distilled water (Section IV of Table VI).

The results (Table VI) showed that in garden soil rich in humus the various stages of maturity of the seed had little or no effect upon the *yield per plant* as shown in his table, but a better *total yield* was obtained from

TABLE VI.

1. *Seeds sown in garden soil rich in humus.*

60 seeds sown in each experiment.

Stage of ripeness at which the seeds were harvested	Total yield after 3 months' growth				Yield per plant after 3 months' growth			
	I.	II.	III.	IV.	I.	II.	III.	IV.
i. Seeds small, soft, and green. Straw not fully green	97 g.	719 g.	476 g.	617 g.	24.2 g.	15.3 g.	10.1 g.	15.8 g.
ii. Juice beginning to turn milky	13 g.	667 g.	685 g.	553 g.	13.0 g.	14.8 g.	14.5 g.	19.7 g.
iii. Juice thick and milky white. Straw still moderately green	86 g.	825 g.	785 g.	897 g.	12.3 g.	17.5 g.	14.5 g.	16.9 g.
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	370 g.	1010 g.	380 g.	907 g.	16.8 g.	19.0 g.	13.6 g.	15.1 g.
v. Seeds free in the glumes. ("Ueberreife")	795 g.	880 g.	875 g.	1142 g.	14.2 g.	15.0 g.	17.5 g.	20.7 g.

2. *Seeds sown in a poor sandy soil.*

60 seeds sown in each experiment.

	I.	II.	III.	IV.	I.	II.	III.	IV.
i. Seeds small, soft, and green. Straw not fully green	3.0 g.	25 g.	35 g.	42 g.	1.5 g.	0.5 g.	0.9 g.	1.3 g.
ii. Juice beginning to turn milky	5.0 g.	52 g.	69 g.	93 g.	1.2 g.	1.3 g.	1.8 g.	2.0 g.
iii. Juice thick and milky white. Straw still moderately green	8.0 g.	135 g.	134 g.	252 g.	2.0 g.	2.8 g.	3.3 g.	5.1 g.
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	82.0 g.	170 g.	90 g.	172 g.	3.9 g.	3.8 g.	6.0 g.	3.6 g.
v. Seeds free in the glumes. ("Ueberreife")	190.0 g.	117 g.	242 g.	145 g.	4.3 g.	3.0 g.	4.7 g.	3.3 g.

the riper seeds; this result was due to the larger percentage of germination in the case of the ripe seed.

In a parallel series of growth experiments conducted in very poor sandy soil, however, an effect of the degree of ripeness of the seed under these unfavourable growth conditions became visible in the yield per plant as well as in the total yield, better plants on the whole being produced from seeds gathered in the later stages of maturity.

The results obtained by Lucanus are borne out by those of Nowachi (22) with winter wheat grown in the field. Unfortunately his paper does not make it clear whether the immature seeds used by Nowachi which were not after-ripened (*i.e.* which were not allowed to dry off in organic connection with the parent-plant after harvesting) were sown green, or whether they were allowed to dry before sowing as was the case in the experiments conducted by Lucanus. His results, however, appear to show that the plants produced from the immature seeds were quite as good as those produced from the fully ripe seeds. In fact, the figures given in his table (Table VII) point to their being better.

It is seen that Nowachi found very little difference in the germination percentages.

The results of Lucanus and of Nowachi referred to above introduce the third point to be considered in discussing the question of immature seed. How far does the process of drying-off in organic connection with the parent-plant have any effect upon the "potentiality" of the

seeds owing to the transference of food-material from the haulm allowing them to advance a stage in maturity? Looking at the figures for yield per plant given in Table VI no important difference can be detected; this is not surprising in view of the fact that practically no difference is observable in yield per plant between plants from fully ripe and those from the most immature seeds.

TABLE VII.

Stage of ripeness at which the seeds were harvested	Average number of ear-bearing haulms		Average weight per plant		Germination percentage	
	I.	II.	I.	II.	I.	II.
Milk ripe (seeds still enclosed in the glumes; contents of seeds milky)	7.7	7.5	66 gms.	63 gms.	84	100
Yellow ripe (seeds yellow, shining; contents of seeds doughy)	5.4	5.2	44 gms.	44 gms.	100	98
Fully ripe	5.9	5.5	41 gms.	39 gms.	100	100
Dead ripe	5	—	43 gms.	—	98	—

I. Seeds, which were not after-ripened.

II. Seeds, which were dried on the haulm.

With regard to germination, on the other hand, the results obtained by Lucanus (Table VIII) certainly show that the immature seeds dried off in organic connection with the haulm retain their capacity for germination far better than those separated from the parent-plant before drying, except, of course, in the case of the fully ripe seeds<sup>1</sup>.

Turning to the more recent investigations planned to determine whether the use of somewhat immature seed is to be recommended as an agricultural practice, we find that from the available evidence no good case can be made out in its favour.

Georgeson, Burtis, and Shelton (10) compared the yield from ripe wheat seed with that from seed harvested in the milk stage and found that the immature seed yielded 19.75 bushels of grain and 0.80 ton of straw per acre as compared with 22 bushels of grain and 1.04 tons of straw per acre produced from the mature seed. With oats, however, the same investigators (9) found that seeds harvested in the dough stage gave the best results, their figures being as follows (Table IX):

<sup>1</sup> Both Lucanus (16) and Nowachi (22) worked out elaborately the differences in weight and the detailed changes in contents which occur during the process of drying-off in seeds separated from the haulm immediately after harvesting as compared with those which take place in seeds allowed to dry off attached to the parent-plant.

TABLE VIII.

1. *Seeds sown in garden soil rich in humus.*

100 seeds sown in each experiment.

Stage of ripeness at which the seeds were harvested	Germinations			
	I.	II.	III.	IV.*
i. Seeds small, soft, and green. Straw not fully grown	6	82	85	67
ii. Juice beginning to turn milky	4	77	85	48
iii. Juice thick and milky white. Straw still moderately green	13	82	86	92
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	37	88	50	100
v. Seeds free in the glumes. ("Ueberreife")	95	97	84	92

2. *Seeds sown in a poor sandy soil.*

100 seeds sown in each experiment.

	I.	II.	III.	IV.*
i. Seeds small, soft, and green. Straw not fully grown	3	80	70	55
ii. Juice beginning to turn milky	6	67	70	77
iii. Juice thick and milky white. Straw still moderately green	6	82	71	82
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	35	80	27	82
v. Seeds free in the glumes. ("Ueberreife")	73	72	92	77

\* The columns I, II, III, and IV correspond to those shown in Table VI.

TABLE IX.

Stage of ripeness at which the seed was harvested	Yield in bushels per acre
Seed in the dough stage	38.99
Seed in the hard dough stage	28.68
Seed ripe	26.66

Zavitz<sup>(24 & 25)</sup> gave the average results of five years' experiments with winter wheat in which the yield obtained from seed which was allowed to become thoroughly ripened before it was harvested was compared with that obtained from seed harvested at various stages of immaturity. The thoroughly ripened seed gave a better yield both of grain and of straw and a heavier weight of grain per measured bushel than that produced from grain harvested at either of the earlier stages of maturity.

The results of Kedzie's<sup>(14)</sup> experiments quoted by Duggar, in which the seeds used are characterised as having been harvested in the "milky juice," "dough," "full yellow ripe," and "dead ripe" stages respectively<sup>1</sup>, showed the marked superiority of the ripe seed as compared with the unripe (Table X), and indicated that a slight advantage accrued from the use of the yellow ripe as compared with the use of the dead ripe seed, the yield being 30 bushels per acre from the former as against 28 bushels per acre from the latter.

TABLE X.

Stage of ripeness at which the seed was harvested	Yield per acre (in bushels)
Milky juice stage	11
Dough stage	25
Full yellow ripe stage	30
Dead ripe stage	28

Goff<sup>(11)</sup> in an experiment with Indian Corn extending over a period of five years found that the largest yields of corn and stalk were obtained from corn gathered slightly immature, and Tracy<sup>(23)</sup> bears this out in the case of Sweet Corn in a paper, dealing with the production of vegetable seeds, in which the conclusion is reached that for seed purposes the crop should be harvested as soon as the grain has fully passed into the dough condition. Goff found that the use of very immature seed gave smaller yields of corn and stalks, but slightly earlier maturity than fully mature seed.

The scanty results which have been recorded in the case of plants other than cereals with reference to the influence upon subsequent growth and yield of the use of immature seeds as compared with fully ripe seeds, appear to bear out the same general conclusions. Immature seeds germinate badly (probably due to changes during storage). They give rise to seedlings which may be in the first place less vigorous than those produced from mature seeds. But the resulting plants at a later stage differ very slightly from those arising from mature seed. The experiments of Arthur<sup>(1)</sup> and of Goff<sup>(11)</sup> with Tomatoes, in which a closer analysis of the growth and yield was made than in the case of cereals, indicate that the use of immature seed leads to an increase of reproductive parts in proportion to the vegetative parts. A greater number of fruits and seeds, but individually smaller and more rapidly ripening, were borne on the plants from immature seed.

<sup>1</sup> Janson<sup>(13)</sup> records in detail the changes which take place in the seed-reserves of oats and barley at different stages of maturity.

## THE "POTENTIALITY" OF THE SEED AS INFLUENCED BY THE WEATHER CONDITIONS AT THE TIME OF HARVESTING.

Nothing of a definite nature from the point of view of physiological pre-determination can be stated in this connection as there are no critical observations available. The general effect of dry climatic conditions during the maturation and harvesting of the seed crop will be to hasten maturity. Districts which have been found most valuable for industrial seed-production are those in which uninterrupted dry weather conditions prevail during late summer and far into the autumn. Wet weather conditions during maturation and at the time of harvesting will obviously not only affect the degree of maturity of the seed, but will also be unfavourable for gathering and storing the crop.

It has been shown repeatedly (*e.g.* Duvel(7); Dorph-Petersen(5)) that the deterioration of seeds during storage runs parallel to the percentage of moisture in the air-dry seed. A slight difference in the amount of water present in the air-dry seed at the time of storing causes marked differences in its subsequent germination capacity, the lower water-content being in the majority of cases the best.

Duvel's(7) conclusion is that the deterioration of seeds in dry storage is due to oxidations (*cf.* also Babcock(2); Becquerel(3), and others). The amount of CO<sub>2</sub> produced by seeds stored air-dry can be correlated with their percentage moisture-content and with the loss of vitality subsequently observed.

## CONCLUSIONS.

A consideration of the results reviewed above makes it clear that the question as to whether differences in the resulting plant are pre-determined by the use of seeds differing in degree of ripeness cannot be regarded as satisfactorily answered in the case of any single species.

This is due to the fact that all the recorded comparisons between plants grown from immature seeds and plants grown from mature seeds appear to have been complicated by some period of storage. Immature seeds are less tolerant of storage in the dry condition than mature seed, so that in the case of the comparisons which have been made, the total yields from immature seeds are usually less than those from mature seeds owing to the fact that a smaller percentage of the immature seeds germinate.

When in such experiments comparisons are made between yield per plant, however, the difference in favour of the plants from mature seeds

tends to disappear or even to be reversed. This result may be significant, but it must be remembered that while the yield per plant in the case of the mature seeds represents an average based on a whole population (*i.e.* both vigorous and weak plants), the yield per plant in the case of the immature seeds, on the other hand, probably represents an average based on the more vigorous members of the population only, the others having perished during storage in the seed stage.

From the point of view of the grower seed harvested at a stage somewhat previous to maturity may, under certain conditions, give a better yield than seed allowed to become dead-ripe upon the parent-plant; but it must be borne in mind that immature seed does not withstand storage as well as seed which has been allowed to become fully ripe, so that—as a general practice—the use of immature seed is not to be recommended.

(*To be continued.*)

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## THE STRUCTURE, BIONOMICS AND FOREST IMPORTANCE OF *CRYPHALUS ABIETIS* RATZ.

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AMONGST systematists who have worked on the Scolytid or bark-boring beetles there are great differences of opinion as to the limits of the genus *Cryphalus*. Following Fowler<sup>1</sup> the genus comprises 24 different species which are widely distributed throughout the world. In his *Coleoptera of the British Isles* he records six different species some of them amongst the smallest of our indigenous beetles. All of them are of economic importance in forestry. Of our native species two, *Cryphalus abietis* Ratz. and *Cryphalus piceae* Ratz., choose as their hosts coniferous trees; the others are found on broad-leaved species.

Till quite recently these two coniferous species were considered rare in Britain but the increasing number of records of *C. abietis* in Scotland makes it no longer possible to describe this beetle as rare.

In view of new schemes of afforestation it is urgent that we should have exact information on the relative forest importance of the various insect enemies of trees. Further, for purposes of intelligent control a knowledge of the species in its various stages and of its life-history and habits is necessary. With these principles in view the following research on *C. abietis* was undertaken.

The research is based on an investigation of its life-history and habits, carried out by means of observations and control experiments, conducted in the open at Aboyne, Aberdeenshire, and Banchory-Devenick, Kincardineshire, and of a series of anatomical studies and breeding experiments made in the laboratory at Edinburgh University on and with material collected in the woods in the vicinity of the places named above and in the neighbourhood of Edinburgh.

Following Fowler the genus *Cryphalus* possesses the following characters: (1) eyes entire or slightly emarginate, (2) antennae with the sutures of the club distinctly marked, the club itself being somewhat variable in shape, (3) thorax tuberculate in front, margined at base,

<sup>1</sup> Fowler's *Coleoptera of the British Isles*, v, 428-430.

(4) scutellum small punctiform, (5) elytra not excavate at apex, clothed with a scale-like pubescence and sometimes in addition with fine raised hairs.

DESCRIPTION OF *C. ABIETIS* RATZ.

The following is Fowler's<sup>1</sup> description:

*C. abietis* Ratz. (Fig. 1). Oblong, subcylindrical, compressed and very convex: fuscous or fuscous-brown, dull, antennae and legs reddish-

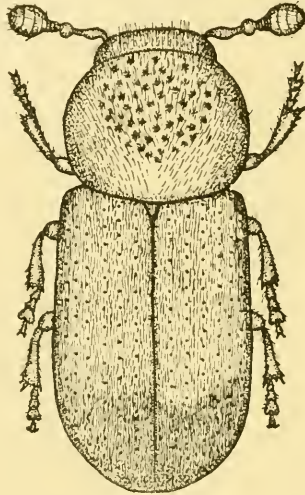


Fig. 1. Adult of *Cryphalus abietis* Ratz. (greatly magnified).

brown, club of the former usually darker, rounded at apex: thorax subglobular, very finely punctured at sides and behind, front part confusedly granulate: elytra rather more than double as long as thorax with distinct punctured interstices, covered throughout with extremely short scale-like hairs, and also very diffusely with short crect hairs, which are wanting behind: the colour of the antennae and the legs is somewhat variable: the species may easily be recognised by the tubercles on the anterior portion of the thorax being few in number and irregular in their distribution and by the regular comparatively strong rows of punctures and very short pubescence of the elytra. Length 1-2 $\frac{3}{4}$  mm.

My own examination of numbers of *C. abietis* leads me to emphasise the following characters:

(1) Club of antennae rounded at apex, antennal funicle four-jointed (Fig. 2).

<sup>1</sup> Fowler's *Coleoptera of the British Isles*, v, 431-432.

(2) Tubercles on prothorax irregular in distribution (not in concentric circles) and wide apart.

(3) Elytra covered with very short scale-like hairs, their interstices with a diffuse row of short erect hairs, which are absent on the apical parts.

From the measurement of a large number of specimens of various origin I find the average length to be 1.75 mm.

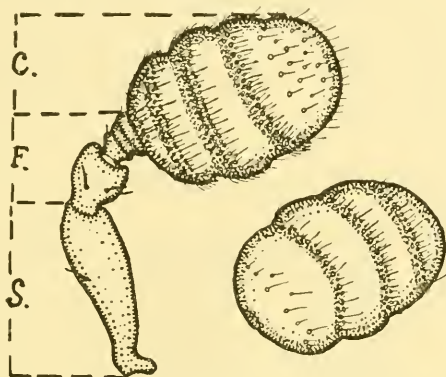


Fig. 2. Antenna of *Cryphalus abietis* Ratz. Posterior face of club is shown on the right (both greatly magnified). C. = club; F. = funicle; S. = scape.

#### SEXUAL DIFFERENTIATION IN *C. ABIETIS*.

There are no reliable external differentiating sex-characters although sometimes the female is slightly larger than the male.

Owing to the close resemblance in feeding habits, similar size, and external naked eye appearance of *C. abietis* and *C. piceae*, these two species may be readily confused.

I have compared by aid of the binocular microscope my *C. abietis* with *C. piceae* from Central Europe in Dr Stewart MacDougall's collection and give in tabular form the outstanding differences between the two beetles.

##### *C. abietis*

Tubercles on prothorax irregular in their distribution (not in concentric circles) and wider apart.

Sides and posterior margin of prothorax bear no marked greyish-white hairs.

Interstices of elytra covered throughout with scale-like hairs, and each has a row of diffuse short erect greyish-white hairs which are absent on the apical parts.

##### *C. piceae*

Tubercles on prothorax fairly regular in their distribution (in concentric circles) and closer together.

Sides and posterior margin of prothorax bear long raised greyish-white hairs.

Interstices of elytra covered with a few scale-like hairs and each has a row of long, raised, greyish-white hairs, which are most marked on the lateral margins and apical portions of the elytra.

EGG OF *C. ABIETIS*.

The egg is oval in shape, whitish in colour, translucent; and has a smooth shiny surface. The egg measures about .6 mm. in length and a little less than .3 mm. in breadth.

LARVA OF *C. ABIETIS* (Fig. 3).

The larva, in general appearance, is typically Scolytid. It is a soft legless grub, with a curved body. The colour of the larva is yellowish-white save the hard chitinous head and mouth-parts which are darkish brown. The body is much wrinkled, with fine hairs scattered over it.

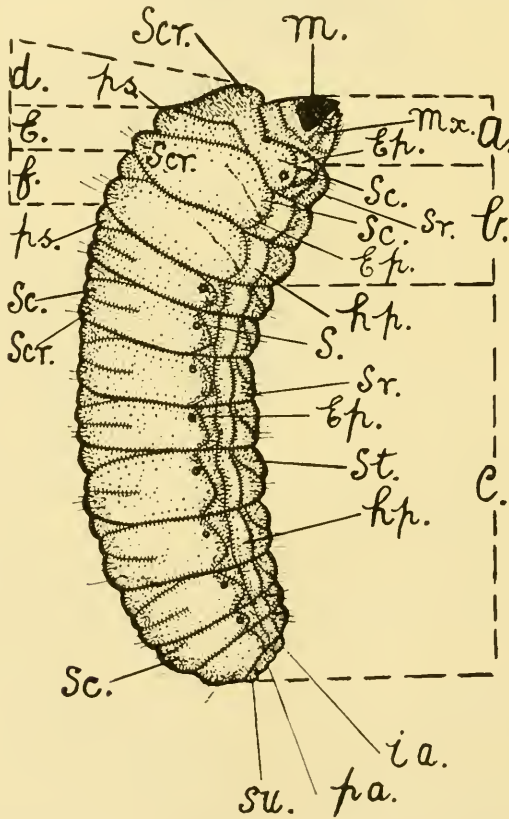


Fig. 3. Larva of *C. abietis*, side view (greatly magnified).

The larva is made up of the oblong chitinous head-piece—two-thirds of which is retractile within the first body segment or prothorax—and thirteen distinct body segments. The first three body segments form the

thorax, the other ten the abdomen. The thoracic segments are larger than the abdominal ones. The first segment of the thorax is more flattened dorsiventrally than the others and bears on its dorsal surface a rectangular patch covered with a felt of fine reddish-brown hairs. The 8th and 9th abdominal segments are much smaller than the others. In a ventral view (Fig. 7) the 10th or last segment is seen to consist of four distinct lobes around the anus. Spiracles, circular in shape, are present on the first thoracic segment and the first eight abdominal ones. The length of the full-grown larva is, on an average, 2.25 mm.

#### HEAD OF LARVA (Fig. 4).

With the aid of a binocular microscope the following parts can be made out in a dorsal view,

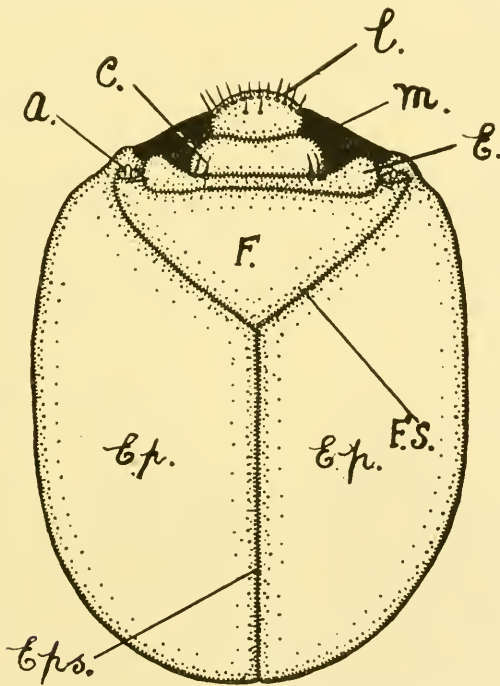


Fig. 4. Head of larva of *C. abictis* seen from above (greatly magnified).

Most anteriorly lies the labrum (*l.*) or upper lip which bears a number of fairly strong bristles on its front margin. Posterior to the labrum lies the clypeus (*c.*) while still further back may be seen the epistome (*E.*), a thickened band of chitin carrying a few strong bristles and forming a

support to the clypeus. At each end of the epistome lies a single-jointed antenna (*a.*) sunk in a pit. In each pit, externally to the antennae four chitinous bristles are usually placed. These details are more clearly shown in the enlarged view of the epistomal region (Fig. 5). In this figure *Ep.* stands for epistome.

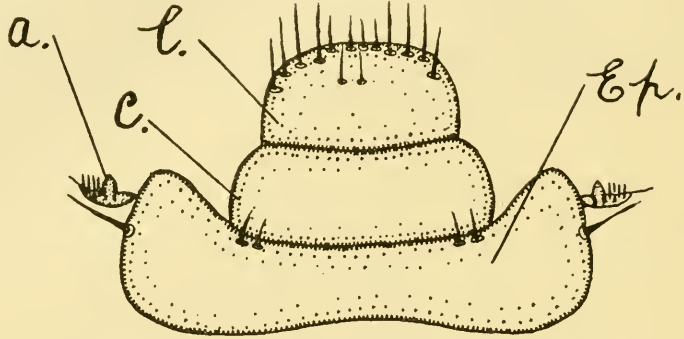


Fig. 5. Region of epistome of *C. abietis* larva (greatly magnified).

Posterior to the epistome and adjacent to it lies a triangular area, the frons (*F.*), bounded on each side by the frontal sutures (*F.S.*). On each side of the frontal sutures lies the epicranium (*Ep.*), a large area which occupies the greater portion of the surface of the head. The epicranium in turn is divided posteriorly into two parts by the epicranial suture (*Ep.s.*).

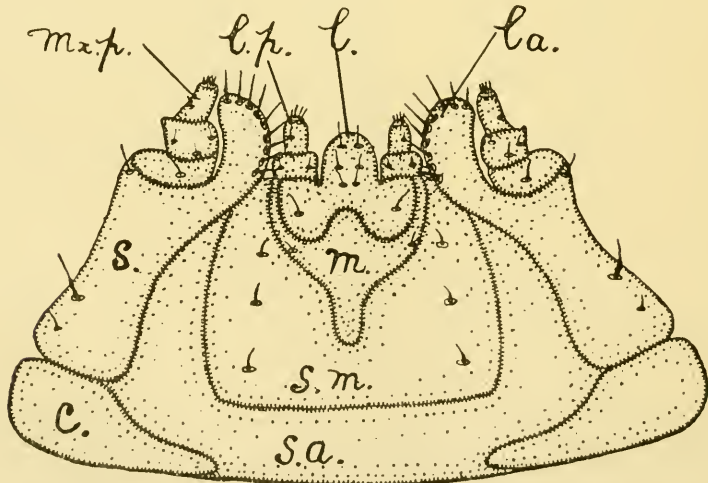


Fig. 6. Maxillae and labium of larva of *C. abietis* (greatly magnified).

On each side of the labrum and partly overlapped by it, are the mandibles. Each mandible (*m.*) is dark brown in colour, highly chitinized and bears three teeth, the posterior one being the smallest.

On the ventral aspect of the head lie the maxillae (Fig. 6).

1st Maxillae: These lie one on each side of the labium and are composed of the usual three parts: posteriorly the cardo (*c.*), more anteriorly the stipes (*s.*), bearing a three-jointed maxillary palp (*mx.p.*) and a few scattered bristles, and thirdly the lacinial lobe (*la.*) which has a number of stout chitinous bristles on its outer margin.

2nd Maxillae: In the centre of the field lies the labium or fused 2nd maxillae, made up of the mentum (*m.*) with two labial palps (*l.p.*) each two-jointed and with the ligulae (*l.*) lying between them. Posterior to the mentum is the submentum (*s.m.*), often indistinct from the submental area (*s.a.*) which lies still further back.

#### THE THORAX (Fig. 3 *b*).

The thorax of the larva is made up of the usual three segments, namely the prothorax, lying behind the head, the mesothorax, and the metathorax.

In a side view of the prothorax (Fig. 3 *d*) one can make out the following five folds: the scutellar (*scr.*) forming the dorso-lateral portion and bearing the rectangular patch of fine hairs already referred to; the scutal (*sc.*) bearing a spiracle on its most ventral portion; the epipleural (*ep.*) and the hypopleural (*hp.*) forming the lateral portion (the two last-named folds are more ventral than the first); the sternellar (*sr.*) forming the ventral portion.

The mesothorax (Fig. 3 *e*) in side view shows six folds: the prescutal (*ps.*) forming the anterior dorsal portion: the scutellar (*scr.*) forming the dorso-lateral portion: the scutal (*sc.*), epipleural (*ep.*) and hypopleural (*hp.*) forming the lateral portion; the sternellar (*sr.*) forms the ventral portion. There are no spiracles borne by the mesothoracic segment. The metathoracic segment (Fig. 3 *f*) is similar to the mesothoracic in structure and is of a corresponding size and shape.

#### THE ABDOMEN (Fig. 3 *e*).

The first seven abdominal segments are similar in structure although they vary in size. In side view each segment shows seven folds: the prescutal (*ps.*), scutal (*sc.*) and scutellar (*scr.*) form the dorso-lateral portion; the epipleural (*ep.*) and the hypopleural (*hp.*) form the lateral portion: while the sternal (*st.*) and the sternellar (*sr.*) form the ventral portion. On each segment, between the epipleural (*ep.*) and the scutal

(*sc.*) and scutellar (*scr.*) folds there is a deep crescent-shaped hollow or groove; on the anterior dorsal side of this groove lies a spiracle (*s.*).

The 8th abdominal segment, in side view, shows a similar composition to the first seven segments except that the prescutal and the scutellar folds are just traceable. The 9th abdominal segment is similar to the 8th except that the prescutal fold is absent and there are no spiracles. The 10th segment, in side view, shows three lobes surrounding the anus: the infra-anal lobe (*ia.*) situated ventral to the anus; the supra-anal (*su.*) dorsal and the para-anal (*pa.*) between the above two.

Looking at the larva from the ventral side (Fig. 7) two other folds may be seen on the thoracic segments, namely the sternal (*st.*) and the poststernellar (*ps.*).

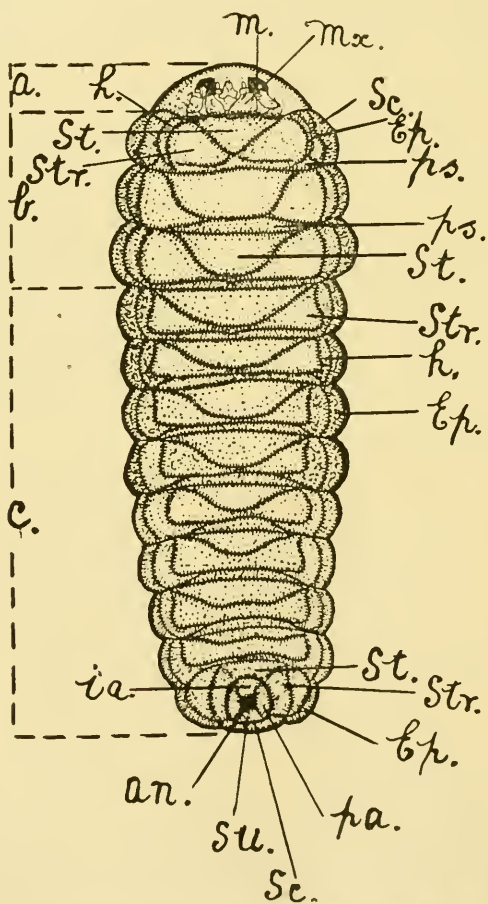


Fig. 7. Ventral aspect of larva of *C. abietis* (greatly magnified).

In a ventral view of the abdomen (Fig. 7 *c*) one other fold, namely the poststernellar, is discernible in addition to those already seen in the side view. The poststernellar fold is present in all the abdominal segments except the last three: in the 8th and 9th it is absent: in the 10th both poststernellar and sternal folds are wanting. In this figure *Str.* stands for sternellar fold and *h.* for hypopleural fold.

#### THE PUPA OF *C. ABIETIS*.

At first the pupa has the general colour of the larva but soon darkens, the mandibles being the first of the appendages to reveal themselves as two brownish patches.

In a dorsal view of the pupa the main divisions of the body are visible. On the vertex or front portion of the head one can make out a few frontal spines. These are fairly conspicuous and are widely separated.

On the sides of the pronotum may be seen a few scattered spines. Lying at the base of the elytra is the scutellum which is easily distinguishable.

Rows of dorsal and pleural spines are absent on the dorsal and lateral surfaces of the abdominal segments, a noteworthy feature as these spines are usually present on the corresponding parts of many Scolytid pupae.

On the ventral aspect of the pupa the usual appendages on the several divisions of the body can be made out. On the head portion the antennae and at the base of the antennae the eyes; lying posteriorly the gena or cheek region between the antenna and the labrum; mandibles, 1st maxillae and labium are also distinguishable.

The legs are folded along the surface of the body, the last pair for the most part obscured from view by the overlapping elytra. On the abdomen only the last few segments are visible in the ventral view; the 9th bearing two prominent fleshy projections or spines is the most conspicuous one. The presence of these spines is characteristic of Scolytid pupae.

On each side of the body lies an elytron or wing cover from under which projects the tip of a flying wing.

#### THE BROOD GALLERIES OF *C. ABIETIS* (Fig. 8).

In some of our bark-boring genera the parent beetles make a comparatively straight strong burrow or mother gallery. Unlike these the typical mother gallery of *C. abietis* rather takes the form of a circular burrow which is cut or gnawed round the base of a branch or twig. If

the branch round which the burrow is cut happens to be a fairly strong one it may be only partially eaten round. On the other hand, if the branch be weak, as is very often the case, the burrow completely girdles the branch. The length of the gallery varies. When the mother gallery is short it is broader, when long it is usually narrower. On an average the distance between the beginning of the mother gallery and its termination, measured along its course, is about  $\frac{3}{4}$  inch in length, while in breadth it measures from  $\frac{1}{8}$ – $\frac{3}{16}$  inch.

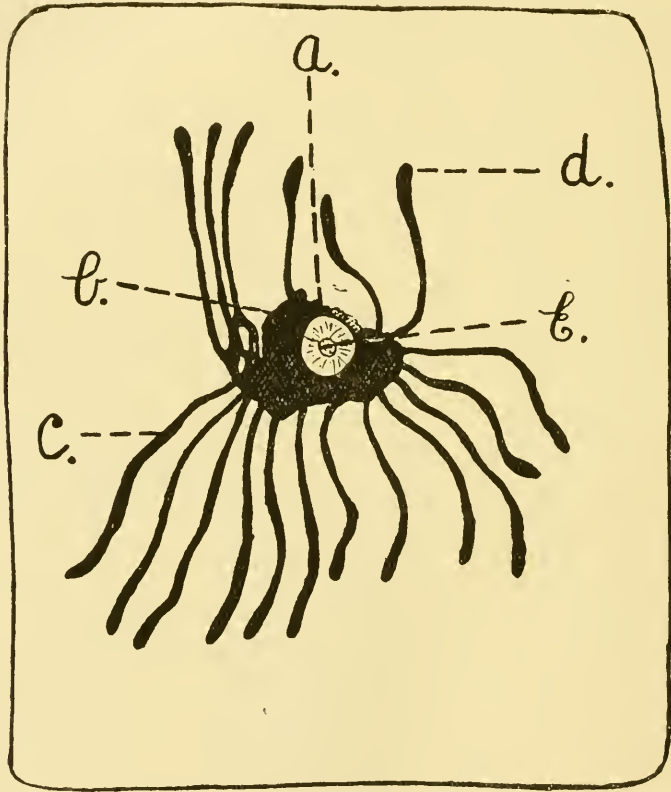


Fig. 8. Typical brood galleries of *C. abietis* on a branch of Silver Fir (*Abies pectinata* D.C.). Note how the mother gallery is cut round a smaller branch (*E.*). *a.* = beginning of mother gallery; *b.* = mother gallery widened in parts through the feeding of the young larvae; *c.* = larval gallery; *d.* = pupal bed; *E.* = base of smaller branch round which mother gallery is cut.

The larval galleries naturally run almost at right angles to the mother gallery, radiating out from it on all sides. Some of these larval galleries

run vertically upwards along the main branch, others run vertically downwards, while others run obliquely. Very frequently the larval galleries run along the branch or twig the base of which has been girdled by the mother gallery. The larval galleries, like the mother galleries, vary considerably in length. The shortest one I have measured was about  $\frac{1}{2}$  inch in length, while the longest was about  $1\frac{1}{2}$  inches.

As is usually the case in monogamous species of Scolytids the female does all the work in the cutting of the mother gallery, right from the entrance hole to its terminating point. In a few cases, however, prior to the disappearance of the female underneath the outer bark I found the male cutting a separate hole close beside her, evidently feeding on the gnawed material. As soon as the female had made a burrow long enough to accommodate herself underneath the bark the male at once repaired to her aid and helped her to widen the mother gallery, following her closely, gnawing first at one side of the gallery then at the other. The chief work of the male however is to throw to the outside of the entrance hole of the gallery the fine bore dust, shovelling it out with his legs. The sexes meet on the surface of the bark.

In many genera of Scolytids, *e.g.* *Myelophilus* and *Tomicus*, the eggs laid by the female are deposited in notches cut by her, as she bores, at more or less regular intervals along both sides of the mother gallery. In the case of *C. abietis* the eggs are laid irregularly and no notches are cut by the female; in fact the eggs usually occur in batches. In some cases I found that the female after she had cut a part of the burrow turned back towards the entrance hole and then laid four eggs; after she had laid this set of eggs she again proceeded to tunnel her gallery, returning after a time to lay another set of eggs. The female lays from 14 to 24 eggs and takes from 5 to 7 weeks to complete her gallery.

The larvae when hatched burrow irregularly for some time, eating along the sides of the mother gallery and usually altering its shape. As a result it is often impossible to determine the original shape of the mother gallery after the eggs have hatched. After boring along the sides of the mother gallery for some time the larvae separate and each gnaws a separate burrow in the inner bark layers, feeding on the gnawed material. This gnawed material is passed through the alimentary canal and the undigested waste material fills the burrow behind the larva.

The mother galleries never penetrate the sapwood but show on the inner bark layers. The young larvae while feeding in their tunnels do not cut the sapwood but for some time prior to pupation they often do groove the sapwood. In other cases the larvae do not groove the

sapwood at all until about to pupate when they invariably cut a pit or bed in the outer surface of the sapwood. This bed or pit excavated by larvae about to pupate lies in no constant direction. Sometimes it may be in the vertical direction, at other times horizontal, and at others oblique.

Thus when a piece of bark is removed from an infested branch the brood galleries cannot be traced on the sapwood at all. As a rule one can trace only that portion of the larval galleries which was cut previous to pupation and the pupal bed or pit on the exposed wood surface. While this is the typical occurrence other appearances are possible. For example, in further observations I noticed that when the bark was somewhat thick, as in the case of strong branches, the larval galleries often did not groove the sapwood at all and usually on these branches pupation took place in the bark. Where the bark was thin on the other hand, as on twigs and on small branches, the larval galleries throughout their entire length grooved the sapwood deeply while the pupal beds in such places were very marked on the surface of the sapwood. As a result when the outer bark was removed from an infested branch with fairly thick bark only the pupal beds could be traced. While if this same operation was performed on an infested twig or weak branch when the bark was thin the larval galleries and pupal beds could easily be traced on the wood surface.

After the period of pupation has passed the young imagos first feed on the patches of the inner bark which surround their pupal beds and then finally bore to the outside through the bark and issue by the small exit holes.

As I point out later in this paper the parent beetles do not all die after egg-laying but in many cases feed anew prior to a possible second egg-laying. I have frequently found these old parent beetles after their egg-laying has been completed cutting galleries which resembled in shape and in direction larval ones.

#### IRREGULAR GALLERIES.

Overcrowding of both mother and larval galleries is not uncommon and takes place on badly infested stems and branches (Fig. 9) with the result that the galleries may be very irregular both in shape and in direction. In many cases it is extremely difficult or impossible to trace, in the confused workings, individual galleries. As a rule on badly infested branches the larval galleries are much shorter than those found on not so badly attacked ones. As a common instance of overcrowding we

may take the case figured here, where the bases of two branches of the same whorl have each been girdled by mother galleries. Here the larval



Fig. 9. Piece of branch of Silver Fir with irregular brood galleries of *C. abietis* due to overcrowding. A side view is shown of the bases of two small branches which have been girdled by mother galleries—represented in the figure as dark projecting portions one on each side of the main branch. Note how the larval galleries arising from the mother galleries have intermingled and so have completely girdled the main branch. The original shape of the mother galleries is here obliterated completely by young larval galleries (dark patches on the main branch) running together; later the larval galleries separate, running upwards and downwards on the main branch.

galleries which arise from each set of mother galleries usually intermingle and as a result completely girdle the main branch. Further in such cases (see figure) it is quite impossible to determine from which set of mother galleries the larval ones arise.

Even more confused workings than the above example are quite common. For instance, where two or more females have chosen the same axil of the branch or twig for brood purposes, the entrance holes of the mother galleries are very near to one another, which leads to

great confusion of mother galleries and larval galleries. The galleries in such cases intersect each other in all directions, forming a network underneath the outer bark layer.

Again where the bases of branches of a whorl have already been badly infested by beetles other parent beetles may commence boring brood galleries on the main branch between the whorls. This occurrence is very common on badly infested stems and branches and leads to still greater confusion of brood galleries.

An exceptional irregularity was found where a number of males and females had used the same entrance hole from which to bore their galleries. Each pair of parent beetles entered underneath the bark by this common entrance hole and immediately proceeded to make a separate mother gallery. These mother galleries radiated out in all directions from the common entrance burrow (see Fig. 10). I have taken as many as five pairs of beetles from such a set of galleries.

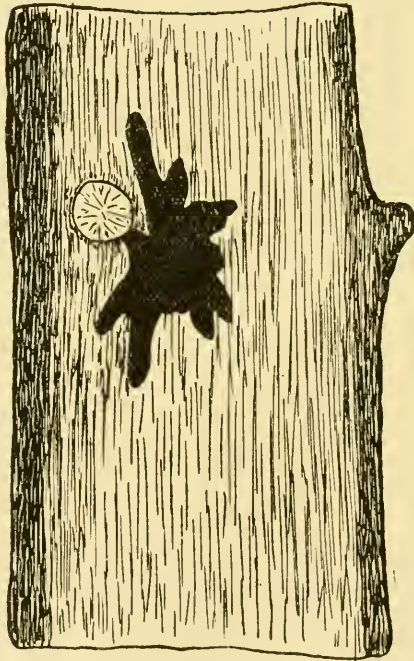


Fig. 10. Irregular mother galleries (not finished) on a piece of Silver Fir stem.

In dealing with the brood galleries of *C. abietis* it is quite impossible in most cases to trace either mother or larval galleries on the removal of the outer bark.

Instead one usually finds all the inner bark layers converted to dust by the work of parent beetles and their larvae. The best way to ascertain the shape of a typical mother gallery is to dissect the gallery immediately after the female has completed her egg-laying and before any of the eggs have hatched. To trace the larval galleries accurately it is essential in most cases to follow up the larvae as they tunnel their respective galleries.

#### LENGTH OF LIFE-CYCLE IN A SINGLE GENERATION.

Many observations repeated under different conditions proved to me that the period of the life-cycle from the laying of the egg to its culmination in the adult stage was extremely variable. The time varied according to the season of the year at which the eggs were laid, the quality of the food material, and the position of that material with relation to the sun: and consequently the environmental temperature.

In the vicinity of Aboyne, Aberdeenshire, field observations were carried out in early April, 1917, in Silver Fir woods badly infested with *Cryphalus abietis*. Careful examination was made of all likely places for females to have chosen for new brood galleries but no adults were found at work. The weather up to this time had been exceptionally unfavourable.

On the 28th September, 1916, however, I had collected some badly infested material consisting of branches and twigs from these same Silver Fir woods. Examination of this material at the time of collection showed that *Cryphalus abietis* was present underneath the bark layers in exceedingly large numbers both as immature fresh young adults and as larvae. This badly infested material—referred to later in this paper as my “stock material”—was kept in the open air throughout the winter months and examined at intervals. On the 20th of April, 1917, one adult issued. Several more adults issued up to 27th April, 1917. Some of these were killed and dissected for the study of their reproductive organs but 50 others were liberated in a muslin bag containing a few branches of Silver Fir and Spruce. These branches had been paraffined at their cut ends to keep them from becoming too dry. This bag was then closed and placed in the open air. Three days later, *i.e.* on 30th April, 1917, the branches in the bag were carefully examined. Some females had just commenced to bore into the Spruce and Silver Fir branches and in a number of cases the male beetle was found resting on the surface of the bark close by the female.

In another experiment carried out in a similar method and under similar conditions 60 adults were liberated on May 2nd, 1917. Dissections of many mother galleries were made at intervals with a view to collecting all the data possible on the making of the gallery and the egg-laying.

In one dissection made 16 days after the commencement of the gallery I found one egg laid while in another four eggs were laid by the end of a month.

The incubation period of the eggs was on an average 10 days. Large numbers of adults continued to escape from my "stock material" up to June 15th, 1917.

The time taken by the parent beetles to bore the mother gallery varied from 5 to 7 weeks.

Some larvae fed for 69 days and then pupated, the pupal period lasting about 29 days.

Thus in the case of eggs laid on June 4th, 1917, *i.e.* a month after the commencement of the mother gallery, the total period until the imago stage was reached on September 21st, 1917, was 108 days.

In my control experiments in natural conditions, some badly infested Silver Fir branches in the woods at Aboyne examined on June 26th, 1917, were found to contain hundreds of eggs of *C. abietis* and in many cases the females had not yet completed their egg-laying. These branches were examined at intervals throughout the summer and the length of the various stages was found to be as follows, *viz.* egg on an average 10 days: larva 71 days: pupa 22 days. That is to say the life-cycle from the egg stage at the end of June to the adult stage on September 27th was 93 days.

While in the above cases many individuals of the same brood reached the adult stage in the average period, quite a number of others were still in the larval stage at the end of September, 1917, and hibernated as larvae.

As showing the variations found in the length of the life-cycle I have set out in the following diagrams the life-cycles which I met with in my control experiments and in the open.

*Diagram A.*

	+ = adult. • = egg. - = larva. ○ = pupa.											
Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	+ •	- -	- -	- ○	○ +	+	+	+
1917	+	+	+	+	+ •	• -	-	- ○	○ +	...	...	...

*Diagram B.*

This diagram is for comparison with Diagram A showing the possible development of the last laid eggs of the same beetles.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	++	•	-	-	-	-	-	-
1917	-	-	-	-	-	○○	++	...	...	...	...	...

*Diagram C.*

Life-cycle found where the brood material was lying under dense shade and hence summer temperature low—here whole of young brood hibernates as larvae.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	+•	•-	-	-	-	-	-	-
1917	-	-	-	-	-	○○	+	+	+	...	...	...

Length of life-cycle, egg to adult, here is about  $11\frac{1}{2}$  months.

*Diagram D.*

Exceptional case in length of life-cycle—here brood material was of poor quality and in dense shade.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	...	...	+•	•-	-	-	-	-
1917	-	-	-	-	-	-	-	-	...	...	...	...

From the diagrams it will be seen that the length of the larval period is extremely variable. In the typical life-cycle it is from 69 to 71 days, whereas where the beetles hibernate as larvae it may be about  $11\frac{1}{2}$  months or longer.

Further, it is obvious that owing to this great variation in the length of the life-cycle there is a great deal of overlapping of generations of beetles.

LENGTH OF LIFE OF *C. ABIETIS* AND THE NUMBER OF  
GENERATIONS IN A YEAR.

It is now recognised amongst workers on Curculionids and Scolytids that many of these beetles may not only have a long individual life but that the newly issued young brood of beetles cannot proceed at once to an efficient copulation followed by egg-laying. Eichhoff and his school believed the contrary. More recent workers however, including Von Oppen, Nusslin, and MacDougall for Curculionidae, and Pauly, Nusslin and Knocke and Fuchs for Scolytidae, proved that Eichhoff's view was erroneous.

My own recent work<sup>1</sup> on the Scolytids *Myelophilus piniperda* Linn. and *Myelophilus minor* Hart. has corroborated the view of these later workers. From the results of the researches of these workers it has also been definitely proved that a large number of forest insects belonging to the Scolytids and the Curculionids do not die after pairing and a first egg-laying, but that after a period of renewed feeding in order to recuperate and to render their sexual organs once more functional, it is possible for them to proceed to a second pairing and a second egg-laying. Von Oppen and others also showed that the imago on its transformation from the pupal condition might be quite unripe and unable to proceed to an efficient copulation followed by egg-laying, and that in such a case an intervening feeding period was necessary for the reproductive organs to become mature.

Further, the question of whether two broods in the relationship of parents, children, and grandchildren are possible in a year is greatly dependent on two things, viz. whether a preliminary feeding is necessary before breeding and if this feeding period be short or long. If this feeding period be short then a second brood in the year is possible, whereas if the period is long a second brood is impossible.

The proving of the facts is not an easy matter in the case of *C. abietis* where the most of the feeding previous to exit for mating takes place under the bark in the place where the insect has reached its imago stage. As underneath the bark of an infested branch or stem it is possible to find *Cryphalus* beetles that have already bred and beetles that have just reached the imago stage and have not bred at all, the true facts as to length of life, number of broods possible, and the generations possible in a year can only be ascertained by a dissection and comparison of the reproductive organs of new imagos, beetles ready to pair, beetles that are laying eggs and beetles that have completed egg-laying.

#### THE MALE REPRODUCTIVE ORGANS OF *CRYPHALUS ABIETIS*.

Fig. 11 shows the male reproductive organs dissected out. These comprise the testes, vasa deferentia, seminal vesicles, accessory glands, common vas deferens or duct and the penis. The testes are translucent glandular bodies and as usual one lies on either side of the abdomen ventrally. These produce the spermatozoa. Each testis (*T.*) is made up of two lobes somewhat circular in shape and closely united along their inner surfaces. From the posterior or under side of each testis, a duct

<sup>1</sup> *Trans. Royal Society Edin.* vol. LII, Part 1, No. 10.

or tube arises known as the vas deferens (*V.d.*). The vasa deferentia unite later to form a common duct (*C.d.*) which leads to the penis. The vas deferens is much swollen but there are constrictions on it at two points. The first constriction occurs at a point distant from the testis of about one-quarter of its total length, while the second is at a point about a corresponding distance from the other end of the vas. The first constriction is most marked, the second is not so conspicuous. The swollen

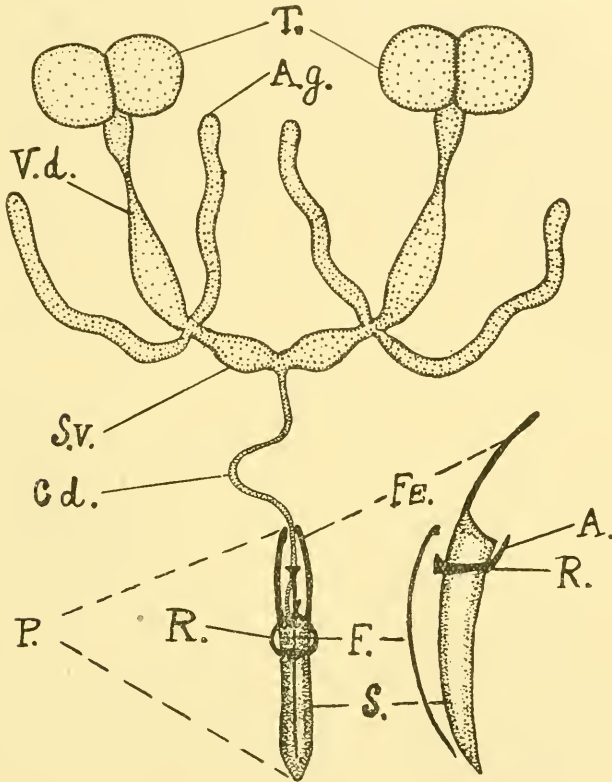


Fig. 11. Male reproductive organs of *C. abietis* (greatly magnified). On the right the penis is shown in side view (more highly magnified).

portion of the vas lying between the second constriction and its union with the vas deferens from the other testis, *i.e.* the most posterior portion of each vas, is called the seminal vesicle (*S.v.*). Two blind diverticula, the accessory glands (*A.g.*), one on either side and placed opposite each other, open into the vas deferens just at its second constriction. The chitinous portion of the penis (*P.*) is composed of the fork (*F.*), ring (*R.*) and sheath (*S.*). The fork gradually tapers to a point while anteriorly

it widens out slightly into a triangular-shaped knob showing very frequently rounded projections on either side. The ring, on the whole, is circular in shape and surrounds the sheath of the penis. In a lateral aspect (Fig. 11) of the chitinous portion of the penis, the dorsal portion of the ring is seen to be drawn out to a point which projects anteriorly. This drawn-out portion of chitin is called by Hopkins<sup>1</sup> the apodemal process (*A.*).

The sheath, roughly speaking, may be considered as a hollow chitinous cylinder tapering posteriorly and bearing on its anterior edge two chitinous rods known as the femora (*Fe.*). In the following columns I contrast the main characters of unripe and ripe reproductive organs of the male, which proved useful to me in differentiating them.

UNRIPE	RIPE
Testes white.	Testes yellowish.
Vas deferens, <i>i.e.</i> portion between testis and seminal vesicle, dirty white in colour.	Vas deferens, <i>i.e.</i> portion between testis and seminal vesicle, yellowish in colour.
Seminal vesicle small.	Seminal vesicle swollen.
Accessory glands short and thin, only slightly developed.	Accessory glands greatly lengthened.

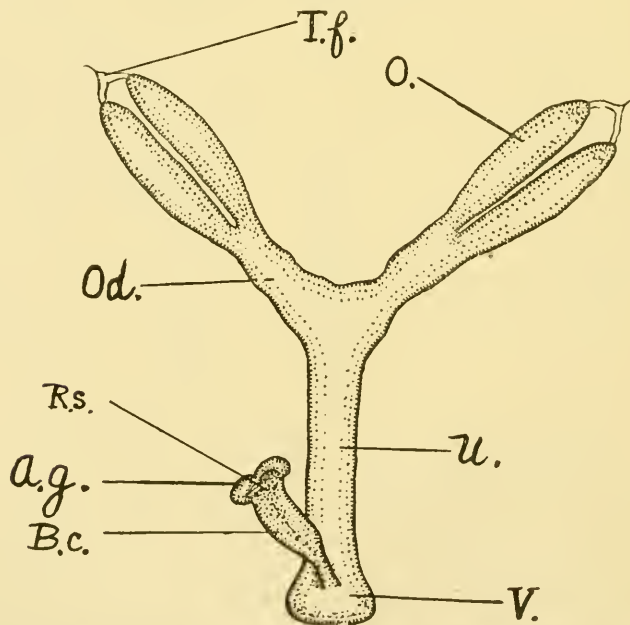


Fig. 12. Immature female reproductive organs of *C. abietis* (greatly magnified).

<sup>1</sup> Hopkins, Preliminary Classification of the Superfamily Scolytoidea, Technical Series, No. 17, Part II, U.S. Bureau of Entomology, 1915, p. 193 *et seq.*

FEMALE REPRODUCTIVE ORGANS OF *C. ABIETIS*.

Fig. 13 depicts the reproductive organs of a female about to proceed to egg-laying.

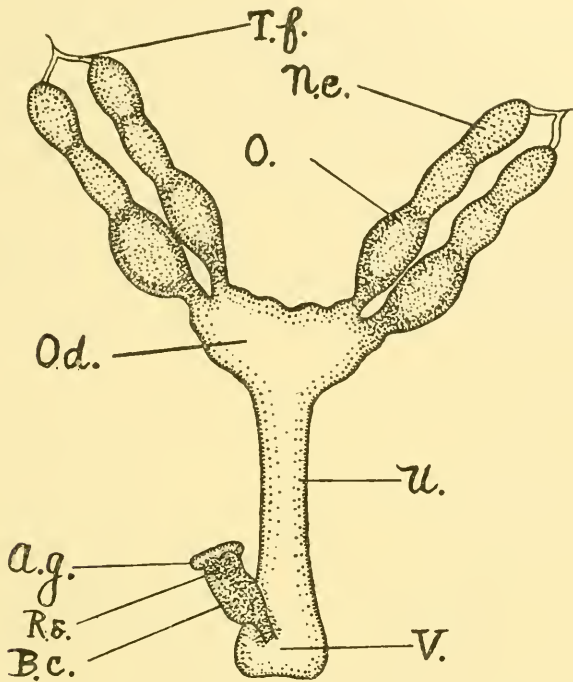


Fig. 13. Reproductive organs of female *C. abietis* about to lay eggs (greatly magnified).

There are two ovaries, one on each side of the abdomen. Each ovary (*O.*) consists of two egg-tubes, which open into the paired oviduct. At the anterior extremities of each egg-tube there is a terminal nutritive chamber (*N.e.*) and at its apex a terminal filament (*T.f.*). The eggs pass from the egg-tubes to the oviducts which unite posteriorly to form a common duct—the uterus (*U.*) and the vagina (*V.*). Uniting with the posterior portion of the uterus we have the bursa copulatrix (*B.c.*) enclosed in the anterior end of which is the receptaculum seminis (spermatheca) (*R.s.*) and bearing anteriorly also the accessory gland (*A.g.*).

Repeated dissections of the reproductive organs of numerous females, both immature and mature, were made with the object of ascertaining definitely whether a slime or a pair of slime glands were present or not, but in all these I failed to observe any trace of them. (Such slime glands are present in the female reproductive organs of many Scolytids and

usually enter the lower portion of the uterus (the vagina) prior to the entrance of the bursa copulatrix.)

According to Nusslin<sup>1</sup> the bursa copulatrix in the genus *Cryphalus* is obscure or absent. From repeated dissections of the female reproductive organs in all stages of development for the purpose of investigating this point I should say rather that the receptaculum seminis is the obscure portion of the reproductive apparatus, for it is only in the reproductive organs of females that have just completed egg-laying that the position and outline of this part is traceable at all. In all stages of the development of the reproductive organs of the female I have found the bursa copulatrix quite easily discernible but at the same time there is no distinct line of demarcation between it and the receptaculum seminis. In my opinion the bursa copulatrix encloses the receptaculum seminis in its anterior end and this can be a possible reason for its obscurity.

The sequence of changes which I observed to take place in the reproductive organs of the female during their transition from the immature to the mature state and to their condition after egg-laying may be summarised as follows:

In the immature state (Fig. 12) the egg-tubes are colourless and are comparatively uniform throughout their length. The bursa copulatrix is colourless and empty while the receptaculum seminis enclosed within it is scarcely traceable. The accessory gland of the receptaculum is small and inconspicuous.

The first noticeable change in the reproductive organs is the slight narrowing of the lower portion of the egg-tubes while the contents of this portion become muddy coloured. Later some of this muddy coloured substance passes down into the oviduct which now becomes much swollen. Following on this, the egg-tubes, by a shunting-off process which takes place in the middle or posterior portion of each tube, become more elongated. Soon the egg-tubes divide up in bead-like fashion, each bead or egg-chamber containing an egg. In this stage, depicted in Fig. 13, we see that the oviduct is still swollen; the bursa copulatrix is full and is muddy in colour and the receptaculum seminis enclosed in the bursa copulatrix is still obscure. As soon as an egg has passed through the neck or lower portion of the egg-tube (see Fig. 14), this portion contracts, swelling out and contracting again each time an egg passes through it. From Fig. 14 it might seem that an egg is passed into the oviduct first from one ovary then the other in turn.

<sup>1</sup> See Hopkins, p. 195.

Egg-laying being completed the egg-tubes are now empty or contracted as shown in Fig. 15. The oviduct also is contracted while the outline of the receptaculum seminis enclosed in the anterior end of the bursa copulatrix is now traceable.

In the case of females which had completed egg-laying and had fed for a period of about four months prior to a possible second egg-laying, I found that, with the exception of a slight increase in the size of the terminal or nutritive chamber, the parts of their reproductive organs had undergone little further change in appearance.

In all my dissections of the reproductive organs of females both in the egg-laying and after egg-laying stages I failed to notice any trace of the so-called corpora lutea, or heap of degenerate yellowish tissue, which in many insects frequently collects at the bases of the egg-chambers as soon as eggs have passed into the oviduct.

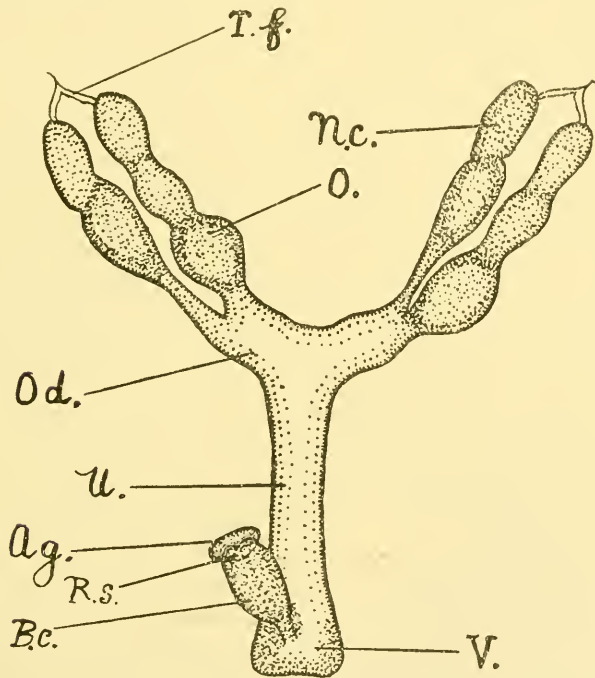


Fig. 14. Reproductive organs of female *C. abietis* egg-laying (greatly magnified).

In the following columns I emphasize the significant characters which appeared to be most useful in determining the unripeness and ripeness of the female reproductive organs.

## UNRIPE

The nutritive chamber at the apex of the egg-tubes is small and apparently seated directly on the oviduct.

Egg-tubes diminutive, short, not prominent, not separated off into ovarian chambers.

Bursa copulatrix empty. Gland associated with the receptaculum seminis empty.

## RIPE

Nutritive chamber large.

Egg-tubes long and pointed so as to suggest strings of beads. The egg-chambers increase in size gradually from the nutritive chamber to the oviduct.

Bursa copulatrix and gland associated with receptaculum seminis well filled.

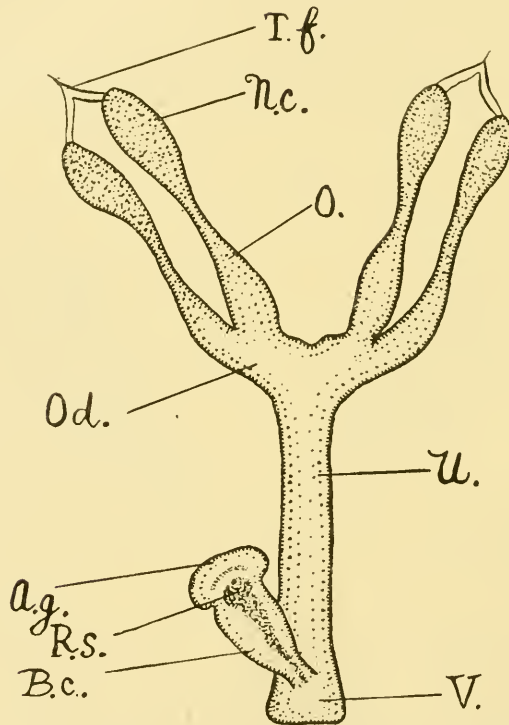


Fig. 15. Reproductive organs of female *C. abietis* after egg-laying (greatly magnified).

## QUESTION OF THE NUMBER OF GENERATIONS IN A YEAR.

From repeated observations made in the open and from my experiments I am convinced that even under the most favourable conditions the occurrence of a double generation in the succession of parents, children and grandchildren within a single year is most unlikely.

In Table No. I, I have summarised my observations and results of the control experiments already referred to under the paragraph dealing with the length of a life-cycle in a single generation. From this table it will be seen that the new generation developed from eggs laid in May of the year and issuing in September is unable to proceed to an egg-laying, *i.e.* a new generation, in the same year. At the earliest it would be the next spring before they laid eggs. Similar results were also obtained from experiments and dissections from material bred in the open in the summer and autumn of the year 1917.

TABLE I.

Date of liberation of adults proceeding to make gallery	Boring mother gallery	Adult stage of new generation reached	Reproductive organs of females dissected out	Results of microscopic examination	Remarks
2 May 1917	4 May 1917	27 Sept. 1917	9 Oct. 1917	Immature	Egg-laying would not take place till following spring as little or no feeding takes place in the months November to March
do.	do.	do.	22 Nov. 1917	do.	
do.	do.	do.	3 Dec. 1917	do.	

Even adults derived from overwintering larvae and which issue in midsummer do not have a new generation in this year as is proved by the undernoted observations.

Some larvae that hibernated during the winter of 1916-17, the first of which pupated on June 5th, 1917, issued as adults from July 21st, 1917, to August 20th, 1917. The majority of these young adults however never swarmed at all during the year 1917 but remained underneath the bark where they were reared and hibernated the second winter as immature adults. That they were immature was proved from a large series of dissections made of their reproductive organs in November and December, 1917.

Some of the reproductive organs of those adults that did swarm in July and August of 1917 were also examined as the beetles issued from the material where they had been reared but they too were found to be immature. The others that issued I liberated on August 14th, 1917, in muslin cages enclosed within which were paraffined branches of Silver Fir, on which they could feed or breed as they chose. On the 16th of August, 1917, a number of them were found to be boring on the Silver Fir branches, evidently feeding. Examination of these branches was made at intervals up to Dec. 3rd, 1917, but in no case were eggs found in any of their

borings. This is remarkable as a number of males and females were working together. The dissection of the reproductive organs of a number of these beetles on November 29th, 1917, and up to December 3rd, 1917, however showed that although they had been feeding for some time the reproductive organs were not ready for egg-laying.

ARE TWO BROODS IN THE RELATIONSHIP OF BROTHERS  
AND SISTERS POSSIBLE IN A YEAR?

My observations show that when the parent beetles have bred and their brood gallery is completed sometimes the male dies before the female has laid her last egg, the female beetle surviving. Very frequently the females die immediately after laying is completed and in many cases the males survive. In some cases both parents die, in others both survive after a first breeding. The mortality amongst parents that have already bred is considerable. Those survivors, male or female, tunnel galleries of a much similar appearance to those of the larval ones and feed on the gnawed material, obtaining nourishment from it and so recuperate their reproductive organs for a possible second egg-laying.

In my experiments a number of parent beetles that had completed egg-laying in the end of June, 1917, tunnelled and fed. The results of these experiments are shown in Table II.

TABLE II.

Date of completion of 1st egg-laying	Found feeding in pseudo-larval galleries after 1st egg-laying	Reproductive organs of females dissected out	Result of microscopic examination	Remarks
26 June 1917 approx.	2 July-20 Nov. 1917	20 Nov. 1917	Immature	A 2nd egg-laying would not take place if at all till following spring.
do.	do.	27 Nov. 1917	do.	
do.	do.	3 Dec. 1917	do.	
do.	do.	10 Dec. 1917	do.	

HOST TREES.

From observations made in the field I find that *C. abietis* confines itself in Scotland to breeding on the stems, branches and twigs of unhealthy, dying, or dead trees of three closely allied genera of conifers, namely, *Abies*, *Picea*, and *Pseudotsuga*. Like many other injurious insects *C. abietis* has a preference for certain genera and species, but if these are found wanting, deficient or in an unsuitable state for brood purposes others may be chosen.

My experience in Aberdeenshire, Kincardineshire and Midlothian leaves me with no doubt that *C. abietis* prefers, in Scotland at least, the

genus *Abies* (Silver Fir family) for brood purposes, having a special preference for the species *Abies pectinata* D.C. (Common Silver Fir). I have also found *Cryphalus* breeding on *Abies cephalonica* Link. (Grecian Silver Fir) while in my breeding experiments the same insect readily took to *Abies nordmanniana* Spach. (Norman's Silver Fir), and *Abies pinsapo* Boissier (Spanish Silver Fir). It has also been recorded in Scotland on *Abies nobilis* Lindl., a North American species. It is possible that all the species of the genus *Abies* may be used for brooding purposes if in a suitable condition.

Next in order of preference, *C. abietis* takes the genus *Picea* (Spruce family), *Picea excelsa* Link. or Norway Spruce being the host plant on which I have found it.

Last in order but by no means of least importance *C. abietis* may choose for brood purposes the genus *Pseudotsuga* (Douglas Fir family). I have found the insect breeding freely in Aberdeenshire on the sickly branches of standing Douglas Firs, *Pseudotsuga Douglasii* Carr., the only species of the genus planted in this country.

We see then that *C. abietis* possesses a wide range of host trees, an exceedingly important factor which would have to be reckoned with in dealing with the control of the species.

As far as my observations go I am convinced that *C. abietis* in most cases only takes to the Spruce and Douglas Fir families when the preferred Silver Fir family is deficient or is in an unsuitable state for brooding purposes.

On the continent of Europe, according to Nusslin<sup>1</sup> and other writers, *C. abietis* is typically a Spruce species. Nusslin also states that, although it prefers the species of the genus *Picea* it also takes the genus *Abies* and occasionally the genus *Pinus*. Of the species of the genus *Pinus* he states that it prefers *Pinus strobus* L. or Weymouth pine.

Kaltenbach<sup>2</sup> quoting Ratzeburg names the species as attacking *Pinus strobus* and the dry branches of Silver Fir. Eichhoff<sup>3</sup> names as host plants Spruce, Silver Fir and Pine.

#### ECONOMIC IMPORTANCE OF *C. ABIETIS* IN SCOTTISH FORESTRY.

Occasional references in the forest literature of Central Europe indicate that *C. abietis* has been known to be harmful especially if in numbers it attacked very young stems.

<sup>1</sup> Nusslin, *Leitfaden der Forst Insektenkunde*, 1905, pp. 201-2.

<sup>2</sup> *Die Pflanzen-Feinde aus der Classe der Insekten*, p. 685.

<sup>3</sup> *Die Europäischen Borkenkäfer*, by W. Eichhoff, p. 177.

So far as my observations in Scotland show, *C. abietis* has not proved of any great forest importance in the sense of having proved destructive to live trees, but the species must not be overlooked or observation on it neglected.

A knowledge therefore of its habits as well as the recognition of the presence of the beetle in our woods at the present time is opportune.

Its favourite breeding places are dead or almost dead trees, twigs and branches, of practically all ages, that have been spoiled or killed by some agency or other such as wind, breakage, etc. The positions most commonly chosen by the parent beetles for tunnelling their brood galleries are around twigs and branches, the female commencing her gallery in the axil of a side branch. No doubt she chooses this position because a good foothold is secured for her while boring the entrance hole of the gallery. Boring gradually round the base of the side branch she cuts the inner bark layers, namely the bast and cambium, leaving only the thin layer of outer bark. Where the twig or branch around which she has excavated her burrow or gallery is a small one it may be completely girdled and isolated from the main branch. Even when the twig or branch is strong and although only partially girdled by one gallery it may be completely girdled and isolated from the main branch or stem by other galleries. Were such workings then to be cut on living twigs and branches it is quite evident that serious damage would be done to trees, for no food material from these isolated portions could pass down to the main stem and roots.

A point worthy of mention in connection with *C. abietis* is that it is negatively heliotropic, the parent beetles preferring bushy twigs and branches in shady places unexposed to the sun. For example, the topmost branches of heaps of brushwood lying in the open are not commonly chosen for brood purposes, while the lower branches of such heaps as well as entire heaps in the shade of standing trees may be badly infested. Most likely those branches which are exposed to the sun are too dry for breeding on and this can be a reason why they are not chosen by the parent beetles.

To ascertain if beetles are present in a wood one has only to examine carefully the axil of a dead twig or branch, when, if beetles are at work, a minute heap of fine bore dust, reddish yellow in colour, will be seen. If a number of beetles have issued a series of minute exit holes may be seen at irregular intervals on the surface of the bark. Frequently one will find on examination of branches where the majority of the beetles

have issued that the outer bark layer is broken and the wood surface exposed to view.

#### NATURAL ENEMIES OF *C. ABIETIS*.

From observations made in the field during the last two years I am of the opinion that the bark fungi play little or no part in controlling the numbers of *C. abietis*. Only on a few occasions have I found beetles killed by fungoid attack.

The larvae are destroyed in numbers by the larvae of a Hymenopterous parasite belonging to the family Chalcididae. On the removal of a piece of the outer bark layer of a badly infested branch or twig one repeatedly met this parasite either in the larval or pupal stage. Only one parasitic larva was found on each host. No cocoon is spun by this Chalcid larva prior to pupation but the pupa lies naked in the Cryphalus gallery or pupal bed. As soon as these parasites have reached the adult stage each gnaws a minute puncture through the outer bark and escapes into the open.

From some Silver Fir branches badly infested with *C. abietis* which I collected in Aberdeenshire in October, 1916, large numbers of these Chalcids issued from July 21st to August 6th, 1917, just at a period when large numbers of these *C. abietis* larvae would be found on infested branches.

The number of these Chalcids varied to a great extent in different localities. From one lot of badly infested material collected in one particular area in the Aboyne district only a few parasites issued. On the other hand, from badly infested material collected from another area a little over a mile from the first exceedingly large numbers of parasites issued. In a single day as many as 30-40 individuals escaped from a few pieces of badly infested material. In this particular case I estimate about 75 per cent. of the larvae of the beetles must have been destroyed.

The abnormal conditions prevailing in our forest areas during the past three years have undoubtedly been the means of creating an excessive number of breeding places for our bark-boring beetles. Foresters throughout the country ought therefore to be on the alert. The intensive study of the life-history and habits of this beetle and of other such forms is for this reason of more than usual interest at the present time.

In conclusion my thanks are due to Dr R. Stewart MacDougall for the encouragement and facilities he has given me throughout this work.

## A COPPER EMULSION AS A FUNGICIDE.

BY H. WORMALD AND L. K. WORMALD.

*(Research Department South-Eastern Agricultural College, Wye, Kent.)*

(With Plate XI.)

IN the report of the Agricultural and Horticultural Research Station, Long Ashton, for 1917, A. H. Lees described methods of preparing an emulsion containing copper by mixing a solution of copper sulphate with soap solutions.

In conjunction with other experiments, a very similar emulsion was made and used at Wye early in 1917. Since the observations made at Wye as to the nature of this emulsion corroborate those of Mr Lees, and since additionally the fungicidal properties of this emulsion have been examined, it seems desirable to record the work so far done, although further experiments must be carried out before an emulsion of this kind can be recommended as a practical spray fluid.

The emulsion prepared at Wye contained rather more copper than that made by Mr Lees. It contained the equivalent of 0.4 per cent. copper sulphate ( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ) and 2 per cent. of soft soap<sup>1</sup> and was made by pouring slowly a 0.8 per cent. solution of copper sulphate into an equal volume of 4 per cent. soft soap solution, stirring well all the time. The emulsion made in this way did not settle, even on standing for several weeks; it could not be filtered and turned chocolate colour on addition of potassium ferrocyanide. When the soap solution was added to the copper solution a quite different result was obtained, and instead of an emulsion (probably of copper stearate in part) green sticky masses having a putty-like consistency were formed.

In order to determine whether the emulsion made as above described possessed fungicidal properties, the following experiment was carried out on August 8, 1917.

Fresh potato shoots were brought into the laboratory, cut under water and placed with ends in water in flasks the mouths of which were under water. On each of two shoots, three leaves at successive nodes were

<sup>1</sup> The soap used throughout these experiments is that sold under the name of "Chiswick Soft Soap."

selected; the uppermost and lowest leaves were sprayed with freshly made copper emulsion by means of an atomiser and the middle leaf left unsprayed. When the sprayed leaves were dry, drops of distilled water containing motile zoospores of *Phytophthora infestans* were placed on all three leaves by means of a platinum loop, two drops being placed on each side of the midrib of the lower side of the terminal leaflet and the second pair of leaflets in each case. The zoospores were obtained by placing affected leaves with ends in water under a bell jar on the previous day and leaving overnight. From one to two hours before the zoospores were required, the portions of the leaves bearing sporangiophores were brought in contact with a few drops of distilled water in a watch glass; numerous sporangia became free in the water and zoospores were liberated within an hour.

Three days later, on August 11, there were black spots on both unsprayed leaves but none on any of the sprayed leaves. On August 13, one of the sprayed inoculated leaves had fallen off so the observations were not continued.

On August 15, a second experiment was carried out on growing potato plants in the garden. Three healthy leaves were selected on successive nodes; two of these, the uppermost and lowest, were sprayed with freshly made emulsion and the other left unsprayed. About two hours after the leaves had been sprayed, there was a heavy thunderstorm lasting about ten minutes, so the leaves were not inoculated until the next morning. These were inoculated in the way described in the previous experiment.

On August 20, the unsprayed leaf showed seven distinct diseased spots though there were no spots on either of the sprayed leaves and on September 11, when the whole of the unsprayed leaf was destroyed, the whole of one of the sprayed leaves was quite uninjured; on the other sprayed leaf, one leaflet, though not one of those inoculated, was withered but otherwise the leaf was quite green and uninjured. On this date, the shoot was removed from the plant and photographed (see figure).

The two lowest leaves shown in the photograph had become naturally infected; the two healthy leaves seen on the right had been sprayed with the emulsion and then inoculated, and the diseased leaf occurring between the two healthy ones had been left unsprayed but had been inoculated.

The accompanying table shows in detail the observations made on the inoculated leaflets.

## Detailed observations of Experiment II.

Inoculated August 16	August 20	August 23	August 28	Sept. 11
Leaf <i>a</i> sprayed { terminal leaflet left        " right       "	no diseased spots do.   do. do.   do.	no diseased spots do.   do. do.   do.	no diseased spots do.   do. do.   do.	Whole leaf uninjured
Leaf <i>b</i> unsprayed { terminal   " left       " right      "	1 distinct spot of blight 2 distinct spots of blight 4 distinct spots of blight	1 spot 1 cm., another 0.3 cm. diam. The two spots have coalesced Whole leaflet blackened and withered	All three leaflets destroyed	Whole leaf destroyed
Leaf <i>c</i> sprayed { terminal   " left       " right      "	no diseased spots do.   do. do.   do.	no diseased spots do.   do. do.   do.	no spots do. do.	no spots do. do.

On the same date as the last experiment, a plant with many badly diseased leaves was sprayed with the emulsion but the disease extended in all the affected leaflets.

From these experiments, it is evident that the emulsion acted as a preventive against infection by zoospores of *Phytophthora infestans* and justified trials on a larger scale.

Later in the year, two small plots of potatoes, each measuring approximately 120 sq. yds, were sprayed with the emulsion and on this occasion when tap water was used instead of distilled water hitherto employed in these experiments, a little difficulty was experienced in spraying the fluid owing to the accumulation in the nozzles of the sprayer of the green sticky substance referred to already.

At the time the crop was lifted the leaves of the sprayed plots were certainly much greener and showed far less damage by blight than those of the unsprayed control plot, but owing to the lateness of the appearance of the blight, all three plots had approximately the same low percentage of diseased tubers although the two sprayed plots showed a slightly greater total yield than the control plot.

In 1918, these trials were repeated and two more small plots, each approximately 36 sq. yds in area, were sprayed, the control plot of the same size being between them. On Plot I, the emulsion described (*i.e.* containing the equivalent of 0.4 per cent.  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$  and 2 per cent. soft soap) was sprayed. On Plot III, an emulsion containing twice as much copper and twice as much soap was used. The plots were sprayed on August 7. Each plot received six gallons, applied by means

of a knapsack sprayer, and both emulsions were made with rain water and were applied in the usual way by a man accustomed to the work, but no unusual care was taken to effect complete treatment of the plot.

To make six gallons of emulsion for Plot I, three gallons of soap solution containing 1.2 lbs. (544.3 gms.) of soap were put in a perfectly clean wooden pail; 0.24 lb. (108.9 gms.) of copper sulphate was dissolved in three gallons of water and this solution was added slowly to the soap solution, which was stirred well all the time.

On August 19, both plots were sprayed again, each receiving six gallons as before. On this occasion both emulsions were made with tap water and Plot I was actually sprayed with emulsion made from tap water though a small amount of a putty-like substance was formed; this remained in the strainer and the whole of the spray went on satisfactorily. In the case of the stronger emulsion, a mass of green "putty" was formed, clogging up the tube and nozzles of the sprayer, even after straining, which was a very long process; this was therefore rejected, the sprayer thoroughly cleaned and the emulsion made again with rain water. Although some "putty" was formed, the emulsion which was put on Plot III contained considerably more copper than that put on Plot I.

The green putty-like substance has strongly adhesive properties and some method has yet to be found for retaining all the copper in the emulsified condition.

The effect of the spray on the leaves was most striking. The control plot began to blacken about three weeks before the sprayed plot showed any signs of being affected and on September 25, when the sprayed plots were still fairly green and healthy, not one green leaf could be seen on the control plot.

From the results given, it will be seen that the sprayed plots gave an appreciably higher yield than the unsprayed and the percentage of diseased tubers was much higher in the unsprayed plot than in either of the sprayed plots.

*Plot I.* Sprayed twice with an emulsion containing approximately the equivalent of 0.4 per cent.  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ .

Ware	63 lbs.	70.8
Chats	18½ "	20.8
Blight	7½ "	8.4
Total	89 "	

*Plot II.* Unsprayed.

		%
Ware	34 lbs.	61.8
Chats	13 "	23.6
Blight	8 "	14.5
Total	55 "	

*Plot III.* Sprayed twice with emulsion containing approximately the equivalent of 0.8 per cent.  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ .

		%
Ware	72½ lbs.	81.9
Chats	13 "	14.7
Blight	3 "	3.4
Total	88½ "	

From these experiments, it would appear that the copper emulsion at the lower strength (containing the equivalent of 0.4 per cent.  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$  and 2 per cent. soft soap) is an efficient preventive against blight when used on potato foliage, and when carefully prepared with rain water it can be applied without difficulty. Further experiments, however, are necessary, particularly with respect to its preparation when only hard water is available, before it can be generally recommended as a practical spray fluid. Although this fluid was originally prepared and examined from another point of view, on account of the small amount of copper used in its preparation and of its fungicidal value, it is worth while trying to overcome the difficulty experienced in making the emulsion under practical conditions. From an economic point of view, the large amount of soap required is partly compensated for by the small amount of copper necessary and the property of spreading over the foliage which soap gives to the fluid.

The fungicidal value of the emulsion, which contains much less copper than Burgundy or Bordeaux mixtures as commonly used, is probably due, in part, to the fact that the particles, owing to their extreme fineness, must come in intimate contact with the leaf surface and to the adhesive nature of the copper compound which it contains.

*Summary.* An emulsion containing the equivalent of 0.4 per cent. copper sulphate ( $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ) can be made by mixing solutions of copper sulphate and soft soap, and this exhibits preventive action against the attacks of the potato blight fungus.





In conclusion, we should like to thank Dr Eyre, who indicated the possibility of preparing an emulsion by the method adopted, and at whose suggestion the above experiments were carried out.

#### DESCRIPTION OF PLATE XI

Photograph of potato shoot described on p. 201. The two healthy leaves seen on the right had been sprayed with copper emulsion and then inoculated with zoospores of *Phytophthora infestans*; the diseased leaf occurring between these had been left unsprayed and had been inoculated. The remaining leaves on the shoot had become naturally infected.

STUDIES IN BACTERIOSIS II<sup>1</sup>.A BROWN BLOTCH DISEASE OF CULTIVATED  
MUSHROOMS.

By SYDNEY G. PAINE.

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## INTRODUCTION.

DURING the spring of 1918 a disease of mushrooms was observed in the beds of a large nursery in Brentford, Middlesex. Mushrooms have been cultivated there for upwards of forty years, and although the disease was not entirely new to the grower there would seem to have been no outbreak in the past of comparable severity. Previous occurrences had been of little importance and had been attributed to the effect of draughts. The disease was first noticed in April, and threatened to assume serious proportions. On examination of one of the houses in the first week of May about one-third of the crop in certain parts of the house was found to be affected<sup>2</sup>. The financial loss at this time when the wholesale price of mushrooms was at its maximum must have been considerable, affected mushrooms being so disfigured as to be unsaleable. Later on in the month, however, the disease became less prevalent, and towards the end of June had become insignificant in amount. The reason for this rapid falling off will be discussed later.

## THE SYMPTOMS OF THE DISEASE.

Circular or irregular spots of a chestnut brown colour appear on the surface of the cap of the mushroom when this has attained a diameter of an inch or so; they spread rapidly and coalesce to form large patches which occasionally cover the entire surface of the pileus. (See Fig. 1.) The stalks also may show the disease, but it is characteristically a disease

<sup>1</sup> The first of this series of studies appears in *The Journal of Agricultural Science*, vol. viii, 1917.

<sup>2</sup> The areas most affected were those within ten feet of either door; this seemed to indicate that draughts were in some way connected with the spread of the disease.

of the cap. The patches become slightly depressed, dry up and crack radially as the mushroom grows. They arise at or near the margin of the mushroom or at the point of contact of one with another, *i.e.* places at which water is likely to remain for some time after the sprinkling of the bed. At the outset it seemed likely that some micro-organism finds entrance at these spots after multiplying in such standing water. The disease spreads rapidly from one diseased head to others in the same



Fig. 1. Mushrooms naturally infected.

cluster in a way which supports the above view as to the mode of dissemination of the disease, the organism presumably being carried by insects or by splashings from infected drops of water during watering.

The disease is very superficial; on peeling off the "skin" the underlying tissue is found to be affected to a depth of, at most, one to three millimetres (the diagrammatic sketch, Fig. 3, shows clearly the slight extent of penetration of the tissue by bacteria, in this case less than half a millimetre), and very frequently is found to be perfectly white and healthy. The affected underlying tissue has a rather water-soaked appearance and a mouse grey or yellowish grey colour.

## ISOLATION OF THE CAUSAL ORGANISM.

Microscopical examination of a section of the grey tissue underlying the brown spot shows that the hyphae are invaded by crowds of bacteria. The preparation from which Figs. 3 and 4 are taken shows the pileus completely disorganised and penetration of bacteria to a depth of about half a millimetre; the organisms are mainly within the cells of the hyphae as is shown in Fig. 4.

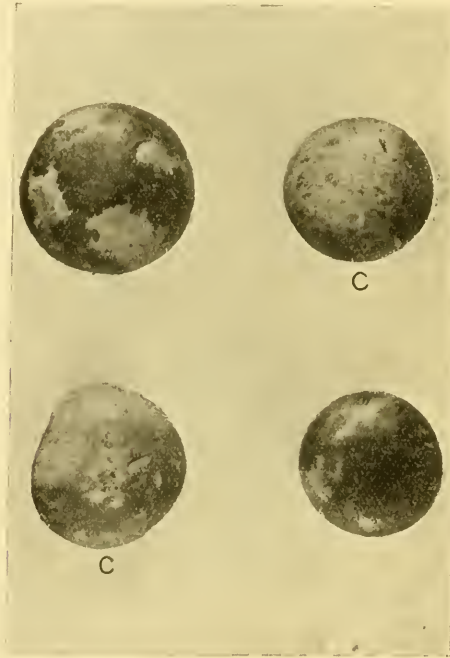


Fig. 2. Mushrooms artificially infected. *cc* controls.

Removal with aseptic precautions of some of the bacterial tissue and inoculation into mushroom-extract or other nutrient media yielded, without the slightest difficulty, pure cultures of an organism which was identical in every case, leaving no doubt that the causal organism had been obtained. The organism was plated several times on mushroom-extract agar and on bouillon-agar in order to ensure purity and from the first the colonies were all of one type.

## INFECTION EXPERIMENTS.

Numerous infection experiments have been made upon young mushrooms growing in the beds at Brentford and upon mushrooms removed from the bed and kept in fresh condition with their stalks embedded in moist soil covered with bell-jars. A suspension in sterilised mushroom-

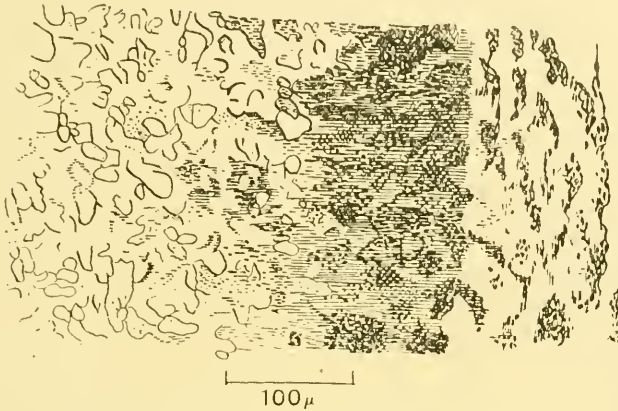


Fig. 3. Camera drawing from a  $3\mu$  radial section through the cap of a diseased mushroom, showing complete disorganisation of the outer hyphae and penetration of the tissue by bacteria to a depth of not more than half a millimetre.



Fig. 4. Camera drawing from same section as Fig. 3, showing hyphae penetrated by bacteria.

extract of the organism from an agar slope was painted over the surface of the mushroom with a sterilised camel-hair brush, numerous control experiments with the uninoculated extract being made at the same time. In every case typical brown streaks corresponding closely to and spreading irregularly from the margins of the pattern painted resulted from such inoculations. (See Fig. 2.) The controls showed either no sign at all, or a slight indentation caused by the mechanical injury of the soft tissue of the mushroom. The infections at Brentford were examined only after three days, but in those made in the laboratory the pattern was well developed overnight and did not extend far afterwards. In some of these the browning was distinctly visible in as short a time as five hours; this led to the suspicion that ammonia might be the direct cause of the browning, and that the organism invading the hyphae was one of the common ammonifiers of the soil which had entered dead tissue resulting from the lethal action of ammonia upon the cells, a mode of entry of a saprophyte into a living plant which the work of Jensen<sup>(4)</sup> has shown to be possible.

To test this hypothesis control experiments were made with mushroom-broth containing additions of ammonia; when these additions were quite small, sufficient only to render the broth just alkaline to litmus, no coloration whatever was produced, but with addition sufficient to make the liquid smell distinctly of ammonia a brown coloration was obtained but of a dull tint easily distinguishable from the warm chestnut shade characteristic of the disease. Further control experiments were made with suspensions of *Bacillus fluorescens liquefaciens*, *Bacillus Proteus*, and *Bacillus mesentericus*, all of which are powerful ammonifying organisms of the soil, and, although repeated on many occasions with cultures of various ages, no browning of the tissue resulted.

The organism was, then, to be regarded as a parasite and this was later definitely established by the loss of virulence in some agar cultures of two months' standing, and in sub-cultures of 24 hours' growth made from these.

#### DESCRIPTION OF THE ORGANISM.

##### I. MORPHOLOGICAL CHARACTERS.

*Form and Size.* The organism is a short rod with rounded ends. In common with most others it varies considerably in size, according to the rate of growth and the medium employed. Measurements are held by the author to be of little significance, but for the purpose of comparison, measurements were made upon a 24 hours' growth on bouillon-

agar, the sixth transfer from the original, incubated at 22° C. The colony had attained a diameter of 4 mm. The film was fixed by ten minutes' immersion in 4 per cent. formalin, stained for ten minutes in aqueous methyl violet, and examined in oil. The length of the organism varied from 0.9  $\mu$  to 1.7  $\mu$  and the breadth from 0.4  $\mu$  to 0.5  $\mu$ . The growth was very viscous and suggested the presence of a capsule; when a suspension of the organism in normal saline was examined by dark-ground illumination, however, no sign of a capsule was discovered.

*Motility and Flagella.* The organism is actively motile in young cultures in broth and upon agar, but it comes to rest early, frequently after 24 hours at air temperature on solid media. The movement is of a free swimming type without other specific characteristic. The flagella have been stained by Stevens' modification of Van Ermengen's stain and by a new method devised by the late Professor H. G. Plimmer<sup>1</sup>. The flagella are two to four times the length of the organism, one or two in number, occasionally three and more rarely four or five, arranged at one pole. (See Fig. 5.) The organism is therefore a *Pseudomonas*.



Fig. 5. Camera drawing from a preparation stained by the method of Plimmer.

*Staining.* The organism stains well with carbol fuchsin, gentian violet and methyl violet, does not stain by Gram's method, is not acid fast, and gives negative results with the usual capsule stains.

<sup>1</sup> I hope with Dr R. H. A. Plimmer's permission to publish a description of this staining method if the details can be worked out from the data left by Professor Plimmer.

## II. CULTURAL CHARACTERS.

The organism grows equally well in mushroom-extract and in beef-extract (Jardox) bouillon + 10, and on solid media from these. It also grows luxuriantly upon potato-mush agar.

*Bouillon + 10.* Turbidity was strongly marked after 24 hours at 22° C. A strong pellicle and faint fluorescence were formed in cultures made during the first two weeks after isolation, but both these characters disappeared in later cultures. The pellicle was easily broken by shaking and did not re-form. A strong pellicle also formed on mushroom-extract. In all cases a slight ring was formed, and after a week or so the liquid was very viscous and mucus-like. It had become strongly alkaline to litmus and smelt of ammonia.

*Bouillon-gelatine Stab.* After 48 hours at air temperature liquefaction had commenced, the top 3 mm. being completely liquid with a funnel-shaped depression extending to a depth of some 10 mm. The bottom of the funnel was occupied by a yellowish white granular mass. Growth along the stab was barely perceptible. Complete liquefaction occurred in about 10 days, at air temperature.

*Bouillon-gelatine Plate.* After 24 hours at 22° C. the colonies had a diameter of 5 or 6 mm. and liquefaction was basin-shaped with a granular deposit at the bottom. In three days the gelatine was completely liquid with a strong ammoniacal odour, resembling somewhat that of stale urine.

*Bouillon-agar Stab.* After 24 hours at 22° C. surface growth was yellowish white and about 4 mm. in diameter. Growth along the stab was perceptible only in the top half centimetre. After 72 hours growth could still be seen only towards the top of the stab. The tube was left in the incubator from June 5th till October 2nd, and growth to the bottom of the stab could then be observed, but only by the use of a strong light. The organism was still viable after four months' incubation at 22° C.

*Bouillon-agar Slope.* The streak was well developed after 20 hours at 22° C. as a dirty bluish-white wet-shining streak 2 mm. wide, with slightly raised flat contour. When collected in mass by a wire the colour was faintly yellow tinted. The surrounding medium was bluish-green but without fluorescence.

*Bouillon-agar Slope under Anaërobic Conditions.* Growth was slight but distinctly perceptible. The organism is a facultative anaërobe with a very marked preference for aërobic conditions.

*Bouillon-agar Plate.* Growth was very rapid at air temperature. After 20 hours colonies had a diameter of 1 mm., and after 49 hours of 4 or 5 mm. The colonies were round, raised, wet-shining, and of a dirty greenish-white colour, the margins later became lobed and spreading. There was no fluorescence but a greenish precipitate was formed in the gel surrounding the colonies. Colonies in the depth of the medium were broadly lenticular.

*Optimum Temperature for Growth.* Tubes of bouillon were inoculated each with one loopful from a broth culture and incubated at 6°, 13°, 18°, 20°, 22°, 25°, and 30° C. After two days' incubation clouding was most dense at 25° C.; growth at 6° C. was not apparent until the fifth day.

*Thermal Death Point.* Tubes of bouillon were seeded each with 1 cc. of a 24 hours' culture at 25° C. They were immersed in a bath at the usual range of temperatures, the temperature of the tubes being controlled by a thermometer immersed in a control tube of broth. Ten minutes heating was allowed at each of the temperatures given below and the tubes were then incubated at 25° C. for seven days.

Temperature of bath	Temperature of control tube	Result
46°	45° rising to 46°	Living
48°	46° .. 48°	..
49°	47° .. 49°	..
49.5°	48° .. 49.5°	..
51°	50° .. 51°	Dead
52°	51° .. 52°	..

### III. PHYSIOLOGICAL CHARACTERS.

The culture used for these experiments was the fifth transfer from the original and had been on no other medium than bouillon-agar + 10. A tube of bouillon was heavily inoculated and a loopful from this used for each test. The temperature of incubation was 22° C.

*10 per cent. Witte Peptone + 1 per cent. Glucose.* Acid on the second day, no gas formed in Durham tube; no change after 15 days.

*10 per cent. Witte Peptone + 1 per cent. Lactose.* No acid and no gas; a thin film with an oily appearance, a slight ring formed and liquid became slightly turbid.

*10 per cent. Witte Peptone + 1 per cent. Saccharose.* No acid and no gas; growth as above.

*Bouillon + 2 per cent. Glucose.* Acid after 24 hours, no gas, no pellicle, no ring; no further change up to 15 days.

*Bouillon + 2 per cent. Lactose.* No acid, no gas, slight pellicle, no ring.

*Bouillon + 2 per cent. Saccharose.* No acid, no gas, slight pellicle, no ring.

*Bouillon + 2 per cent. Mannite.* No acid, no gas, no pellicle, no ring; slightly bleached at bottom of tube after 15 days.

*Ushinsky's Solution.* Alkaline on second day, no gas, loose pellicle, no fluorescence. After 15 days: completely bleached, no gas, no fluorescence, thin pellicle and strong ring. After two months: blue above, bleached below, no fluorescence, very viscous deposit. After four months: the ultramarine colour had completely returned.

*Litmus Milk.* Curd separated after the fourth day, the reaction was neutral but became slightly alkaline later. On the seventh day the curd occupied only one-third of the volume of liquid, the litmus was bleached and a strong green fluorescence developed in the whey. Most of the curd was digested but some remained at the bottom of the tube after six weeks.

*Milk.* The curd formed and was partially digested as above, and the whey became strongly fluorescent.

*Potato Plug.* After two days the streak was visible as a white, wet-shining, raised mass; after five days the colour had assumed a faint yellow tinge; the potato was not discoloured. Pulped in water after three weeks, the iodine test showed slight diastatic action.

*Dunham's Solution.* Became slightly turbid on the second day; no pellicle and no ring formed. After 30 days a trace of indol was present.

*Nitrate Bouillon.* A loose pellicle formed after 24 hours, the liquid became very viscous and of a yellowish-green colour. Nitrate was not produced, but ammonia was formed. This was probably a product of the breakdown of protein since nitrate was still present after two months' incubation. The presence of nitrate was not due to the death of the organism previous to destruction of all the nitrate since the culture was found to be still viable at the end of two months. No gas was formed.

#### GENERAL DISCUSSION, COMPARISON OF THE ORGANISM WITH ALLIED STRAINS.

In searching for the mode of entry of the organism to the sheds the possible sources to be considered were: (1) the manure used in making the beds; (2) the spawn; (3) the mould used for casing; (4) the straw litter for covering the beds after spawning; (5) the water used for sprinkling; and (6) the air. Suspicion of the manure was removed by

the fact that during fermentation the temperature usually rises to 120° or 130° F., a moist temperature sufficiently near to the thermal death point of the organism to eliminate this source. The other materials used on the bed, though not free from suspicion, were hardly likely to have introduced the organism, since, as stated in the Introduction, the disease did not appear uniformly distributed over the beds. The water used for sprinkling the beds was deemed to be a likely source. This was taken from the town main and from an old well. Both of these supplies were sampled on two occasions and platings made upon mushroom-extract agar, many colonies of ammonifying organisms developed on the plates and most of these were tested by inoculation upon growing mushrooms, but in no case was there any production of the disease symptoms. Early suspicion fell upon the air as the carrier of the organism since, as stated in the footnote on p. 206, the disease, originating near the doors and windows of the sheds, seemed to be associated with draughts. The litter when removed from the beds was dumped down outside the sheds and some was packed at the bottom of the doors to exclude draught as much as possible; dust from this litter would be carried into the shed each time the door was opened. A search for the organism upon this material, however, proved abortive.

The disease commenced to decrease in early June, and towards the end of June had practically ceased to exist. This may have been, and probably was, in large measure due to the rapid growth of mushrooms during this warm period, the organism, though a tremendously vigorous grower at air temperature, presumably not being able to keep pace with its active host. Another interpretation is, however, possible; the onset of the disease in March and its fall in June, coupled with the fact that the sheds were surrounded by fruit trees in a large orchard, drew the author's attention to the synchronising of the disease with the period of fruit-blossoming, and suggested that the cause of the disease might be identical with that of the "Pear-blossom Blight," investigated by Barker and Grove(1) in this country, and by Doidge(2) in S. Africa.

This disease had not been specially noticed by the grower but practically no fruit set this year and the disease might well have been partially responsible for this failure.

Comparison was therefore made of the morphological and physiological characters of the mushroom organism with the published records of those of the Pear Blight organism(1, 2 and 3). In most of these the two organisms seemed to be identical. Through the courtesy of Professor Barker, a culture of the latter organism was obtained and careful com-

parative experiments were made. The table given below shows how closely the two organisms agree in their physiological behaviour; certain morphological and cultural characters, however, point to differences which although they may not be specific differences at least serve to differentiate the two organisms as separate strains; these characters were constantly observed even after the two had been cultivated simultaneously through a succession of transfers during two months over which the experiments were made. Barker and Grove's organism does not grow so rapidly as the mushroom organism, it forms long thread-like involution-forms on the second day at 25° C. which the latter does not, it has its optimum for growth at 18° C. whereas the latter grows best at 25° C., the thermal death point which may be conceived to be one of the most secure of criteria is two degrees lower than that of the mushroom organism. Finally, a marked difference is found in the viscosity of liquid cultures: Barker's organism produces in bouillon and Uschinsky's solution<sup>1</sup> a gelatinous deposit in old cultures, whereas the whole solution becomes mucus-like in three-day-old cultures of the mushroom organism.

The organism described by Miss Doidge(2) as the cause of Pear-blossom Blight in S. Africa and named *Bacterium nectarophilum* has many characters in common with the mushroom disease organism. It differs only in the length and number of its flagella, both of which may be merely cultural variations, in the possession of a capsule and in its inability to liquefy gelatine. This last is a very striking character, but we have not as yet sufficient evidence to be able to judge in how far it is a constant one. The work of Morse(5) has shown that in one case, namely that of *Bacillus solanisaprus*, the power to liquefy gelatine could be developed under suitable cultural conditions and that this organism was really a strain of a vigorous liquefier, *Bacillus atrosepticus*. The identity of *Bacterium nectarophilum* with the organism described in this paper is then not beyond the region of possibility, and the hypothesis that Pear-blossom Blight and the Mushroom Disease may be produced by one and the same organism may yet prove to have some foundation in fact. Barker's organism was used in inoculation of mushrooms and found to have no effect upon them, but this has little significance since the organism had been in artificial culture for a considerable time and

<sup>1</sup> Barker and Grove's organism was found by Miss Doidge (2, p. 58) to give no growth in Uschinsky's solution. This was not my experience. Slight growth resulted and the liquid became strongly alkaline, then bleached at the bottom and a gelatinous precipitate was formed.

might well have lost its original parasitic properties. Careful observation will therefore be made next spring for signs of either disease, and it is hoped that the question of identity in etiology may then be definitely settled.

A disease of Mushrooms has previously been found by Tolaas<sup>(6)</sup> in which the symptoms were identical with those here described. His description of the causal organism is rather meagre, but in such reactions as are given, except in two instances, there is complete agreement with those of the organism described in this paper. The exceptions are in the reduction of nitrates and in the action upon starch (see comparative schedule, p. 218). It is not clear from his brief statement "Nitrates are reduced" how Tolaas arrived at this conclusion, and, in fact, it is possible that both in this and in testing the action of the organism upon starch the methods of technique employed by Tolaas were different from those employed by the authors, and have led them to opposite conclusions. Putting aside these two characters the organisms are closely similar, and, since the symptoms of the disease correspond exactly with those described by him, there seems little doubt that we have here the disease discovered by Tolaas. He suggests that the organism may be a parasitic strain of *Pseudomonas fluorescens*. This may indeed be the case, but until it is proved it seems well to give the mushroom disease organism a distinguishing name, and, in spite of the slight disagreement in physiological behaviour, the organism here described is believed to be identical with that of Tolaas and the name *Pseudomonas Tolaasi* is suggested. The organism, however, may yet be shown to be identical with that of Barker and Grove, in which case it will be necessary to re-name it in order to give due priority to these investigators.

*Control Measures.* Means of controlling the disease have not been investigated for the reason that it subsided and disappeared naturally. Tolaas found an efficient method of prevention of the disease in the fumigation of the beds with sulphur previous to spawning. In this connection it is of interest to note that sulphur fumigation has been the general practice in the houses at Brentford, but was abandoned for the season in which the outbreak occurred.

## Comparative Schedule.

## Pear Blossom Blight.

## Mushroom Disease.

	ORGANISM OF TOLAAS	ORGANISM OF PAINE	ORGANISM OF BARKER AND GROVE	ORGANISM OF DOIDGE
1. Dimensions	1.0 $\mu$ -1.5 $\mu$ $\times$ 0.5 $\mu$	0.9 $\mu$ -1.7 $\mu$ $\times$ 0.4 $\mu$ -0.5 $\mu$	2 $\mu$ -4 $\mu$ $\times$ 0.5 $\mu$ -0.8 $\mu$	0.5 $\mu$ -3 $\mu$ $\times$ 0.45 $\mu$ -0.7 $\mu$
2. Flagella	Polar 1 to 2	Polar 1 to 2, occasionally 3, 4 or 5	Polar 3 to 6	Polar 1 to 5
3. Capsule	—	Absent	Absent	Present
4. Optimum temperature	—	25° C.	18° C.	25° C.
5. Thermal death point	—	49°-50° C.	47°-48° C.	49° C.
6. Colour	Fluorescent	Fluorescent	Fluorescent	Fluorescent
7. Bouillon	Well clouded in 36 hours; pellicle and ring—very thick in some cases	Well clouded in 24 hours; thick pellicle in early cultures; thin pellicle and ring in later cultures; very viscous—mucoid	Slightly clouded in 24 hours; slight rim and pellicle; gelatinous precipitate	Well clouded in 24 hours; tendency to pellicle formation; considerable viscid sediment
8. Gelatine stab	Liquefaction saccate	Liquefaction infundibuliform; granular precipitate; growth in upper part of stab only	Liquefaction crateriform; white precipitate; no liquefaction along stab	No liquefaction; growth in upper part of stab only
9. Agar colonies	Shining greyish-white; greenish pigmentation of the medium	Round, raised, wet-shining; later lobed and spreading; greenish precipitate in medium	Round, raised, wet-shining; later lobed and spreading	Spreading irregular margins
10. Uschinsky's solution	No acid; no gas	Alkaline; no gas; bleached; mucoid deposit	Alkaline; no gas; bleached; very little growth	Heavy viscid deposit
11. Litmus milk	Coagulated; alkaline whey; complete digestion of casein	Coagulated; alkaline whey; partial digestion of casein; fluorescence	No coagulation; alkaline; complete digestion of casein	No coagulation; colour unchanged at first; bleached later; slow digestion of casein
12. Indol formation	Slight	Slight	None	None
13. Nitrate reduction	Reduced	Not reduced	Not reduced	Not reduced
14. Diastatic action	None	Feeble	Feeble	Feeble
15. Group number	221-2333133	221-2332123	221-3332123	222-2332122

## SUMMARY.

A disease of cultivated mushrooms is described in which patches of a chestnut brown colour so disfigure the pileus as to render the affected crop quite unmarketable.

The disease is identical with that described in America by Tolaas, but left unnamed by him.

The cause of the disease is a small bacterial parasite which may possibly be a strain of *Pseudomonas fluorescens* and may prove to be identical with the organism which produces Pear-blossom Blight.

Until its identity is established by further experiment it seems well to give it a distinguishing mark, and the name *Pseudomonas Tolaasi* is suggested.

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PHYSIOLOGICAL PRE-DETERMINATION: THE  
INFLUENCE OF THE PHYSIOLOGICAL CONDI-  
TION OF THE SEED UPON THE COURSE OF  
SUBSEQUENT GROWTH AND UPON THE YIELD.

IV. REVIEW OF LITERATURE. CHAPTER III.

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CHAPTER III

THE EFFECT OF CONDITIONS DURING GERMINATION AND IN  
THE EARLY SEEDLING STAGE UPON SUBSEQUENT GROWTH  
AND FINAL YIELD.

INTRODUCTION.

THE external conditions operating upon the seed during the critical stages of germination play an important part in determining the vigour of growth and the yield of the resulting plant. A variety of methods have been employed in endeavours to stimulate and accelerate seed-germination, but in few cases have the effects upon subsequent growth and final yield been studied. The experiments in which this has been

done, although few in number, are of considerable interest because they point to methods by means of which an action induced during germination may favourably or otherwise affect the whole course of development.

In many cases treatments of the seed previous to or during germination have been devised primarily with a view to seed-sterilisation and fungus control or with a view to increasing the percentage of seeds able to germinate. It has thus happened that observations on the physiological behaviour of the plants produced from these treated seeds have in most cases been incidental. This is unfortunate because in many cases an increase in the vigour and size of the seedlings has been noted, and because there is considerable evidence to show that a very close correlation exists between the size and vigour of the seedling, even in its earliest stages, and the final yield of the adult plant.

For instance, in the last report of the Experimental and Research Station of the Nursery and Market Garden Industries Development Society, Cheshunt, it is recorded as a result of a series of careful quantitative experiments carried out by Mr F. G. Gregory<sup>(16)</sup> that in the case of cucumbers a correlation exists between the area of the cotyledons and the dry weight of the plant after 30 days<sup>1</sup>, also between the growth rate of the main stem and laterals and the weight of fruit produced in the first two "flushes." It is obvious that such observations are of great importance to horticulturists since they enable the practical man to forecast the future efficiency of a plant from the seedling stage.

On the one hand recent work is tending to establish that the ordinary variations observed in the size and vigour of seedlings are reflected in the size of the final yield independently of the environmental conditions obtaining throughout the main period of the plant's life. On the other hand it is known that a large number of easily applicable, brief treatments of seeds previous to and during germination, favourably affect the size and vigour of the seedlings produced. But practically no attempt has hitherto been made to bring these two facts together and to discover whether increased size and vigour of seedlings due to seed-treatments will pre-determine an increase in the size of the final yield independently of the conditions obtaining during the main period of growth, in other words, whether increased yields can be obtained as the result of simple

<sup>1</sup> The authors are indebted to Mr Gregory for permission to make use of the following unpublished data:—

For correlation between	(i) Maximum area of the cotyledons	} $r = +.36.$
	(ii) Dry weight of the entire plant after 30 days	
For correlation between	(i) Maximum area of the cotyledons	} $r = +.54.$
	(ii) Maximum area of the first foliage leaf	

seed-treatments. When once the position is defined it becomes apparent that such tests might give positive results, and, if so, would be of considerable practical value owing to the simplicity, brevity, and cheapness of the operations involved.

In the following review we shall have to deal with a very wide range of seed-treatments. It therefore seems advisable to briefly consider, under the headings of the various arbitrary methods employed, the results which have been reported in the literature, and subsequently to deduce as far as possible our general conclusions from the whole of the available evidence.

#### TREATMENTS OF THE SEED AFFECTING THE NUTRITION OF THE SEEDLING.

We may classify the treatments affecting nutrition and deal with them under the following headings:

- (a) Removal or Partial Removal of the Cotyledons, Endosperm, etc.
- (b) Soaking Treatments;
- (c) Seed Impregnation Treatments (*i.e.* treatments in which the seeds are soaked in solutions of nutrient salts);
- (d) Enzyme Treatments.

##### (a) *Removal or Partial Removal of the Cotyledons, Endosperm, etc.*

An obvious method of varying the amount of reserve food-material available for the developing embryo has been to remove, or partially remove, the cotyledons of exalbuminous seeds or the endosperm of albuminous seeds. In this way series of plants with decreasing initial supplies of food-material available for the seedling have been compared with plants from untreated seeds. But it should be borne in mind that not only have the food-reserves been removed with the cotyledons, but also a certain proportion of the initial assimilating surface of the plant. This factor appears to have been entirely overlooked by the original workers.

Experiments conducted on these lines are worthy of considerable attention for although the treated seeds do not, of course, give results showing increased yields, yet they clearly demonstrate the potentiality for pre-determination which exists during the early stages in the development of the seedling. The effects of the amount of nutrient material originally available for the embryo are found in the case of annuals to last throughout the life of the plant, and to be clearly visible during the stages of vegetative development, of flowering, and of seeding.

Some of the earliest workers to record results of experiments dealing with the effects of removing part of the seed-reserves are Tautphoeus (35), Marek (28), and F. Haberlandt (18). These investigators worked with a considerable number of annuals, including plants with albuminous and exalbuminous seeds. They carefully cut off fractions of the endosperm or cotyledons and sowed the seeds on damp blotting paper, but the embryos were not provided with any artificial food-material. The seedlings thus produced were compared with normal seedlings grown under similar conditions<sup>1</sup>. The main facts which emerged from their results were, that the life-duration of the embryo plant in the absence of other food supplies was directly related to the amount of food-material supplied from the cotyledons or endosperm, and that the size of all the organs developed also bore a direct relation to the amount of food-material originally available.

The interesting implication of these early experiments, namely, that the effect of the food-reserves of the seed on the early growth of the embryo would continue throughout the life of the plant if the seedlings were afterwards artificially supplied with nutrient salts, was followed up by Wollny. In a series of experiments with peas grown in water-culture solutions Wollny (41) first showed that the amount of growth made by plants during the first month of development was directly proportional to the amount of food-material originally available for the embryo. The following table summarises the results of two of his experiments:

<sup>1</sup> The question has sometimes been raised as to whether embryos which have been completely deprived of their food-reserves immediately previous to germination are able to develop at all. There seems to be no doubt, however, that if the requisite food be artificially supplied in the form of simple substances, such as sugar and simple salts, development can take place.

Dubard and Urbain (9) reported that the endosperm was never indispensable to the development of the plant. They supplied embryos of wheat, oats, barley, *Ricinus*, etc. with Knop's solution during their early stages of growth, and subsequently planted them in ordinary soil and obtained mature plants. Brown and Morris (3) reared perfect plants from excised barley embryos fed during their early stages with cane-sugar and mineral nutrient-solutions, and kept in the light.

With regard to exalbuminous plants, on the other hand, such as the bean, cauliflower and savoy cabbage, Dubard and Urbain (10) found that they could not obtain development under the same conditions unless the cotyledons were left attached to the embryo for a period varying from 7 to 10 days, but Buekner and Kastle (4), who carried out experiments with Lima bean embryos deprived of their cotyledons, found that while development could not take place in the presence of salt solutions only, yet development became possible if reducing sugars were supplied to the embryos.

TABLE I (after Wollny).

*Experiment I (1874).*

Pea seedlings from entire seeds compared after 30 days with those from seeds from which one cotyledon had been removed. The seedlings were provided with nutrient solutions. Six seedlings in each experiment.

	Entire seeds (weight of a single seed = 0.405 gm.)	Treated seeds (weight = 0.202 gm.)
Average weight of the aerial parts of the plants ... ..	2.380 gm.	1.207 gm.
Average weight of the roots... ..	0.872 gm.	0.403 gm.
Average breadth of the main root ... ..	118 units*	108 units*
Average length of the plants ... ..	35.16 cm.	29.63 cm.
Average breadth of the internodes ... ..	185 units*	151 units*

*Experiment II (1875).*

Pea seedlings from entire seeds, seeds with  $\frac{1}{2}$ , and seeds with  $\frac{3}{4}$  of their cotyledons removed, compared after 4 weeks. The seedlings were provided with nutrient solutions. Four seedlings in each experiment.

	Entire seeds (weight of a single seed = 0.405 gm.)	Seeds with $\frac{1}{2}$ cotyledons	Seeds with $\frac{3}{4}$ cotyledons
Average weight of the aerial parts of the plants... ..	3.423 gm.	2.016 gm.	1.209 gm.
Average weight of the roots... ..	1.205 gm.	0.679 gm.	0.635 gm.
Average length of the plants... ..	51.9 cm.	43.7 cm.	33.8 cm.
Average breadth of the internodes ... ..	168 units*	146 units*	127 units*

\* 1 unit = 0.01428 mm.

Wollny subsequently conducted experiments with peas, vetches and winter rye in which the development of the plants, which were grown in soil under ordinary conditions, was followed through its *whole course*. The results obtained from entire seeds were compared with those obtained from seeds from which  $\frac{1}{3}$  and  $\frac{2}{3}$  of the cotyledons or endosperm had been removed. These results are given in Table II.

The total yield was very much larger in the case where entire seeds were used than in the case of seeds with  $\frac{2}{3}$  cotyledons or endosperm, and likewise very much larger again in the case of seeds with  $\frac{2}{3}$  cotyledons or endosperm than in the case of seeds with only  $\frac{1}{3}$  of their food-reserves available; but in contrast to the results obtained from the short-period experiments, the ratio of the final yields was not the same as the ratio of the amounts of initial food-reserves. The yield relative to the amount of reserve-material originally present was greater where the original food-reserve was small (see column X in Table II). Wollny (*l.c.*) summarises

his results in the following words: "Die Erträge in dem Grade steigen, als das Saatgut reicher an Reservestoffen ist, oder mit anderen Worten, die Verletzungen, welche die Reservebehälter der Samen treffen, in dem Grade ihres Umfanges das Produktionsvermögen der Pflanzen schädigen. Das relative Produktionsvermögen der Pflanzen im umgekehrten Verhältnisse zur Menge der Reservenernährung des Saatgutes steht."

TABLE II.

The seeds were first allowed to swell in water and were then divided into three groups, viz. (i) seeds from which  $\frac{2}{3}$  of the cotyledons or endosperm was removed, (ii) seeds from which  $\frac{1}{3}$  of the cotyledons or endosperm was removed, and (iii) seeds which were not treated (=controls). The seeds were then sown in plots which were 4 sq. m. in area, a distance of 20 cm. being allowed between the seeds.

Name of plant	Condition of the seeds	Weight of 100 seeds sown	Number of plants	Yield, on basis of 100 plants*		Number of plants at the harvest	X Yield relative to the amount of reserve-material originally present
				Seeds	Straw		
		gm.		gm.	gm.		
Peas	Entire seeds	31.5	100	583.5	2012	84	19.5
	Seeds with $\frac{2}{3}$ cotyledons	21.0	100	499.0	1482	83	24.8
	Seeds with $\frac{1}{3}$ cotyledons	10.5	100	310.5	1169	63	30.6
Vetches	Entire seeds	34.2	100	310.8	1138	87	10.9
	Seeds with $\frac{2}{3}$ cotyledons	22.8	100	291.2	922	77	13.8
	Seeds with $\frac{1}{3}$ cotyledons	11.4	100	196.6	526	49	18.2
Winter rye	Entire seeds	3.6	100	863.4	1510	96	241
	Seeds with $\frac{2}{3}$ endosperm	2.4	100	677.6	1148	81	283
	Seeds with $\frac{1}{3}$ endosperm	1.2	100	580.8	909	22	485

\* If the number of plants actually present at the harvest be taken into consideration, the differences in yield become much greater.

The results of these German agriculturists do not appear to have attracted much attention. Some thirty years later a number of French workers (Delassus, Dubard and Urbain, and Urbain) turned their attention to the same subject. These investigators were not working so directly from the economic point of view and their results, while confirming those of the earlier German workers, enter into greater details, and we may profitably describe the results obtained by them.

E. Delassus(7) experimented with beans, vetches, and lupins, new seeds of the same origin, and, as far as possible of the same weight, being selected. These seeds were soaked in water for 24 hours, after which treatment they were divided into four lots, viz.:

*Lot I.* Entire seeds (= controls);

*Lot II.* Seeds from which one half of one of the cotyledons was removed;

*Lot III.* Seeds from which one whole cotyledon was removed;

*Lot IV.* Seeds from which  $1\frac{1}{2}$  cotyledons were removed.

The seeds were then planted in uniform soil and received similar cultural methods. Morphological differences manifested themselves throughout the course of development. The suppression of a part of the food-reserves of the seed resulted from the outset in a retardation in the growth of the stem which lasted throughout the life of the plant. This fact is brought out in the following table, where the mean height of the stems of the beans and vetches at the end of the first three months of their development is indicated.

TABLE III.  
Mean height of stem after

	1 month's growth		2 months' growth		3 months' growth	
	Beans	Vetches	Beans	Vetches	Beans	Vetches
<i>Lot I</i>	82 mm.	103 mm.	204 mm.	225 mm.	362 mm.	770 mm.
<i>Lot II</i>	39	76	96	187	328	675
<i>Lot III</i>	30	73	78	177	260	670
<i>Lot IV</i>	36	63	60	154	200	590

The number and size of the leaves and also the total fresh and dry weights of the aerial parts of the plants at each stage in their development remained approximately proportional to the amount of reserve food-material originally at the disposal of the embryo, as the following figures show:

TABLE IV.

		Number of leaves produced after											
		1 month's growth				2 months' growth				3 months' growth			
		Lot I	Lot II	Lot III	Lot IV	Lot I	Lot II	Lot III	Lot IV	Lot I	Lot II	Lot III	Lot IV
Beans	...	10	6	4	5	21	12	9	8	34	21	14	13
Vetches	...	29	23	24	17	165	117	126	77	327	240	228	176
		Dimensions of the leaves											
		mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Beans	{ Breadth ...	33	18	17	18	35	34	31	21	38	40	36	33
	{ Length ...	51	31	27	28	54	50	34	28	55	57	49	45
Vetches	{ Breadth ...	6	4	4	3	10	8	9	7	—	—	—	—
	{ Length ...	52	45	41	31	75	74	69	64	83	84	70	78
		Weight of the aerial part of the plant in gms.											
Beans	{ Fresh weight	49.9	35.2	17.4	16.5	—	—	—	—	—	—	—	—
	{ Dry weight	5.3	2.6	1.7	2.2	—	—	—	—	—	—	—	—
Vetches	{ Fresh weight	18.5	9.9	11.3	4.9	185	102	138	51.5	890	417	406	260
	{ Dry weight	2.6	1.5	1.7	0.7	25.5	14	18	8	183	83	77.5	49.1

A study of the root system is also interesting. Removal of the food-reserves appears to bring about a progressive disappearance of the secondary roots. The main root in the case of plants belonging to Lot I, is not always clearly distinguished; on the other hand, in the case of the plants belonging to Lots II, III, and IV, it shows a vigorous development.

The time of flowering and the total number of flowers produced were also influenced by the amount of reserve food-material available for the embryo. Every plant flowered, but, in the case of the plants belonging to Lots II, III, and IV, the flowers were produced later than in the case of the controls; and whereas there were on an average 36 flowers per stalk in the case of the beans belonging to Lot I (*i.e.* the controls), there were only 20, 16, and 10 flowers per stalk respectively in the plants belonging to Lots II, III, and IV.

The fruits were heavier and more numerous on the control plants, the average weight of 100 bean seeds harvested the same day being as follows:

<i>Lot I</i>	<i>Lot II</i>	<i>Lot III</i>	<i>Lot IV</i>
245 gm.	170 gm.	137 gm.	119 gm.

In conclusion the author made a further interesting observation, namely, that the suppression of the seed-reserves markedly decreased the power of the resulting plant to resist the attack of parasitic fungi.

In a later investigation Delassus(8) examined in detail the morphological modifications brought about by the complete or partial removal of the cotyledons of a number of leguminous plants, including the bean (*Vicia Faba*) and lupin. He followed the same routine as in the previous experiment. It was found by microscopical examination that the various tissues of all the organs of the plants produced from the treated seeds were reduced in size in proportion to the amount of cotyledonary tissue removed, and that this reduction was not only in the number of the constituent cells but also in the dimensions of individual cells. This reduction in tissue development was observable at the outset and persisted throughout the life of the plant<sup>1</sup>.

With regard to albuminous seed (into which class the cereals fall) the method usually adopted has been to completely remove the endosperm (or perisperm) before germination or at various intervals after the commencement of germination. The effects upon the subsequent

<sup>1</sup> The influence of food-reserves is most marked in the earliest hours of germination, but their removal at quite a late stage in the development of the seedling may still give results similar in nature to those reported above, as is shown by the results obtained by Gain (14), who removed the cotyledons from lupin seedlings on the 12th day after sowing.

development of the plant of the removal at an early stage of the endosperm of albuminous seeds are in the main quite similar to those that occur in the case of exalbuminous seeds deprived wholly, or in part, of their cotyledons.

J. A. Urbain<sup>(36)</sup> in 1913 carried out experiments with oats, maize, fennel, *Saponaria* sp., *Nigella hispanica*, *Papaver somniferum*, and *Ricinus communis*. As in the case of Delassus' experiments, this author found that the effects produced as the result of removal of the seed-reserves were not merely temporary, from which the plant might recover after it had become established, but persisted throughout the whole course of its development. In all the species tested the effects were the same in character; the suppression of the endosperm (or perisperm) led to a dwarf habit, obvious modifications in the external morphology of the leaves, precocious flowering, sometimes followed by a second flowering, and frequent sexual anomalies in the course of the first flowering period.

It is of interest to record in some detail a single experiment of Urbain's in illustration of his results. Embryos of *Ricinus communis* were isolated from their food-reserves on the second day of germination and were kept in a greenhouse at 25° C. until the 12th day, when they were "potted out." On the 35th day they were transplanted to open ground together with controls. On the 47th day the controls were 1 metre in height whereas the experimental plants were only  $\frac{1}{3}$  metre in height. The controls had the usual 9-lobed leaves, but the leaves of the treated plants possessed only 4 lobes. Flower spikes had appeared in the axil of the 4th leaf only in the case of the treated plants, the male flowers on these flower-spikes exhibiting various abnormalities. During this flowering period the growth of the treated plants was arrested, but the plants subsequently continued their growth. About the 74th day the controls produced flowers, and at the same time the plants from the treated seeds produced a second crop of flowers, the controls being at this stage 2 metres high as against  $\frac{1}{2}$  metre in the case of the experimental plants.

Results of a similar nature were obtained with the other albuminous seeds investigated by Urbain (*e.g.* oats, maize, fennel, etc.).

Consideration of the above experiments, both of the earlier German agriculturists and of the more recent French school, strongly suggests that the influence exercised upon the plant throughout its development by the food-reserves of the seed is a phenomenon which needs further examination.

The work of Gressler(17), Hackenberg(19), Kiltz(23), and Gericke(15) throws perhaps the best light upon this question. These authors obtained dry weight measurements from week to week. From the data so obtained a complete analysis of the normal growth as compared with the growth of plants from which various amounts of the initial food-reserves had been removed, can be made.

The following table and figures (Table V and Figs. 1-3) summarise some of the results obtained by Gericke (*l.c.*) with *Helianthus annuus*, var. *Bismarckianus*. The results obtained with (a) normal plants, (b) plants from which one cotyledon and one foliage leaf were removed at a very early stage, and (c) plants from which both cotyledons were removed, are represented.

TABLE V.

*Increase in dry weight of A. normal plants of Helianthus annuus Bismarckianus; B. plants from which one cotyledon and one foliage leaf had been removed; and C. plants from which both cotyledons had been removed.*

Growth period in weeks	Dry weight of five plants				
	A	B	C	Ratio $\frac{B}{A}$	Ratio $\frac{C}{A}$
1	·0571	·0489*	·0343*	·856	·601
2	·159	·0742	·0671	·466	·422
3	·579	·145	·182	·255	·314
4	2·008	·525	·463	·261	·231
5	6·225	1·863	1·163	·299	·187
6	→ 16·871	6·325	2·594	·375	·154
7	38·23	17·81	4·877	·465	·127
8	70·73	42·11	7·657	·595	·108
9	108·68	69·27	11·635	·638	·107
10	157·00	114·48	—	·729	—
11	230·00	—	—	—	—
12	310·43	—	—	—	—
13	403·00	—	—	—	—
14	504·00	—	—	—	—
15	631·00	—	—	—	—
16	707·00	—	—	—	—
17	769·00	—	—	—	—

The arrow indicates the point at which flower-bud formation begins in the case of normal plants.

\* These figures may be taken as values of the *original* amount of food-reserves. The initial dry weight of the embryo, apart from the reserves, is negligible, and the seeds are exalbuminous. The cotyledons and foliage leaves were removed from the experimental plants during the first week of growth after the embryo had absorbed part of the food-material stored in them.

With regard to the growth of the normal plant the general law was formulated to the effect that during the vegetative growth period *the dry weight of the plant increases according to the principle of a geometric series*<sup>1</sup>. This law amounts to a statement that the total dry weight of the plant increases on a "compound interest" basis. From this law it follows that there are two main factors which control the final yield:

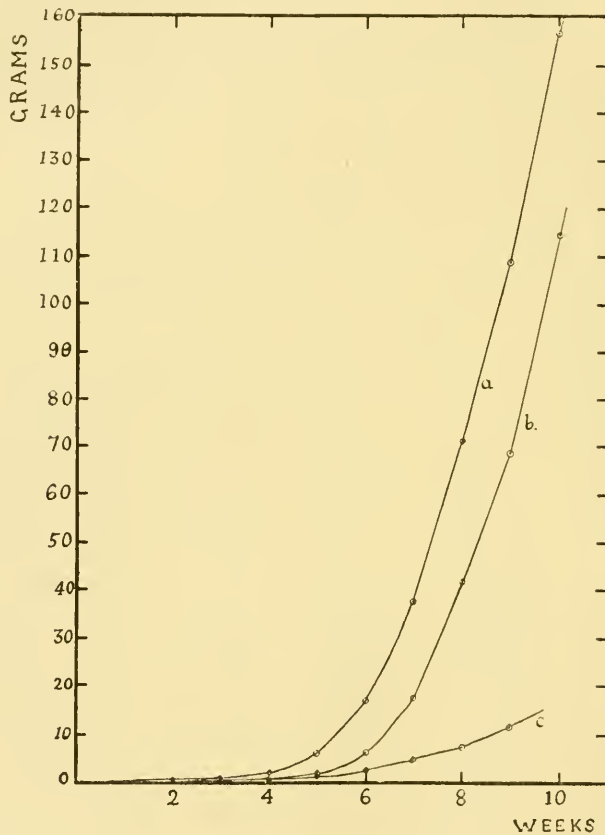


Fig. 1. Total dry-weight increase in the case of *a*, normal plants of *Helianthus annuus* *Bismarckianus*; *b*, plants from which one cotyledon and one foliage leaf had been removed; *c*, plants from which both cotyledons had been removed. (After Gericke.)

<sup>1</sup> The results of a series of investigations, which were carried out in Germany on the suggestion of the Ministry of Agriculture, and which were recorded in the *Landwirthschaftliche Jahrbücher*, 1877-79, supply a mass of detailed data with regard to the normal growth, the increase in dry-weight, and the change in leaf-area of a number of cultivated plants. These data appear to support the general law formulated above.

(1) the initial "capital," and (2) the "rate of interest<sup>1</sup>." The first of these factors has a pre-determining effect upon the development of the plant and cannot be influenced by subsequent environmental conditions, but the second factor would naturally be under the influence to some extent of the environmental conditions obtaining during the main growth period of the plant.

Curve *a* in Fig. 2 shows the change occurring from week to week in the "rate of interest" of the growth of normal plants. In this case the "rate of interest" or, in other words, the "efficiency" of the plant is at its maximum during the second week of growth and subsequently gradually falls throughout the course of later development<sup>2</sup>.

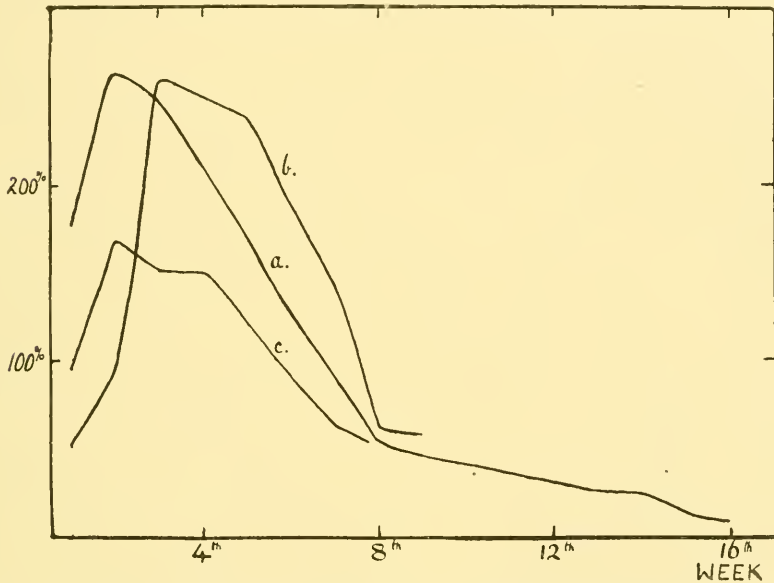


Fig. 2. Change in the percentage increase in dry weight from week to week (*i.e.* "rate of interest") in the case of *a*, normal plants of *Helianthus annuus Bismarckianus*; *b*, plants from which one cotyledon and one foliage leaf had been removed; *c*, plants from which both cotyledons had been removed.

<sup>1</sup> The German authors used the expression "Substanzquotient," which is the dry weight of the plant at time  $n$  divided by the dry weight of the plant at the time  $n - 1$ . The unit of time taken is arbitrary and is one week. It seems to us more suitable to use the expression "rate of interest." The "rate of interest" = 100 (Substanzquotient - 1).

<sup>2</sup> In the case of the data obtained by Gericke the question which immediately presents itself is how far the fall in the "rate of interest" curve is due to inherent causes and how far it is due to the limiting factors of the environment, *e.g.* light. Gericke's data allow one to rule out temperature, but the author himself suggests the possibility of light as the limiting factor. The seeds were sown during the end of May and the beginning of June.

We may now consider for comparison with the normal plant the results obtained with plants from which different proportions of the initial food-reserves had been removed. Curves *b* and *c* (in Figs. 1 and 2) show that the removal of part of the initial food-reserves affects the subsequent growth and yield of the plant in two distinct ways. In the first place, broadly speaking the growth made by the plant, and consequently its final yield, is *approximately* proportional to the amount of food-material originally present; this may be called the pre-determining effect of the initial "capital." Secondly, the partial removal of the food-reserves has a specific pre-determining effect upon the "rate of interest," and it is in consequence of this fact that strict proportionality between the experimental and the control plants is not maintained.

The effect of loss of food-material upon the "rate of interest" is brought out in Fig. 2. In the case of the removal of one cotyledon and one foliage leaf the "rate of interest" is less than that of the control during the first three weeks. Later it increases rapidly, surpasses, and remains higher than that of the normal plant during the remainder of the growth period. Where both cotyledons are removed, however, the consequences are different. The "rate of interest" remains less than that of the normal plant throughout the whole course of development.

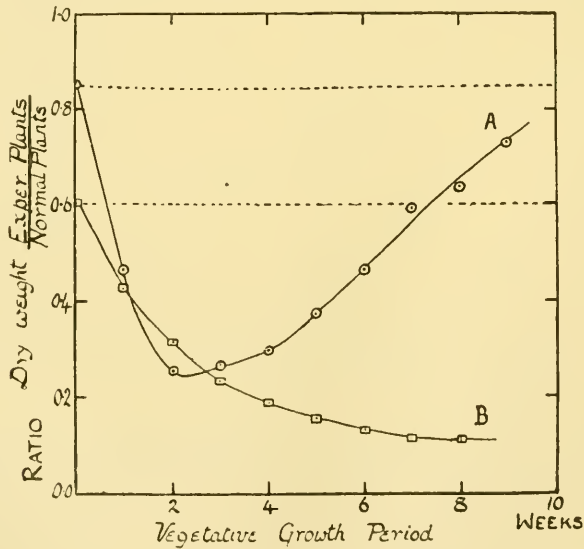


Fig. 3.

$$A = \frac{\text{Dry weight of the plants from which one cotyledon and one foliage leaf had been removed}}{\text{Dry weight of the normal plants.}}$$

$$B = \frac{\text{Dry weight of the plants from which both cotyledons had been removed}}{\text{Dry weight of the normal plants.}}$$

The manner in which this influence of the removal of part of the initial food-reserves upon the "rate of interest" affects the dry weight ratio is shown in Fig. 3, which is constructed from Gericke's data. Both sets of experimental plants are at the outset less productive relatively to the original dry weight than the controls. The ratio

$$\frac{\text{Dry weight of the experimental plants}}{\text{Dry weight of the control plants}}$$

decreases. In the later weeks of growth the development of the experimental plants from which one cotyledon and one foliage leaf had been removed differs widely from that of the plants from which both cotyledons had been removed. In the first case recovery sets in and the *relative* productivity rapidly increases and surpasses that of the controls so that at the end of the vegetative period the ratio  $\frac{\text{Yield from the experimental plants}}{\text{Yield from the control plants}}$  is nearly the same as the ratio of the initial "capital."

In contrast, the plants from which both cotyledons had been removed, do not recover. They remain relatively less productive than the controls throughout their development and as a result, the final yields from the controls is nine times that from the experimental plants, whereas the initial "capital" of the controls was only  $1\frac{1}{2}$  times that of the experimental plants.

Wollny, taking the weights of the final yields found, as we have stated above, that his plants, from which  $\frac{1}{3}$  or  $\frac{2}{3}$  of the cotyledons had been removed, were *relatively* more productive than those from untreated seeds, and it is seen that Gericke's data throw much light on Wollny's results.

We have still to seek an explanation for the following facts which were especially expressed by the French school of workers, namely—(1) that the seedlings which have been deprived of a large part of the food-materials elaborated by the parent-plant show symptoms characteristic of starvation although they may be equipped with all the organs necessary for the elaboration of their own food-supply (the removal of the parental supply would naturally be expected to cause only a slower and smaller initial growth); (2) that such seedlings commonly show in addition to starvation symptoms definite morphological abnormalities.

These two facts, taken together, seem to give some grounds for the view that the seedlings obtain from the food-reserves elaborated by the parent some nutritional elements necessary for normal growth and development which they cannot elaborate themselves except at some considerably later stage in their development.

In concluding this section dealing with the effect upon subsequent growth and final yield of the total or partial removal of the initial food-reserves of the plant, the main generalisation to be made on the basis of the evidence reviewed is that the yield from the plant is approximately proportional to the initial amount of food-reserves available for the embryo.

(b) *The effects of soaking seeds in water.*

The pre-determining effects of soaking seeds in water are often pronounced. From the point of view of growth and yield, it appears from the evidence we are about to review that these effects may be good or bad, the result depending upon the external conditions during the soaking treatment and upon its duration. How far this form of treatment is properly included here under the head of treatments affecting nutrition, is debatable. There is certainly a considerable exosmosis of soluble food-reserves from seeds soaked in water, and on the basis of such results as are described above, this should cause a depression in growth and yield. On the other hand, owing to the fact that actual growth is inhibited in the embryo under water, time is allowed for a complete mobilisation of food-reserves in readiness for very active growth as soon as the seed is sown, so that the early stages of development may be unusually vigorous. The advantage of considering in this place the question of the pre-determining effects of soaking seeds in water is that in dealing later with other seed treatments it will be found that soaking the seed in water is necessarily bound up with many of these<sup>1</sup>.

In the late seventies and early eighties of last century a group of German workers, notably C. Kraus<sup>(25)</sup> and <sup>(26)</sup> and E. Wollny<sup>(42)</sup>, investigated very fully the effect upon subsequent growth and yield of soaking seeds in water and obtained remarkable results. These authors emphasised the importance of the conditions under which the soaking was carried out, especially with regard to the relative amount of water employed. Beneficial effects upon growth and yield were obtained when the soaking of the seed was carried out with the least possible amount

<sup>1</sup> In the Wolfryn process of electrical treatment of seeds for the purpose of increasing the yield, cereal and other seeds are immersed in large tanks containing weak solutions of NaCl or other salts through which a direct current is passed. It is stated by the inventor, Mr H. E. Fry (see *Letter to Agricultural Gazette*, LXXXVIII, No. 2328, 1918, p. 138), that in the course of the experimental tests, it was found that although the electrically treated seeds gave the best results, the *soaking treatment alone* gave better results than no treatment at all.

of water, and they believed that the main effect of using as small an amount of water as possible lay in reducing the loss by exosmosis of essential soluble food-reserves during the process of soaking. It may be pointed out that the minimum amount of water is at the same time a favourable condition for the supply of oxygen to the seed and for the removal of carbon dioxide from the seed during soaking. The time of immersion employed varied from 24–100 hours according to the species of seed under investigation. Generally speaking the time of immersion allowed was just long enough for the swelling of the seed to become complete. These authors, in view of the possible economic application of this seed-treatment, carefully tested how far the re-drying of the seed would affect the results, and found that in general the re-drying of the seed after soaking, especially if carried out slowly, did not appreciably alter the beneficial influence of the process. The following general conclusions may be drawn from their experiments.

(I) *Effect on germination.*

(a) Seeds soaked in the minimum amount of water and afterwards *slowly dried* at ordinary temperatures imbibe water and develop more quickly, when again allowed to take up water and germinate<sup>1</sup>, than untreated seeds.

(b) Seeds which are *rapidly dried* after the initial soaking germinate more slowly than untreated seeds.

(c) Seeds swollen in water and sown in the still moist condition germinate more quickly than untreated seeds.

(II) *Effect on subsequent growth and final yield*<sup>2</sup>.

(a) In general, seeds soaked in water previous to germination give rise to slightly fewer plants than untreated seeds. If the seeds are re-dried too rapidly the number of plants produced may be considerably diminished.

(b) Soaking seeds in water previous to germination tends to accentuate individual differences in the growth of the plants produced from them.

(c) Plants from seeds swollen in water previous to sowing develop at first more quickly than those from untreated seeds, but this initial difference in growth tends to disappear later on.

<sup>1</sup> For detailed experiments dealing with this point see Tautphoeus (35).

<sup>2</sup> It is immaterial whether the seeds after swelling in water are *slowly* re-dried before sowing or whether they are sown at once in the moist condition.

(d) At a later stage the experimental plants take the lead, and flower before the control plants.

(e) The experimental plants have a longer growth-period and flowering-period than the control plants, arrive at maturity at a later date and give larger final yields, and this probably accounts for the fact that plants from seeds which are soaked in water previous to sowing are more productive than plants from untreated seeds.

(f) Soaking the seed in a relatively large volume of water, for instance, ten volumes of water to one volume of seed, reduces the beneficial effect, and may even be harmful.

(g) The soaking treatment is especially useful when the seeds are sown in light dry soil, provided that the seed is well covered with the soil.

In view of the importance of their results we may give in full an account of a few typical experiments carried out by Kraus<sup>(25)</sup> and by Wollny<sup>(42)</sup>. Kraus carefully analysed at all stages of development of the plants the effect of the seed treatment. The following is a summary of the results of three of his experiments carried out with beans, peas, and seeds of *Lupinus angustifolium* respectively.

#### Experimental data.

*Soil.* Deep loamy sand (Keuper).

*Previous History.* Crop maize, stable manure applied.

*Preparation of the Soil.* In the spring the ground was dug deeply with a spade.

*Cultivation of the Ground.* Weeded and hoed.

*Date of Sowing.* April 26th.

*Weather Conditions during Experiment:*

Month	(a) Temperature			(b) Weather			
	Maximum	Minimum	Mean	Fine	Cloudy	Rainy	Changeable
April	7°	3°	5.4°	8	17	4	1
May	14	0	7.5	10	15	6	—
June	19	12	14.6	13	7	3	7
July	15	8	11.6	6	8	15	2
August	19	10	13.6	17	7	6	1

*Kind of Seed used.* Carefully selected large seeds.

*Treatment of the Seed:*

1. Untreated (=controls);
2. Swollen in water for 24 hours, afterwards *quickly* dried;
3. Swollen in water for 24 hours, sown in the moist condition.

(During the soaking-treatment a few of the peas had sprouted.)

*Spacing and Depth of Sowing:*

	Spacing	Depth	Number of seeds in each row
Beans	15 cm.	4 cm.	42
Peas	10 cm.	3 cm.	42
Lupins	15 cm.	3 cm.	30

*Harvested.* August 30th.

The relative degree of development of the experimental and control plants at various stages was noted throughout the experiment. The results obtained were as follows:

XW = plants from seeds which were swollen and sown in the moist condition;  
 XD = " " " " and *quickly* dried;  
 C = controls (= plants from untreated seeds).

(i) *Beans.*

Comparative degrees of development at different periods	{	Order in which seeds sprouted	XW; C; XD
			1. XW = C = XD
			2. XW = C > XD
			3. XW > C > XD
			4. XW > XD > C
		Order in which plants ripened off	C; XW; XD.

(ii) *Peas.*

Comparative degrees of development at different periods	{	Order in which seeds sprouted	XW; C; XD
			1. XW = C = XD
			2. XW = C > XD
			3. XW > C = XD
			4. XW > XD > C
		Order in which plants ripened off	C; XW; XD.

(iii) *Lupins.*

Comparative degrees of development at different periods	{	Order in which seeds sprouted	XW; XD; C
			1. XW = C = XD
			2. XW > C = XD
			3. XW > XD > C

At the time of harvesting a very detailed analysis of every individual plant of the crop was made of which Table VI is a summary.

With reference to the yield it is to be noted in these experiments that the untreated seed is strictly comparable with the seeds sown in the swollen condition after soaking, but not with the seed sown after re-drying, because while in the former case the number of plants is the same per given area, in the latter case the plants are far fewer in number and consequently much wider spacing per plant is allowed.

Where a comparison therefore is legitimate, as between untreated seeds and seeds soaked but sown in the moist condition, the treatment clearly increased the yield in all three experiments; and this increase was correlated with modifications in development at all stages, as described above.

In the case of a comparison between untreated seed and seed quickly dried after soaking the yield *per plant* is markedly larger in the case of the treated seed, but the total yield per given area is smaller. Any conclusions drawn from the figures for the yield per plant are vitiated

TABLE VI.  
Harvest results.

	Beans			Peas			Lupins		
	C	XD	XW	C	XD	XW	C	XD	XW
Number of seeds sown	42	42	42	42	42	42	30	30	30
Number of plants produced	42	9	42	39	17	40	26	15	27
Average length of stem per plant	60 cm.	68.8 cm.	74.7 cm.	139 cm.	151 cm.	216 cm.	40.6 cm.	41.8 cm.	42.8 cm.
Average number of internodes per plant	18.6	24.7	21.8	—	—	—	—	—	—
Average number of pods per plant	6	13.8	8.2	6.4	8	7.6	43	68	53
Average number of pods per main stem	5.7	6.5	6.4	—	—	—	—	—	—
Average number of seeds per plant	15.8	43.8	20.7	22.2	28.7	35.7	—	—	—
Number of successive inflorescences	—	—	—	—	—	—	3.6	3.8	3.7
Percentage of plants that were branched	24	89	45	—	—	—	58	87	56
Percentage of pods fully ripe at harvest	—	—	—	40.6	25.5	9.7	—	—	—
Percentage of plants in which the pods were fully ripe at harvest	74	11	50	—	—	—	—	—	—
Total yield ( <i>i.e.</i> total number of seeds produced)	663	391	869	869	489	1429	—	—	—
Percentage increase or decrease in total yield of experimental plants as compared with the controls	—	-41	+31	—	-44	+65	—	—	—

by the fact that the plants from the treated seed have a much wider spacing owing to the large mortality amongst them.

Wollny's<sup>(42)</sup> experiments extended over a number of years and his attention was directed more to the effect upon final yield of the soaking treatment of the seeds. The following tables give a detailed summary of his results.

The most noteworthy features of these results were firstly, that increased yields of grain were obtained in every case (with the exception of Winter Rye) as the result of the soaking treatment; and secondly, that a reverse effect, *i.e.* a decreased yield, was obtained when the swelling of the seeds was carried out in excess of water.

Since the publication of the work of Kraus and Wollny we have not been able to find in the literature any reference to the subject until

TABLE VII.

*Comparison of Yields from (1) seeds soaked in water and sown in the moist condition, (2) seeds soaked and redried before sowing, and (3) untreated seeds.*

The peas, beans, rye, and the vetch seeds were allowed to swell in the minimum amount of water for 36 hours, the maize for 72 hours. The re-drying process extended over 14 days during which the seeds were left exposed to the sun and air.

Kind of seed	Date of experiment	Treatment of the seed	Number of plants		Yield from 100 plants		Average weight of 100 seeds gm.	Percentage increase or decrease in yield of seeds from experimental plants as compared with controls
			Original	At the harvest	Seeds gm.	Straw gm.		
Victoria peas	1877	{ Swollen, sown moist	64	58	532.9*	1324*	—	+29
		{ Untreated	64	59	413.3*	1443*	—	
Beans	1877	{ Swollen, sown moist	64	57	920.5*	2436*	—	+27
		{ Untreated	64	60	727.6*	2215*	—	
Victoria peas	1878	{ Swollen, sown moist	100	88	1188.6	1778	—	+23
		{ Untreated	100	94	967.0	1658	—	
Victoria peas	1882	{ Swollen, redried	92	74	548.6	1594	—	+9
		{ Untreated	97	76	502.6	1684	—	
Vetch	1882	{ Swollen, redried	90	79	440.4	910	—	+6
		{ Untreated	96	82	417.0	1074	—	
Winter rye	1882	{ Swollen, sown moist	100	96	867.0	1510	—	-6
		{ Untreated	100	100	925.0	1690	—	
Victoria peas	1882	{ Swollen, sown moist	95	84	602.0	2012	—	+10
		{ Untreated	97	90	548.0	1998	—	
Vetch	1882	{ Swollen, sown moist	89	87	414.0	1138	—	+7
		{ Untreated	98	89	388.0	1146	—	
Victoria peas	1883	{ Swollen, sown moist	69	62	445.0	1355	—	+17
		{ Swollen, redried	79	71	511.0	1408	—	+34
		{ Untreated	93	83	382.0	952	—	
Beans	1883	{ Swollen, sown moist	99	99	869.0	1545	46.5	+9
		{ Swollen, redried	100	96	868.0	1459	45.6	+9
		{ Untreated	99	94	798.0	1468	38.8	
Winter rye	1883/4	{ Swollen, sown moist	99	60	1160.0	1983	2.99	-8
		{ Swollen, redried	95	83	1101.0	1831	3.17	-13
		{ Untreated	93	70	1263.0	2314	3.14	
Summer rye	1884	{ Swollen, sown moist	94	80	497.0	975	2.75	+5
		{ Swollen, redried	85	53	559.0	1302	2.38	+18
		{ Untreated	89	78	475.0	1051	2.57	
Maize	1884	{ Swollen, sown moist	27	27	12515.0	46740	38.9	+11
		{ Swollen, redried	27	26	14792.0	47577	36.1	+31
		{ Untreated	27	27	11274.0	41630	36.4	
Victoria peas	1884	{ Swollen, sown moist	96	92	730.0	1282	27.9	+9
		{ Swollen, redried	92	87	705.0	1310	29.4	+5
		{ Untreated	94	87	668.0	1184	28.7	
Beans	1884	{ Swollen, sown moist	95	77	381.0	766	47.2	+3
		{ Swollen, redried	95	82	402.0	792	51.0	+9
		{ Untreated	94	80	369.0	725	47.7	

\* Yield from 64 plants.

TABLE VIII.

*The Harmful Effect of Soaking Seeds in Excess of Water.*

In these experiments the volume of water used was ten times that of the seed.

Kind of seed	Treatment of the seed	Number of plants at the harvest	Yield from 100 plants		Average weight of 100 seeds	Percentage decrease in yield of seeds from experimental plants as compared with controls
			Seeds	Straw		
			gm.	gm.	gm.	
Summer rye	{ Untreated	78	475	1051	25.7	—
	{ Soaked	65	359	877	22.7	-25
Peas	{ Untreated	87	668	1184	28.7	—
	{ Soaked	84	546	1214	27.5	-18
Beans	Untreated	80	369	725	47.7	—
	Soaked	77	264	766	54.4	-28

1907, when two papers by Eberhart<sup>(11)</sup> and Schleh<sup>(33)</sup> respectively appeared. These authors took up the question as it was left by Wollny and Kraus.

Eberhart at the Agricultural Institute of the University of Jena tested the effect upon yield of soaking seeds of barley and beans. The result of a pot experiment carried out in triplicate with barley appeared to be the same in every way as that obtained by Kraus and Wollny, in other words, the soaking of the seed affected the whole course of development and increased the final yield (Table IX).

TABLE IX (after Eberhart).

*Soil.* Clayey loam rich in humus.

*Kind of Seed.* Barley (weight of 100 grains = 5.21 gm.).

*Date of Sowing.* April 21st.

*Period of Soaking.* 48 hours.

*Temperature of the water.* 10° Cel.

*Height of Plants on May 16th.* { From untreated seeds = av. 13.1 cm.  
 { From seeds previously swelled = av. 15.9 cm.

*Harvest results (August 5th).*

	From untreated seed	From treated seed
Number of stems per pot ... ..	18.5	20.5
Average number of stems per plant ... ..	3.08	3.41
Average length of the stems ... ..	49.59 cm.	56.50 cm.
Average total weight of a plant ... ..	9.28 gm.	11.70 gm.
Average weight of heads per plant ... ..	4.52 gm.	5.73 gm.
Average weight of straw per plant ... ..	4.76 gm.	5.96 gm.
Average number of grains per plant ... ..	74.16	89.50
Average weight of the grains per plant ... ..	3.45 gm.	4.56 gm.

In the case of the pot experiments with beans, the effect of different soil-water-content (30 per cent. and 60 per cent.) upon the results obtained by the soaking treatment was ascertained. The effect of the soaking treatment upon yield was found to be independent of the amount of moisture in the soil. Similar results were obtained with oats.

Finally a field experiment with beans was described in which the yield from plants from untreated seeds was compared with that from plants from seeds swelled and afterwards redried. The results obtained are summarised below:

TABLE X.  
*Harvest Results.*

	Number of plants*	Weight of pods	Weight of straw	Average length of the stem	Average number of pods per plant	Weight of seeds
Untreated seed	96	609.0 gm.	776.0 gm.	97.75 cm.	4.19	474.3 gm.
Seed swollen in water previous to sowing	96.6	697.8 gm.	877.6 gm.	103.02 cm.	5.08	543.3 gm. (+15%)
Seed swollen in water and then redried previous to sowing	95.3	677.1 gm.	875.6 gm.	101.74 cm.	5.03	526.3 gm. (+11%)

\* Mean of three experiments.

Schleh reported the following results of large-scale field tests with oats carried out to determine whether the soaking treatment of seeds was of any economic value. On moist soil with a high humus content<sup>1</sup>

<sup>1</sup>

I. *Mechanical Analysis of the Soil.*

Size of sand particles	Surface soil of Plots 1 and 2	Surface soil of Plots 7 and 8
2-1 mm.	0.1 %	0.1 %
1-0.5 mm.	13.4	16.5
0.5-0.25 mm.	22.2	20.8
0.2 mm.	51.1	50.2
Silt	13.2	12.4

II. *Chemical Analysis of the Soil.*

	Surface soil of Plots 1 and 2	Surface soil of Plots 7 and 8
Organic matter ... ..	3.05 %	1.15 %
nitrogen ... ..	0.156	0.122
Mineral matter ... ..	96.95 %	98.85 %
sodium chloride ... ..	0.153	0.146
magnesia ... ..	0.109	0.090
potash ... ..	0.110	0.112
phosphoric acid ... ..	0.138	0.141

an increase of 90 kilograms of grain, 300 kilograms of straw, and 280 kilograms of chaff per hectare in favour of the treated seed was obtained. On dry soil with a low humus content, on the other hand, the plants from the treated seeds gave a slightly smaller yield than the controls to the following extent, 10 kilograms of grain, 4 kilograms of straw, and 20 kilograms of chaff per hectare. The seeds used in Schleh's experiment were soaked for 48 hours in distilled water.

*The importance of the conditions under which the soaking treatment is carried out.*

Although the soaking treatment appears to be simple, the immediate and subsequent effects of soaking seeds in water are complex, and differ widely according to the conditions under which the soaking of the seed is carried out.

During the natural uptake of water preceding germination the whole physiological system of the seed is set in motion. Enzymes are liberated, no doubt, from pro-enzymes, and soluble food-materials increase, etc.

When seeds are immersed in water for the purpose of swelling, the conditions to which the plant is subjected are abnormal, as is shown by the fact that germination is inhibited. Under these abnormal conditions there is no doubt that many of the complex of processes usually accompanying the initiation of germination are modified. In addition, however, it is definitely known that a considerable exosmosis of essential soluble food-reserves occurs<sup>1</sup>, the supply of oxygen to the seed is decreased, and carbon dioxide accumulates in the seed.

It is obvious that both the leaching out of essential food-reserves, and the conditions of oxygen supply and of carbon dioxide escape, must be greatly influenced by such factors as time of soaking, temperature of soaking, relative amount of water used, movement of the water, surface of the water exposed to the air, size of the seed, and density of the seed-mass.

How far the leaching out of food-material and the modification of the rate of gaseous exchange under the abnormal conditions of soaking are related to the beneficial alterations in subsequent development and in yield observed has not been satisfactorily investigated. Wollny and his contemporaries considered that the leaching out of essential food-reserves was always detrimental and comparable to the partial removal of the cotyledons or endosperm as described above, and endeavoured

<sup>1</sup> See especially A. Zöbl (44), F. Haberlandt (18), T. Yokoi (43) and G. André (1). Data published by Zöbl and André show that the phosphorus and potassium of the seed-contents are very rapidly lost when seeds are soaked in pure water.

to eliminate such exosmosis as far as possible by using the minimum amount of water necessary for the complete swelling of the seed.

That the exosmosis of soluble food-material, or the lack of oxygen combined with accumulation of carbon dioxide which must necessarily accompany the immersion of the seed in water, may become sufficiently pronounced to cause very definite injury, resulting in a fall in germination percentage and a decrease in the subsequent yield, is clear from the work of numerous authors, and it is in this connection in particular that the conditions under which the soaking treatment is carried out are important. For example, if the seeds are immersed in a dense mass, even with a minimum amount of water, the lack of oxygen and accumulation of carbon dioxide resulting at normal temperatures from such conditions may in a very short time cause serious injury to the seeds, as the present authors have found. Again, it has been shown that in the case of some seeds (*e.g.* peas and beans) pronounced injury results even after very short periods of soaking when excess of water is used, probably for the same reason (*cf.* Kidd and West (21)).

If the temperature is high (*e.g.* 25°—30° C.) the injurious effects are more difficult to avoid; on the other hand, for some as yet unexplained reason, low temperatures (0°—10° C.) appear in many cases to exert a specific injurious action upon seeds soaking in water (*cf.* Kidd and West (22)).

In any case too long a period of soaking produces injury and death. Coupin (5) has shown that whereas some seeds can withstand only a brief period of immersion in water, others can withstand a long one.

The results of experiments in which stagnant water is compared with running water in its effect upon submerged seeds, indicate that lack of oxygen and accumulation of carbon dioxide, rather than the loss of soluble substances, are chiefly responsible for the injurious effects observed. In running water as compared with stagnant water, although a greater exosmosis of soluble matter occurs, the oxygen supply to the seed is maintained and carbon dioxide accumulation is reduced to a minimum. Under these conditions certain seeds can germinate and form roots and leaves (*cf.* Jodin (20)). In stagnant water, on the other hand, even when leaching is reduced to a minimum, germination is inhibited and injury and death eventually follow.

(c) "*Seed Impregnation*" (i.e. *Soaking Seeds in Solutions of Nutrient Salts*).

Wollny<sup>(11)</sup> and Tautphoeus<sup>(35)</sup> in the first instance, and later Schleh<sup>(33)</sup>, Köch<sup>(24)</sup> and others, investigated the effect of soaking seeds in solutions of various nutrient salts upon their germination and subsequent growth and yield.

Table XI gives the results of experiments recorded by Wollny.

From the table (p. 245) it appears that the results obtained by the use of solutions of nutrient salts are not appreciably better than those obtained with pure water, and this general conclusion is supported by the results obtained by the other authors mentioned above. Schleh used (1) a 20 per cent. solution of potassium nitrate, and (2) a nutrient solution consisting of 5 per cent. phosphoric acid, 10 per cent. nitrogen, and 10 per cent. potassium, and soaked his seed for 48 hours.

(d) *Enzymes*.

The enzymes of the seed are primarily concerned in the physiological processes whereby the food-reserves are prepared for consumption and utilised in growth. Factors influencing in any way the utilisation of the food-reserves of the seed may have an important pre-determining influence upon the whole course of subsequent development of the plant.

In this connection two different lines of experiment have occurred to a number of investigators, namely:—

(i) To supply the seed artificially with those products which are likely to result from the breaking down of its own food-reserves under the action of enzymes (Sharpe<sup>(34)</sup>).

(ii) To supply the seed with the enzymes themselves (Babcock<sup>(2)</sup>, Waugh<sup>(37)</sup> and <sup>(38)</sup>, Lehmann<sup>(27)</sup>). Under this category may be included those treatments which are believed to stimulate enzyme action in the seed (Effront<sup>(13)</sup>).

It is unfortunate that the results recorded stop short either at germination or at the early seedling stage.

Babcock (*l.c.*) reports the results of an experiment conducted at the Wisconsin Agricultural Experiment Station with corn (*Zea Maïs*), less than 50 per cent. of which germinated after soaking in pure water. But seeds from the same lot and treated in the same manner as the controls, except that the water in which they were soaked contained commercial

TABLE XI.

*Comparison of yields from seeds soaked in solutions of various nutrient salts with those obtained from (1) untreated seed and (2) seeds soaked in distilled water.*

The peas were soaked for 24 hours, the beans for 36 hours.

The seeds were sown at a uniform depth of 5 cm.

Name of plant	Date of experiment	Treatment of the seed	Distance apart of the plants	Number of plants		Yield from 64 plants		Percentage increase or decrease in yield of seed from experimental plants as compared with the controls
				Original	At the harvest	Seeds	Straw	
Horse beans	1876	Soaked in distilled water	25 cm.	64	64	gm.	gm.	+ 11
		" .5 % solution of NaCl		64	55	331	642	+ 31
		" .5 % Knop's solution Untreated (sown dry)		64	63	389	740	+ 3
Victoria peas	1877	Soaked in distilled water	25 cm.	64	58	533	1324	+ 29
		" .5 % solution of NaCl Untreated		64	57	693	1639	+ 68
Horse beans	1877	Soaked in distilled water	25 cm.	64	60	920	2436	+ 27
		" .5 % solution of NaCl Untreated		64	57	951	2755	+ 31
Victoria peas	1878	Soaked in distilled water	20 cm.	100	88	1788*	1778*	+ 23
		" .5 % solution of NaCl		100	91	845*	2145*	- 13
		" .5 % soln. of potassium phosphate		100	97	867*	1918*	- 10
		" .5 % " ammonium nitrate		100	71	955*	2049*	- 1
" concentrated "Gyps." solution	100	89	1038*	1983*	+ 7			
Untreated	100	94	967*	1658*				

\* Yield from 100 plants.

diastase, all germinated. The author remarks that "the increased vitality of the diastase lot was very noticeable." 100 per cent. germination was also obtained when seeds from the same lot were soaked for 15 hours in a 3 per cent. solution of glucose instead of water, thus indicating that lack of suitable food-material was the chief reason for the poor germination capacity of the untreated seeds.

Remarkable increases in germination percentages were recorded by Waugh(37) for old tomato seeds soaked previous to sowing in a 5 per cent. diastase solution as compared with similar seeds soaked in distilled water (Table XII). Waugh also remarked that the vigour of the young plants was often enhanced by the enzyme-treatment of the seeds.

TABLE XII (after Waugh).

Kind of seed	Age, years	Time of soaking, hours	Percentage of germination		
			Soaked in water	Soaked in 5 % solution of diastase	
Tomato	Hundred Day	12	168	12 %	84 %
	Hundred Day	12	48	34	70
	Early King Humbert	12	24	14	24
	Essex Hybrid	9	24	0	10
	Long Keeper	5	25	36	46
Cucumber: White Spine	5	48	44	54	
Radish: Carmine Erfert	6	48	46	60	

Although such results as these of Babcock and of Waugh and the similar results reported by others, for example, Lehmann(27), who treated seeds of *Epilobium hirsutum* with solutions of papayotin, trypsin, etc. and obtained increased percentages and vigour of germination, appear to be quite definite, we cannot readily accept the conclusion that they are to be explained as being due to the specific action of the enzymes added, for it is difficult to understand how such enzymes, when applied externally, can enter the seed. In contradiction to the above results White(39) states that the addition of dissolved ferments does not increase the percentage of germination of old seeds, and when any effect at all is produced, it is a tendency to lower it.

Experiments in which diffusible organic food-substances have been supplied to germinating seeds with a consequent increase in the germination percentage are more easily explained. Sharpe(34) obtained increased vigour and percentage of germination by germinating seeds in the presence of leucine or asparagin, substances which are of common occurrence in germinating seeds.

That food-substances can be utilised by the young embryo when it

comes into contact with them is clearly shown by the work of Brown and Morris<sup>(3)</sup>, Buckner and Kastle<sup>(4)</sup>, and others.

Brown and Morris in dealing with the utilisation of sugar by barley embryos, demonstrated the interesting fact that if cane-sugar be supplied to the seed in such a way that it can enter and come into contact with the embryo, it is utilised in growth in preference to the food-reserves in the endosperm, which are left untouched<sup>1</sup>. Barley grains, after 24 hours soaking, had their distal ends cut across and were then set with their proximal ends uppermost in loosely packed glass wool saturated with (a) distilled water, (b) a 3.5 per cent. solution of cane-sugar. Vigorous and normal growth followed in both cases, but when the grains were critically examined at the end of 4 days it was found that whereas in the case of (a) the endosperm was completely disintegrated and the starch had been attacked, in the case of (b) the endosperm was still as tough as before germination and the starch had scarcely been attacked.

Little definite evidence is available as to how far treatments, which stimulate germination, do so in virtue of their influence upon the rate of consumption of food-reserves by the embryo. It is probable, of course, that most of the many arbitrary treatments, which have been found to favour germination, bring about at the same time a quicker consumption of the food-reserves under the action of the specific enzymes concerned, but evidence is lacking in most cases as to the manner in which this result is produced.

In the case of acid treatments, which have been shown to increase the vigour of germination and of subsequent growth (see following chapter in this series), the enhanced rate of food-reserve consumption recorded as the result of these treatments may probably be attributed to the action of acids in liberating enzymes from pro-enzymes. Brown and Morris (*l.c.*) found that they could obtain a larger secretion of diastase from excised barley embryos when these were placed on a slightly acid medium than when laid on a neutral substrate. On a neutral gelatin medium they obtained from 50 barley embryos after 3 days an amount of diastase equivalent to 0.1186 gm. CuO (0.0708 gm. equivalent from the embryos and 0.0478 gm. from the medium). The corresponding figures when 0.0065 per cent. formic acid was added to the medium show a total diastase equivalent of 0.1450 gm. CuO, of which 0.0904 gm. was obtained from the embryos and 0.0546 gm. from the medium. This amounts to an increase of 22 per cent.

<sup>1</sup> Brown and Morris (*l.c.*) showed that the presence of assimilable sugars inhibited the secretion of diastase by the scutellum.

Reynolds-Green and Jackson<sup>(31 & 32)</sup> have also shown that acidity leads to the liberation of enzymes, and we may recall here Plate's<sup>(30)</sup> observation that the food-reserves of seeds treated with concentrated sulphuric acid for a few hours were completely utilised in 10 days, as compared with 15 days in the case of untreated seeds, and that the subsequent development of the plants from the treated seeds was correspondingly more advanced.

The work of Eckerson<sup>(12)</sup> and Efront<sup>(13)</sup> is also important in this connection. Eckerson set out to determine the limiting factor in the delayed germination of embryos of *Crataegus mollis*, which had previously been shown by Davis and Rose<sup>(6)</sup> to have a definite after-ripening period independently of the presence of their carpels and testas. Eckerson's results were not conclusive, but she demonstrated a slow increase in the acidity of the hypocotyledonary region of the embryo during the after-ripening period culminating in a sudden increase towards the end of this period. This sudden increase in acidity was correlated with the formation of enzymes and with germination. She also found that treating the embryos with hydrochloric, butyric, or acetic acid shortened the after-ripening period and hastened the appearance of enzymes.

Efront (*l.c.*) working with barley, found that treatment with lactic acid (2 gm. per litre) favoured germination and at the same time increased the amount of diastase present in the grains.

#### CONCLUSION.

The main conclusion which appears to emerge from this brief review is that the conditions operating during germination and the early seedling stage of the life-cycle of the plant are of the utmost importance, especially in the case of annuals and biennials, *i.e.* in the case of the majority of economic crops. Conditions operating during germination exercise a pre-determining influence upon subsequent growth and directly affect the yield. In many cases the value of the effects obtained are from the economic point of view out of all proportion to the cost of the treatments used.

The selection of vigorous seedlings is a common practice among horticulturists. It is recognised that some sort of correlation exists between the vigour of the seedling and that of the adult plant, and some recent scientific work (Gregory, *l.c.*) has quantitatively established this fact. But the proper deductions have not been made. The vigour of the seedling may be due either to hereditary causes or to environmental

factors which have operated previously to, or during, germination. It is obvious that the environmental conditions which obtain during germination affect the vigour of the seedling, and in the present review of literature attention has been directed to special seed-treatments which have been found to stimulate not only germination but also the growth of the plants produced. The critical question is therefore—Can we propound a law to the effect that increased vigour of seedling development due to environmental conditions as distinct from hereditary causes, is correlated with increased vigour of growth throughout the life of the plant and with increased yield independently of the subsequent environmental conditions?

Experimental work should be concentrated on this distinction. If the principle of physiological, as distinct from hereditary, pre-determination was fully established, many of the methods of seed-treatment which have been found to stimulate germination and the growth of the seedling could probably be developed, and employed in the field and greenhouse as a means of increasing production.

(To be continued.)

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ON FORMS OF THE HOP (*HUMULUS LUPULUS* L.)  
RESISTANT TO MILDEW (*SPHAEROTHECA*  
*HUMULI* (DC.) BURR.); III.

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IN previous articles<sup>(1)(2)</sup> I have pointed out that certain seedlings of the wild hop obtained from Italy show immunity, or resistance, to the attacks of the mildew *Sphaerotheca Humuli* (DC.) Burr.

Under conditions in which other seedlings of the same parentage and age (to the number of several hundreds) became severely infected with mildew, certain individual seedlings remained persistently immune throughout the growing season for the two consecutive years 1916 and 1917. The present paper deals with the behaviour of these and several other seedlings during 1918 and previous years. The manner in which these plants when grown in the greenhouse were artificially inoculated and otherwise exposed to infection has already been described in detail (1), p. 456).

The facts observed as to the degree of immunity shown by the various seedlings can best be described if we take the plants in groups and record their behaviour each season for the years during which they have been under observation. In the annual record of each seedling the following abbreviations are used:

G = grown in greenhouse,	I = immune,
H = „ hop garden,	S = susceptible.

The figures 1 to 3 indicate the amount of mildew present, 1 = mere trace of mildew; 2 = fair amount of mildew; 3 = plant very mildewed. The plants are all seedlings of the wild hop, raised at Wye from seed obtained from Vittorio, Italy.

*Group 1.* 4 seedlings (1-4) sex unknown.

<i>Plants 1, 2, 3, 4<sup>1</sup>.</i>	{	1916 G (1),
		1917 G (1),
		1918 G (1).

These four seedlings, 1-year-old in 1915, have proved persistently immune as 2-, 3-, and 4-year-old plants (non-flowering) in the green-

<sup>1</sup> These are four of the seven seedlings noted in (1), p. 456 and (2), p. 88.

house, under the severest tests as regards constant inoculations, for three years. They have now been planted out (during the winter of 1918-19) in the Experimental Hop-garden (under Reference Nos. 316, OB 26, OE 14, DD 31) with the object of seeing what effect, if any, the different conditions of growth have on their resistance to mildew.

*Group 2.* 5 seedlings (5-9).

*Plant 5.* Ref. No. Z 42 ♂

1917 H (I),

1918 H (I); 3 "cuts" 1917/18 G (I).

*Plant 6.* Ref. No. Z 2 ♂

1917 H (I),

1918 H (I); 3 "cuts" 1917/18 G (I).

*Plant 7.* Ref. No. OD 19 ♀

1917 H (I),

1918 H (I); 3 "cuts" 1917/18 G (I).

*Plant 8.* Ref. No. Z 25 ♀

1916 H (I),

1917 H (I),

1918 H (I); 4 "cuts" 1917/18 G (I).

*Plant 9.* Ref. No. OA 49 ♀

1917 H (I),

1918 H (I); 2 "cuts" 1917/18 G (I).

These five seedlings have all remained immune in the hop-garden, and the "cuts" taken from them in the winter of 1917-18 proved immune in the greenhouse during the growing season of 1918.

The plant Z 25 first attracted attention in the hop-garden in 1916, since no mildew was present on it while the two seedlings (Z 24 ♀ and Z 26 ♀) on either side of it in the same row, and of the same parentage and age, were severely attacked both on the leaves and "hops." The same thing occurred in 1917; Z 24 and Z 26 were excessively mildewed, and it so happened that some lateral branches of Z 24 had grown out, reached the main stem of Z 25 and had climbed up it and produced very mildewed "hops" (strobiles) on branches closely interwound round those of Z 25 which bore perfectly healthy (immune) hops. In the case of the seedling OD 19, a strong lateral shoot grew out and twined round the main stem of OD 18 (a susceptible seedling of the same age and parentage) and produced healthy hops on branches intertwined with those bearing the excessively mildewed hops of OD 18.

It may be pointed out that with respect to all these seedlings (Z 2, Z 25, Z 42, OA 49, OD 19), the incidence of the disease in the hop-garden in both 1917 and 1918 was such as to ensure their natural

inoculation from adjacent mildewed seedlings, most of which were affected to the severest extent. In every case, each of these five seedlings had mildewed plants on either side of it.

The following inoculation experiment was carried out on the seedling Z 25 in 1918. On June 10th several lateral shoots, 9 in. to 1 ft. long, produced from the main stem at about 5 ft. from the ground, were inoculated by "atomising" three leaves on each shoot with water containing conidia of *S. Humuli*. The seedlings Z 24 and Z 26 were of the same age and parentage as Z 25, and had proved in 1917 to be very susceptible (S<sup>3</sup>). On June 30th the following results were noted:

Ref. no.	No. of shoots (3 leaves inoculated on each shoot)	No. of leaves infected on each shoot	Total no. of leaves infected
Z 24	6	2, 3, 3, 2, 3, 1	14
Z 25	6	0, 0, 0, 0, 0, 0	0
Z 26	4	3, 0, 3, 3	9

At this date the patches of mildew were small, but many were densely powdery with conidia. The infected leaves were picked off to prevent the spread of the mildew to the commercial part of the hop-garden.

The evidence would seem to show that these five seedlings of Group 2 (which are all 5-year-old flowering plants) remain immune to mildew, after being grown for four years in a hop-garden under ordinary conditions of cultivation and manuring; although under the same conditions a large number of seedlings of the same age and parentage have proved each season to be exceedingly susceptible.

*Group 3.* 9 seedlings (10 to 18).

*Plant 10.* Ref. No. OR 38 ♀

1914 G (I),

1916 H (S<sup>1</sup>),

1917 H (S<sup>2</sup>); 5 "cuts" 1916/17 G (I\*),

H (S<sup>3</sup>);

1918 { 3 cuts 1916/17, now 2 cuts 1916/17 G (I) 9 cuts 1917/18 G (I),  
in H; Ref. No. W 56 (S<sup>2</sup>),

„ Y 28 (S<sup>3</sup>),

„ Z 4 (S<sup>3</sup>).

\* See footnote 1, next page.

As a 2-year-old seedling OR 38 was persistently immune in the greenhouse (1), p. 456), in 1914; that winter it was planted out in the hop-garden. It flowered there in 1916, and in October of that year it proved

to be susceptible to a slight extent, several of the leaves and one hop (strobile) being slightly affected. In 1917, in October, there was a fair amount of mildew (with perithecia) on the hops; and in 1918 by Sept. 7th there was a fair amount of mildew on the young leaves and by October the hops had become excessively mouldy, a considerable percentage of them being deformed or totally undeveloped owing to the attacks of the mildew.

During the winter of 1916-17, five "cuts" were taken from OR 38 and grown (in pots) during the season of 1917 in the greenhouse; these "cuts" proved to be immune, except that two of them showed a temporary and strictly local susceptibility<sup>1</sup>. Two of these five "cuts" taken in 1916-17 were kept in the greenhouse during 1918, and proved persistently immune. The remaining three "cuts" had been planted out, in the autumn of 1917, in the hop-garden, and, as young, non-flowering plants, all proved in October, 1918, to be susceptible. One plant (Ref. No. W 56), 1 $\frac{1}{4}$  ft. high, showed a fair amount of mildew on the leaves; one plant (Y 28), 5 ft. high, was very mouldy on the leaves and stems; the third plant<sup>2</sup> (Z 4), 5 ft. high, was very mouldy on the leaves.

During the winter of 1917-18 nine "cuts" had been taken from OR 38 and these were grown in pots in the greenhouse during 1918. These plants proved persistently immune, notwithstanding the fact that the parent plant was decidedly susceptible in the hop-garden both in 1917 and 1918.

*Plant 11.* Ref. No. OR 39 ♂

1914 G (I),

1916 H (S<sup>1</sup>),

1917 H (S<sup>1</sup>); 2 "cuts" 1916/17 G (I),

1918 H (? I); 2 "cuts" 1916/17 G (I); 6 "cuts" 1917/18 G (I).

This seedling, after proving immune as a 2-year-old seedling in the greenhouse in 1914, showed slight susceptibility in the hop-garden in October, 1916, one leaf each on two lateral shoots showing small patches of mildew. In 1917, in October, there was one small patch of mildew on the under-surface of one leaf of a lately-developed lateral shoot. In 1918 there was no mildew on the plant; as, however, no actual inoculations were made the immunity cannot be held to be definitely proved. During 1916-17 two "cuts" were taken from OR 39; these proved immune in the greenhouse for two consecutive seasons. Six "cuts" taken in 1917-18 proved immune in the greenhouse during 1918.

<sup>1</sup> The facts have been given in detail, and discussed, in (2), p. 84: 86.

<sup>2</sup> This was the "cut" which in 1917 has proved immune, in the greenhouse, in the Exper. 4 recorded in (2), p. 85.

Plants 12, 13, 14. Ref. Nos. V 91, V 92, V 93. Sex unknown.

Plants 12, 13, 14 { 1916 G (I),  
1917 G (I).

1918. All 3 plants now in H: Ref. No. V 91 (S<sup>1</sup>),  
" V 92 (S<sup>1</sup>),  
" V 93 (S<sup>1</sup>).

These three seedlings as 2-year-old plants proved persistently immune in the greenhouse during 1916, and again during 1917<sup>1</sup>. In the autumn of 1917 they were planted out in the hop-garden, the plants grew during 1918 to the height of 5 ft. and all showed slight susceptibility—a very few patches of mildew being present on a few leaves both of V 91 and V 92, and one patch only on the under-surface of one leaf of V 93.

Plant 15. Ref. No. Z 14 ♂

1917 H (I).

1918 H (S<sup>1</sup>); 3 "cuts" 1917/18 G (I).

Plant 16. Ref. No. Z 22 ♀

1917 H (I).

1918 H (S<sup>2</sup>); 2 "cuts" 1917/18 G (I).

Plant 17. Ref. No. OB 34 ♀

1917 H (I).

1918 H (S<sup>1</sup>); 3 "cuts" 1917/18 G (I).

Plant 18. Ref. No. HH 44 ♀

1917 H (S<sup>1</sup>).

1918 H (S<sup>1</sup>); 3 "cuts" 1917/18 G (I).

The above four seedlings all agree in their "cuts" being immune when grown in the greenhouse, although all the parents show some degree of susceptibility when grown in the hop-garden. Z 14 showed the merest trace of mildew on its leaves; Z 22 a fair amount of mildew on its "hops" and very occasionally a trace of mildew on its leaves; OB 34 was immune in 1918 except for one quite young "hop" (strobile) which alone was smothered in mildew in the conidial stage, and arrested in development, among some hundreds of healthy "hops"<sup>2</sup>; HH 44 showed in both years only a trace of mildew in its "hops."

The evidence given by seedlings in Group 3 shows clearly that one and the same plant<sup>3</sup> may be persistently immune when grown in the greenhouse and susceptible even to the highest degree when grown in the hop-garden.

#### Group 4. 4 seedlings.

Instances of "semi-immunity" have been noticed in the case of four seedlings. With regard to the seedlings Z 15 (♂) and OC 6 (♂), one

<sup>1</sup> These are three of the seven seedlings noted in (1), p. 456, and (2), p. 88.

<sup>2</sup> This case may possibly be compared with the strictly local susceptibility shown by one leaf of the "immune" plant of OR 38 in the greenhouse in 1917 (see (2), p. 86).

<sup>3</sup> Adopting Dr J. Schmidt's terminology (see *Comptes Rendus Trav. Labor. Carlsberg*, xi, 153 (1915)) each "cut" taken from the parent plant is a "clone-plant."—the "hop-clone" being all those plants derived from the same seedling by vegetative propagation.

“cut” of each was taken in the winter of 1917-18, and grown in the greenhouse during 1918. These two plants never became really infected throughout the season. On inoculation infection stopped short, after the formation of small blisters or “humps” on the leaves (which I have already described (3) as being frequently the first sign of infection); on the surface of these “humps” a meagre, scarcely white growth of mycelium with conidiophores took place which soon died away, leaving minute, brown patches of dead, epidermal cells at the place where the mycelium had been. In the hop-garden, Z 15 was recorded as having mildew to the second degree in 1917 and 1918; while OC 6 was recorded as having no mildew in either year.

The seedling Z 23 ( $\sigma$ ), of which three “cuts” were tested in the greenhouse during 1918, was also “semi-immune” in a very similar manner. Inoculation of the leaves was followed by the formation of yellowish, translucent “humps” on the leaf, on which a very weak growth of mycelium took place, the mildew scarcely ever presenting a white patch and the conidiophores soon dying away. In the hop-garden Z 23 was recorded as (S<sup>2</sup>) in 1917 and (I) in 1918.

The seedling OA 33 ( $\sigma$ ), of which two “cuts” were tested in the greenhouse in 1918, was a little more susceptible, the patches of mildew produced after inoculation being larger and white and “powdery” with conidia; unlike the growth of mildew found on really susceptible plants, however, these patches did not remain white and enlarge, but died away, leaving behind yellowish, more or less translucent spots where the mycelium had been. In the hop-garden OA 33 was recorded as having no mildew on it during 1917 and 1918.

In all the cases recorded above, the immunity to mildew shown in the greenhouse by the various seedlings of the wild hop from Italy has been constant for the particular plant year after year; in no single case has a seedling which was immune one season in the greenhouse shown susceptibility in other seasons in the greenhouse, although it may have done so in the hop-garden. The case has been very different with a seedling of American ancestry. This seedling was raised at Wye of the parentage (Oregon Cluster  $\times$  English male hop)  $\times$  English male hop<sup>1</sup>. In 1916 as a 2-year-old plant it proved throughout the season in the greenhouse persistently immune, in spite of the most numerous

<sup>1</sup> The “Oregon Cluster” is a commercial variety cultivated in the United States. In our opinion (see *Journal of Botany*, May 1915) it belongs to the species *Humulus americanus*, and not to *H. Lupulus*, from which the varieties cultivated in Europe derive their origin. The seedling now mentioned must therefore be considered of hybrid origin.

inoculations under conditions in which some hundreds of hop-seedlings of the same age became infected. The plant grew during that season to a height of 4 ft. In 1917 this seedling, which was still kept in the greenhouse, entirely lost its immunity. On April 19 there were small but "powdery" patches of mildew on four of its leaves. The leaves were at this date slightly yellowish, as the result of abnormal weather conditions, viz. rapid changes of temperature<sup>1</sup>. By May 9 the stem of the plant, after having been more or less completely checked in growth, was still growing only very slowly; there were now a few, fairly large "powdery" patches of mildew on four of the (upper) leaves. By May 22 the two stems of the plant were only 8 in. high, and still only lengthening slowly; the plant was clearly highly susceptible; the surface of the stem near its apex was covered all round, for a length of 1½ in., with a continuous growth of the "powdery" conidial stage; several of the young leaves also were infected; and one of the stems had the terminal bud and the two youngest leaves smothered over with mildew and more or less hypertrophied. The plant, which as the result apparently of the severe attacks of mildew never made any very strong growth, reached a height of 2 ft. 10 in. Mildew persisted on it throughout the growing season. This seedling unfortunately died during the winter of 1917-18. It is to be noted that under these same cultural conditions in the greenhouse during 1917 the immune seedlings of the wild hop from Italy all retained their immunity.

We may ask here what is the explanation of the apparent change from immunity to susceptibility when a plant of Group 3 is transferred from the greenhouse to the hop-garden, and, conversely, of the change from susceptibility to immunity when the plant is brought back from the hop-garden to the greenhouse. The explanation may be sought for in two directions.

It is possible that there are different strains of the biologic form of *S. Humuli* on the hop with different powers of infection, and that the plant when in the hop-garden is attacked by a form which is absent in the greenhouse. The work of Barrus(4) would seem to give evidence of the existence of different strains of a parasitic fungus which are regional in their distribution. Whether such is the case with the Hop-mildew I hope to prove next year by inoculating the same (immune) plant in the greenhouse with spores taken from the same (susceptible) plant in the hop-garden.

<sup>1</sup> The conditions of growth at the time are described more fully in (2), p. 84.

On the other hand, the difference may well be not in the fungus but in the plant, which may change its power of resistance as the result of changed conditions of growth. The chief differences between the conditions in the hop-garden and in the greenhouse are the greater atmospheric humidity and (particularly towards the end of summer) the greater variation of temperature in the hop-garden, and the higher temperature reached in the greenhouse. It is noteworthy that the infection of the "immune" seedlings in the hop-garden is most evident in the autumn when low temperatures<sup>1</sup> occur at night. As regards the effect of greenhouse conditions, the statement has been made by Butler(5), p. 124, that "the mere growth of a plant under glass may reduce its resistance. Several varieties of wheat are much less resistant to black rust when grown in greenhouses than in the open, and the same is true of some other rusts and mildews." Butler(5), p. 162, also attributes the change from immunity to susceptibility sometimes shown by Einkorn wheat in India to the effect of high temperature. In the case of these hop seedlings, their transference to a higher temperature is associated, apparently, with a change to immunity.

#### SUMMARY.

1. Certain seedlings of the wild hop when grown in the greenhouse are persistently immune to the attacks of the mildew *Sphaerotheca Humuli*. This immunity has been shown by the same individual seedling for three consecutive years. Under the same cultural conditions other seedlings of the same parentage prove to be very susceptible.

2. Certain seedlings (Group 2) which are immune when grown in the greenhouse are also immune when grown in the open. These seedlings have retained this immunity after four years' residence in a hop-garden under normal conditions of cultivation and manuring.

3. Certain seedlings (Group 3) which are immune when grown in the greenhouse are susceptible when grown in the hop-garden; in some cases the susceptibility shown is of the highest grade.

4. "Cuts" taken from the seedlings of Group 3 in the same year in which the seedling proved to be susceptible in the hop-garden are immune in the greenhouse under cultural conditions in which "cuts" taken from other susceptible seedlings in the hop-garden are very susceptible.

<sup>1</sup> It is possible that the low temperature increases the infection-powers of the conidia of the mildew. In the *Erysiphaceae*, as in the *Uredineae*, "chilled" spores have increased powers of germination.

5. Certain seedlings (Group 4) are semi-immune to the attacks of the mildew.

6. One seedling (of American ancestry) grown in the greenhouse was immune throughout the season in 1916 and very susceptible in 1917.

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- (2) ——— *Idem*, II. *Journ. Genetics*, VIII, No. 2, 83-91 (1919).
- (3) ——— On the Resistance to Fungicides shown by the Hop-mildew (*S. Humuli* (DC.) Burr.) in different stages of development. *Annals of Applied Biology*, III, 93-96 (Plate XV) (1917).
- (4) BARRUS, M. F. Variation of varieties of Beans in their susceptibility to Anthracnose. *Phytopathology*, I, 190 (1911).
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## A LIST OF COCCIDAE AFFECTING VARIOUS GENERA OF PLANTS.

BY E. ERNEST GREEN, F.E.S., F.Z.S.

(Continued from Vol. V, page 156)

- QUERCUS (Fagaceae) 'Oak.'  
   MONOPHLEBUS fuscipennis.  
   DROSICHA corpulenta.  
   ICERVA purchasi.  
   XYLOCOCCUS quercus, napiformis.  
   KUWANIA quercus.  
   SPHAEROCOCCUS sylvestris.  
   ASTEROLECANIUM bornmuelleri, ilicicola, quercicola, variolosum, variolosum-minor, pasaniae.  
   LECANIODIASPIS quercus, tessellata.  
   CEROCOCCUS corticis, chrhorni, quercus.  
   NIDULARIA pulvinata, japonica.  
   OLLIFFIELLA cristicola.  
   KERMES andrei, arizonensis, austini, ballotae, boguei, ceriferus, cockerelli, concinnulus, fuscus, galliformis, galliformis-cueroensis, gibbosus, gillettei, grandis, ilicis, kingii, nakagawae, nawae, nigropunctatus, nivalis, pallidus, perryi, pettiti, pubescens, quercus, roboris, trinotatus, variegatus-corticalis, vermilio, rattani, himalayensis, bacciformis, miyasakii, vastus, shastensis, mirabilis, branigani, cordiformis, essigii, lindingeri, occidentalis, sassceri, waldeni.  
   ERIOCOCCUS quercus, howardi, quercus-gilensis, aceris.  
   PHENACOCCUS quercus, aceris.  
   CEROPUTO koebelei.  
   PSEUDOCOCCUS quercus, agrifoliae, maritimus, quercicolus.  
   TRIONYMUS villosus.  
   LECANIUM antennatum, canadense, cerasifex, ciliatum, cockerelli, fuscum, lymani, pubescens, quercifex, quercitronis, emerici, nigro-fasciatum, coryli, pulchrum.  
   PULVINARIA innumerabilis, sericca, vitis.  
   DIASPIS montana.  
   PROTODIASPIS parvula, agrifoliae.  
   CHIONASPIS planchonii, quercus, chinensis, kinshinensis, salicis.  
   ASPIDIOTUS ancyclus, cryptoxanthus, hederæ, jordani, minimus, osborni, ostreaeformis, zonatus, lilacinus, obscurus, setiger, densifloræ, yulupæ, vitis-suberi, distincta, alni, niger, pseudo-spinosus, tenebricosus, camelliae.  
   LEPIDOSAPHEs citricola, crawii, ulmi.  
 QUINARIA (Vitaceae).  
   ASPIDIOTUS hederæ.  
   LEPIDOSAPHEs ulmi.  
 RADIOLA (Linaceae).  
   RIPERSIA halophila.  
 RAMONA (Labiatae).  
   PHENACOCCUS ramonæ.  
   PSEUDOCOCCUS crawi.  
   PUTO yuccæ.  
 RAPANEA (Myrsinaceae).  
   ERIOCOCCUS cornuus.  
   CEROPLASTES floridensis.  
 RAPHIA (Palmaceae).  
   CEROPLASTES actiniformis.  
   FIORINIA macroprocta.

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- RAUWOLFIA (Apocynaceae).  
   LECANIUM hemisphaericum.  
   PULVINARIA psidii.
- RHAGODIA (Chenopodiaceae).  
   PULVINARIA maskelli.
- RHAMNUS (Rhamnaceae) 'Buckthorn.'  
   KERMES nawae.  
   ERIOCOCCUS gurneyi.  
   PSEUDOCOCCUS alaterni, citri.  
   TACHARDIA lacca.  
   LECANIUM kunoensis, oleae, cilia-  
   tum, corni.  
   CHIONASPIS salicis, furfura-fulva.  
   ASPIDIOTUS camelliae, britannicus,  
   ostreaeformis, perniciosus.  
   PARLATORIA oleae.  
   LEPIDOSAPHEs ulmi.
- RHEEDIA (Clusiaceae).  
   ASTEROLECANIUM aureum.  
   LECANIUM hemisphaericum, oleae.  
   ASPIDIOTUS dictyospermi.
- RHEUM (Polygonaceae).  
   PSEUDOCOCCUS citrophilus.
- RHINOCARPUS (Anacardiaceae).  
   ASPIDIOTUS rossi.
- RHIPOGONUM (Liliaceae).  
   COELOSTOMIDIA zealandica.  
   HEMICHIONASPIS minor.  
   LEPIDOSAPHEs pyriformis.
- RHIZOPHORA (Rhizophoraceae)  
   'Mangrove.'  
   LECANIUM rhizophorae, expansum-  
   rotundum.  
   CTENOCHITON rhizophorae.  
   HEMICHIONASPIS congregabilis.  
   POLIASPIS lanigera.  
   ASPIDIOTUS rhizophorae, fissidens-  
   constricta.
- RHODODENDRON (Ericaceae).  
   ERIOCOCCUS azaleae, bezzii, uvae-ursi.  
   HEMICHIONASPIS rhododendri.  
   ASPIDIOTUS duplex, paconiae, rho-  
   dodendri, ficus.
- RHODOMYRTUS (Myrtaceae).  
   ERIOCOCCUS rhodomyrti.
- RHUS (Anacardiaceae).  
   PSEUDOCOCCUS quaintaneci, capensis.  
   PHENACOCOCUS pettiti, stachyos.  
   LECANIUM robiniae-subsimile.
- PULVINARIA hazeae, maclurac, rhois.  
   ERICERUS pela.  
   TAKAHASHIA jaliscensis.  
   CHIONASPIS platani, mytilaspiformis.  
   ASPIDIOTUS perniciosus, duplex,  
   africanus, pectinatus.
- RHYNCHOSPERMIUM (Compositae).  
   PROTOPULVINARIA pyriformis.  
   DIASPIS pentagona.  
   ASPIDIOTUS ficus.
- RIBES (Grossulariaceae) 'Currant,' etc.  
   ICERYA purchasi.  
   PSEUDOCOCCUS arceae, gahani.  
   PHENACOCOCUS socius, aecris.  
   LECANIUM corni, coryli, rehi, ribis,  
   websteri, nigrofasciatum.  
   PULVINARIA occidentalis, vitis,  
   betulae.  
   DIASPIS pentagona.  
   CHIONASPIS furfurus, salicis.  
   EPIDIASPIS piriicola, lepèri.  
   ASPIDIOTUS ancyllus, forbesi, hede-  
   rae, hunteri, perniciosus, tas-  
   maniae, ostreaeformis, lataniae.  
   LEPIDOSAPHEs ulmi.
- RICHARDIA (Araceae).  
   PSEUDOCOCCUS capensis.  
   PULVINARIA psidii.
- RICINUS (Euphorbiaceae) 'Castor-oil.'  
   ICERYA purchasi.  
   LECANIUM hemisphaericum.  
   PULVINARIA floccifera.  
   DIASPIS pentagona.  
   CHIONASPIS eugeniae.  
   ASPIDIOTUS destructor, orientalis.
- RINORIA (Violaceae).  
   ASPIDIOTUS sylvaticus.
- ROBINIA (Leguminaceae).  
   GUERINIELLA serratulae.  
   PSEUDOCOCCUS capensis, adonidum.  
   PHENACOCOCUS hystrix.  
   HELIOCOCCUS bohemicus.  
   LECANIUM quadrifasciatum, quer-  
   citronis, robiniarum, robiniae,  
   vini, corni, capreae, persicae.  
   PULVINARIA innumerabilis.  
   ASPIDIOTUS juglans-regiae, afri-  
   canus, rapax, hederac.  
   PARLATORIA oleae.

- RODRIGUESIA (Orchidaceae).  
   CONCHASPIIS angracii.  
 ROLLINIA (Anonaceae).  
   PALAEOCOCCUS rosae.  
 ROSA (Rosaceae).  
   ICERYA purchasi, seychellarum, aegyptiaca.  
   PALAEOCOCCUS rosae.  
   ORTHEZIA insignis.  
   TACHARDIA rosae.  
   LECANIUM perornatum, rosae, persicae, oleae, pulchrum, coryli, corni, nigrofasciatum.  
   PULVINARIA coulteri, betulae.  
   DIASPIS rosae.  
   CHIONASPIS salicis.  
   ASPIDIOTUS ficus, aurantii, dictyospermi, articulatus, orientalis, perniciosus, lataniae, tesserata, hederac, camelliae.  
   LEPIDOSAPHES ulmi.  
   PARLATORIA calianthina, proteus, oleae.  
 ROSIMARINUS (Labiatae) 'Rosemary.'  
   ICERYA purchasi.  
   ERIUM rosmarinus.  
   LECANIUM oleae, corni.  
 RUBIA (Rubiaceae).  
   ASPIDIOTUS hederac.  
 RUBUS (Rosaceae).  
   ORTHEZIA urticae.  
   ERIOCOCCUS multispinus.  
   PSEUDOCOCCUS glaucus.  
   PHENACOCOCUS rubivorus, colemani, comari.  
   TETRURA rubi.  
   LECANIUM coryli, fitchii, obtusum, rubi, pulchrum, hesperidum, corni, capreae, persicae.  
   PULVINARIA vitis.  
   DIASPIS rosae.  
   CHIONASPIS dubia.  
   ASPIDIOTUS perniciosus.  
   LEPIDOSAPHES ulmi.  
 RUMEX (Polygonaceae).  
   ICERYA purchasi.  
   ERIOCOCCUS insignis.  
   PSEUDOCOCCUS arcaea, capensis.  
   RIPERSIELLA rumicis.  
   RUSCUS (Liliaceae).  
   CEROPLASTES rusci.  
   ASPIDIOTUS britannicus, hederac.  
   FIORINIA pellucida.  
   RUTA (Rutaceae).  
   CHIONASPIS canariensis, berlesii.  
   SABAL (Palmaceae).  
   COMSTOCKIELLA sabalis.  
   ASPIDIOTUS personatus, pseudospinosus, dictyospermi.  
   ISCHNASPIS filiformis.  
   SACCHARUM (Graminae) 'Sugar-Cane.'  
   ICERYA seychellarum.  
   MARGARODES formicarium.  
   PSEUDOCOCCUS calceolariae, sacchari, saccharifolii, boninsis, virgatus.  
   RIPERSIA sacchari.  
   LECANIUM guerinii.  
   PULVINARIA iceryi, elongata.  
   DIASPIS major.  
   CHIONASPIS depressa, madiunensis, saccharifolii.  
   ASPIDIOTUS sacchari, glomeratus, destructor.  
   SAGITTARIA (Alismaceae).  
   PSEUDOCOCCUS virgatus.  
   SAGUERUS (Palmaceae).  
   ASPIDIOTUS spinosus.  
   SALICORNIA (Chenopodiaceae).  
   CEROPUTO ambigua.  
   PULVINARIA salicorniae.  
   SALIX (Salicaceae) 'Willow,' 'Sallow,' etc.  
   ICERYA purchasi.  
   ERIOCOCCUS borealis.  
   PHENACOCOCUS aceris.  
   LECANIUM nigrofasciatum, coryli, corni, ciliatum.  
   PULVINARIA ehrhorni, innumeralis, occidentalis, vitis, betulae.  
   DIASPIS pentagona.  
   CHIONASPIS lintneri, ortholobis, salicis, salicis-nigrae, wistariae.  
   HEMICHIONASPIS minor.  
   HOWARDIA biclavus.  
   LEUCASPIS kermanensis, salicis.

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SALIX (Salicaceae)—*cont.*

ASPIDIOTUS ancyclus-serratus, perniciosus, camelliae, aurantii, distincta, ostreaceiformis, lataniae, alienus, pectinatus.

LEPIDOSAPHES pallida, ulmi.

SALSOLA (Chenopodiaceae).

CHIONASPIS canariensis, berlesci.

SALVIA (Labiatae).

ORTHEZIA insignis.

CEROCOCCUS zapotlana.

PSEUDOCOCCUS crawii, transvaalensis.

SAMBUCUS (Caprifoliaceae) 'Elder.'

ASTEROLECANIUM pustulans-sambuci, fimbriatum.

PSEUDOCOCCUS obscurus, bakeri.

SAMOLUS (Primulaceae).

ASTEROLECANIUM stypheliae-multi-porum.

SANCHEZIA (Acanthaceae).

ORTHEZIA praelonga.

SANDORICUM (Meliaceae).

PINNASPIS siphonodontis.

SANGUISORBA (Rosaceae).

MARGARODES polonicus.

ASTEROLECANIUM fimbriatum.

SANICULA (Umbelliferae).

ASTEROLECANIUM fimbriatum.

SANTALUM (Santalaceae) 'Santalwood.'

RHIZOCOCCUS fossor.

PSEUDOCOCCUS gallicola.

INGLISIA foraminifer.

DIASPIS santali.

POLIASPIS exocarpi.

ASPIDIOTUS santali.

SAPINDUS (Sapindaceae).

LECANIUM gracilis, tessellatum, nigrofasciatum.

DIASPIS ceylonica.

HOWARDIA biclavis.

FIORINIA nephelii, sapindi.

SAPOTA (Sapotaceae).

ICERYA purehasi.

LECANIUM mangiferae, nanus, tessellatum, oleae.

PULVINARIA psidii.

PROTOPULVINARIA pyriformis.

DIASPIS persimilis, miranda.

SAPROSMA (Rubiaceae).

ASPIDIOTUS transparentis.

FIORINIA rubrolineata, sapsosmae.

PARLATORIA mytilaspiformis.

SAROTHAMNUS (Leguminosae).

LECANIUM pulchrum, coryli, corni.

PULVINARIA betulae.

CHIONASPIS salicis.

ASPIDIOTUS hederac.

LEPIDOSAPHES ulmi.

SASSAFRAS (Lauraceae).

LECANIUM lintneri.

LEPIDOSAPHES ulmi.

SAUVAGESIA (Ochnaceae).

CEROPLASTES ceriferus.

SAXEGOTHAEA (Coniferae).

PSEUDOPARLATORIA chilina.

SAXIFRAGA (Saxifragaceae).

ORTHEZIA cataphracta.

ASPIDIOTUS hederac, dietyospermi.

SCAEVOLA (Goodenovicae).

LECANIUM tessellatum.

SCALEZIA (Compositae).

ORTHEZIA galapagoensis.

ASPIDIOTUS lataniae.

SCHINUS (Anacardiaceae).

LECANIUM hemisphaericum, nigrum.

PULVINARIA psidii.

CEROPLASTES albolineatus, cistudiformis, rusci, sinensis, postperlucidus.

HEMICHIONASPIS aspidistrae.

ASPIDIOTUS africanus.

SCHIZOSTACHYUM (Gramineae).

ASTEROLECANIUM miliaris-longum.

ODONASPIS schizostachyi.

SCHLEICHERA (Sapindaceae).

MONOPHLEBUS stebbingi.

TACHARDIA lacca, albizziae.

SCHOTIA (Leguminosae).

AONIDIA biafrac.

SCIADOPYTIS (Coniferae).

PSEUDOCOCCUS ryani.

LEPIDOSAPHES newsteadi.

SCLERANTHUS (Caryophyllaceae).

MARGARODES polonicus.

SCOLOPENDRIUM (Filices).

LECANIUM hesperidum.

SCOLOPIA (Bixaceae).

PARLATORIA cingala.

- SCORPIURUS (Leguminosae).  
   ASTEROLECANIUM fimbriatum.  
 SCROPHULARIA (Scrophulariaceae).  
   ASTEROLECANIUM fimbriatum.  
   CEROPUTO superbus.  
 SEAFORTHIA (Palmaceae).  
   DIASPIS boisduvali.  
   ASPIDIOTUS fieus.  
   PARLATORIA pergandei.  
 SEDUM (Crassulaceae).  
   ICERYA purchasi.  
   DIASPIS pentagona.  
   ASPIDIOTUS hederac, camelliae.  
 SELENIPEDIUM (Orchidaceae).  
   PARLATORIA proteus.  
 SEMELE (Liliaceae).  
   ASPIDIOTUS laurotorum.  
 SEMPERVIVUM (Crassulaceae).  
   ASPIDIOTUS hederac.  
 SENEBIERA (Cruciferae).  
   PSEUDOCOCCUS capensis.  
 SENECCIO (Compositae).  
   PSEUDOCOCCUS capensis, adonidum.  
   LECANIUM hemisphaericum.  
   ASPIDIOTUS niger.  
 SEQUOIA (Coniferae).  
   PSEUDOCOCCUS sequoiae.  
   PUTO cupressi.  
   DIASPIS visci.  
   ASPIDIOTUS coniferarum.  
 SERRATULA (Compositae).  
   GUERINIELLA scitatulae.  
   LECANIUM pulchrum.  
 SESBANIA (Leguminosae).  
   LECANIUM discrepans, oleae.  
 SHOREA (Dipterocarpaceae).  
   TACHARDIA lacca.  
 SIDA (Malvaceae).  
   ASTEROLECANIUM pustulans.  
   PSEUDOCOCCUS burnerae, virgatus.  
   PHENACOCUS insolitus.  
   LECANIUM nigrum.  
   CHIONASPIS solani.  
   HEMICHIONASPIS minor.  
 SIDEROXYLON (Sapotaceae).  
   LECANIUM sideroxylium.  
   DIASPIS persimilis.  
   ASPIDIOTUS fissidens-pluridentatus.  
 SILENE (Caryophyllaceae).  
   PSEUDOCOCCUS capensis.  
 SIPHONODON (Celastraceae).  
   NEOLECANIUM eribrigerum.  
   PINNASPIS siphonodontis.  
 SMILAX (Liliaceae).  
   ICERYA purchasi.  
   LECANIUM urichi.  
   PULVINARIA convexa.  
   FILIPPICA oleae.  
   DIASPIS rosae-spinosa.  
   ASPIDIOTUS smilacis, lauretorum,  
     britannicus, hederac, rossi.  
   LEPIDOSAPHEs cocculi.  
 SOJA (Leguminosae) 'Soya Bean.'  
   ERIOCOCCUS sojae.  
 SOLANDRA (Solanaceae).  
   PSEUDOCOCCUS citri.  
 SOLANUM (Solanaceae).  
   ICERYA purchasi.  
   CEROCOCCUS hibisci.  
   PSEUDOCOCCUS affinis, citri, solani,  
     secretus, capensis, virgatus, ci-  
     trophilus, corymbatus.  
   PHENACOCUS insolitus, stachyos,  
     solani.  
   LECANIUM pseudosemen, toluacanum,  
     hemisphaericum, oleae.  
   MESOLECANIUM lucidum.  
   PULVINARIA floceifera, psidii.  
   CEROPLASTES cirripediformis.  
   INGLISIA castilloae.  
   DIASPIS pentagona.  
   CHIONASPIS manni, solani.  
   HOWARDIA biclavis.  
   ASPIDIOTUS cydoniae, orientalis,  
     camelliae.  
   LEPIDOSAPHEs alba.  
 SOLDANELLA (Primulaceae).  
   ORTHEZIA cataphracta.  
 SOLENOPSIS (Campanulaceae).  
   PHENACOCUS solenopsis.  
 SOLIDAGO (Compositae).  
   ICERYA purchasi.  
   ORTHEZIA solidaginis, urticae.  
 SONCHUS (Compositae).  
   ICERYA purchasi.  
   PSEUDOCOCCUS capensis.  
 SONERILA (Melastomaceae).  
   LECANIUM hesperidum.

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- SOPHORA (Leguminosae).  
 DIASPIS texensis, penta-gona.  
 CHIONASPIS salicis.  
 ASPIDIOTUS sophorae.  
 SORBUS (Rosaceae).  
 LEPIDOSAPHES ulmi.  
 SORGHUM (Gramineae) 'Millet.'  
 PSEUDOCOCCUS sorghiellus, sorghii-ellus-kingi.  
 SPARTINA (Gramineae).  
 RIPERSIELLA maritima.  
 CHIONASPIS spartinae.  
 SPARTIUM (Leguminosae).  
 ICERYA purchasi.  
 ASTEROLECANIUM algeriense, fim-briatum.  
 LECANIUM mori.  
 ASPIDIOTUS hederæ.  
 LEPIDOSAPHES ulmi.  
 SPARTOCYTISUS (Leguminosae).  
 ASPIDIOTUS lataniae.  
 LEPIDOSAPHES ulmi.  
 SPERGULA (Caryophyllaceae).  
 PSEUDOCOCCUS capensis.  
 SPERGULARIA (Caryophyllaceae).  
 MARGARODES poloricus.  
 PSEUDOCOCCUS calceolariae, luffi.  
 SPHAGNUM (Lycopodiaceae).  
 ORTHEZIA cataphracta.  
 NEWSTEADIA floccosa.  
 PSEUDOCOCCUS sphagni, perrisii.  
 SPIRAEA (Rosaceae).  
 LECANIUM vini, websteri, corni, persicae.  
 PULVINARIA cockerelli, vitis.  
 LICHTENSIA viburni.  
 ASPIDIOTUS perniciosus, hederæ.  
 LEPIDOSAPHES ulmi.  
 SPONDIAS (Anacardiaceae).  
 LLAVELA axin.  
 PSEUDOCOCCUS virgatus.  
 PULVINARIA psidii.  
 ASPIDIOTUS subsimilis-anonae.  
 SPOROBOLUS (Gramineae).  
 RIPERSIA sporoboli.  
 ACLERDA obscura.  
 STACHYS (Labiatae).  
 ICERYA purchasi.  
 ASTEROLECANIUM fimbriatum.  
 PSEUDOCOCCUS eriogoni.  
 PIENACOCCUS stachyos.  
 PUTO yuccae.  
 LECANIUM pilehrum.  
 ASPIDIOTUS labiatarum.  
 STANGERIA (Cycadaceae).  
 PSEUDOCOCCUS longispinus.  
 LECANIUM hemisphaericum.  
 STAPELIA (Asclepiadaceae).  
 ASPIDIOTUS hederæ.  
 STAPHYLEA (Staphylaceae).  
 ASPIDIOTUS ancylus.  
 STATICE (Plumbaginaceae).  
 RIPERSIA halophila.  
 LECANIUM hesperidum, hemisphae-ricum.  
 STELLARIA (Caryophyllaceae).  
 ORTHEZIA urticae.  
 STEPHANOTIS (Asclepiadaceae).  
 CONCHASPIS angræci.  
 RIPERSIA terrestris.  
 ASPIDIOTUS destructor.  
 STERCULIA (Sterculiaceae).  
 LECANIUM hesperidum.  
 HEMICHIONASPIS minor.  
 STEREOSPERMUM (Bignoniaceae).  
 CRIBROLECANIUM formicarum.  
 STILLINGIA (Euphorbiaceae).  
 LECANIUM globulosum.  
 LEPIDOSAPHES ulmi.  
 STRAUSSIA (Rubiaceae).  
 PSEUDOCOCCUS straussiae.  
 STREBLUS (Urticaceae).  
 TACHARDIA lacea.  
 STRELITZIA (Musaceae).  
 CEROPLASTES rusci.  
 DIASPIS boisduvalli.  
 ASPIDIOTUS dictyospermi, ficus, camelliae.  
 FIORINIA fioriniae, pellucida.  
 STROBILANTHES (Acanthaceae).  
 ORTHEZIA insignis.  
 PEDRONIA strobilanthis.  
 CHIONASPIS strobilanthis.  
 HEMICHIONASPIS aspidistrae.  
 ASPIDIOTUS putearius.  
 STROMBOSIOPSIS (Olacaceae).  
 ASPIDIOTUS spünger.

- STRYCHNOS (Loganiaceae).  
   LECANIUM viride.  
   PULVINARIA psidii.  
   DIASPIS stilosa.  
   ASPIDIOTUS fissidens, undulatus.  
   ISCHNASPIS bipindensis.  
 STYPHELIA (Epaeridaceae).  
   ASTEROLECANIUM stypheliae.  
   SPHAEROCOCCUS stypheliae.  
   CTENOCHITON serratum.  
   ASPIDIOTUS immaculatus.  
 SWIETENIA (Meliaceae) 'Mahogany'  
   etc.  
   ASPIDIOTUS orientalis.  
 SYMPHORICARPUS (Caprifoliaceae).  
   PIENACOCCUS colemani.  
   LECANIUM corni.  
   PULVINARIA betulae.  
 SYMPLICOS (Symplocaceae).  
   ERIOCOCCUS japonicus.  
   CEROCOCCUS albospicatus.  
 SYNCARPIA (Myrtaceae).  
   GOSSYPARIA syncarpiae.  
 SYNGONIUM (Araceae).  
   HEMICHIONASPIS aspidistrae.  
 SYRINGA (Oleaceae) 'Lilac.'  
   PSEUDOCOCCUS syringae.  
   LECANIUM corni.  
   PULVINARIA innumerabilis, vitis.  
   DIASPIS pentagona.  
   CHIONASPIS salicis.  
   ASPIDIOTUS diffinis, perniciosus,  
     hederac, pectinatus.  
   LEPIDOSAPHEs ulmi.  
 SYZYGIUM (Myrtaceae).  
   DIASPIS africana.  
   LEPIDOSAPHEs unguolata.  
 TABERNAEMONTANA (Apocynaceae).  
   MARGARODES rileyi.  
   LECANIUM tessellatum, hemisphaericum,  
     hesperidum, viride.  
   CEROPLASTES roseatus.  
   CONCHASPIS angraeci.  
   HOWARDIA biclavus.  
   AONIDIA cornigera.  
 TALINUM (Portulacaceae).  
   PSEUDOCOCCUS virgatus.  
   LECANIUM hesperidum.  
 TAMARINDUS (Leguminaceae).  
   MONOPHLEBUS tamarindus.  
   MARGARODES rileyi.  
   TACHARDIA lacea.  
   LECANIUM oleae.  
   CHIONASPIS acuminata.  
   HEMICHIONASPIS minor.  
   HOWARDIA biclavus.  
   ASPIDIOTUS lataniae, tamarindi,  
     orientalis.  
 TAMARIX (Tamaricaceae).  
   MONOPHLEBUS tamarindus.  
   GOSSYPARIA mannifera.  
   ERIUM lichtensioides.  
   PUTO africanus.  
   LECANIUM oleae, hemisphaericum.  
   PULVINARIA psidii.  
   TRABUTINA elastica.  
   CHIONASPIS etrusca.  
   ADISCODIASPIS tamaricola.  
 TARAXACUM (Compositae).  
   ORTHEZIA urticae.  
 TAXUS (Coniferae) 'Yew.'  
   PSEUDOCOCCUS kraunhiaae, taxi.  
   PULVINARIA floccifera.  
   DIASPIS taxicola.  
   ASPIDIOTUS taxus, aurantii.  
   FIORINIA odinae-multipora.  
   LEPIDOSAPHEs citricola.  
 TECOMA (Bignoniaceae).  
   LECANIUM somereni, corni, persicac,  
     viride.  
   PULVINARIA psidii.  
   HOWARDIA biclavus.  
   ASPIDIOTUS hederac.  
 TECTONA (Verbenaceae) 'Teak.'  
   MONOPHLEBUS tectonae.  
   ICERYA sulfurea-pattersoni.  
   LECANIUM nigrum.  
   PULVINARIA psidii.  
 TEINOSTACHYUM (Gramineae).  
   ANTONINA zonata.  
 TELOPEA (Proteaceae).  
   CHIONASPIS eugeniae.  
 TEMPLETONIA (Leguminosae).  
   ASTEROLECANIUM fibriatum.  
   ASPIDIOTUS ceratus.  
   LEPIDOSAPHEs chitinosae.

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- TEPHROSIA (Leguminaceae).  
 CEROCOCCUS hibisci.  
 PSEUDOCOCCUS virgatus.  
 PHENACOCCUS iceryoides.  
 ASPIDIOTUS orientalis.
- TERMINALIA (Combretaceae).  
 PSEUDOCOCCUS erotonis.  
 LECANIUM terminaliae, begoniae,  
 nigrum, oleae.  
 HOWARDIA biclavis.  
 ASPIDIOTUS destructor, ficus.
- TETRANTHERA (Lauraceae).  
 CHIONASPIS minuta, megaloba.
- TETRASTIGMA (Vitaceae).  
 LECANIUM luzonicum.
- TEUCRIUM (Labiateae).  
 ORTHEZIA delavanxii, urticae.  
 ASTEROLECANIUM fimbriatum.  
 ASPIDIOTUS labiatarum.
- THEA (Ternstroemiaceae) 'Tea.'  
 ICERYA aegyptiaca, purchasi.  
 MARGARODES rileyi.  
 ORTHEZIA insignis.  
 TACHARDIA decorella, decorella-  
 theae.  
 CEROCOCCUS ficoides.  
 PSEUDOCOCCUS citri, theaeicola.  
 PHENACOCCUS ornatus.  
 RIPERSIA theae.  
 LECANIUM notatum, viride, watti,  
 formicarii, discrepans, nigrum,  
 hemisphaericum, colemani.  
 PULVINARIA aurantii, psidii, theae.  
 LICHTENSIA japonica.  
 CERONEMA japonica.  
 ERIOCHITON theae.  
 CEROPLASTES ceriferus, floridensis,  
 rubens.  
 DIASPIS pentagona-theae.  
 CHIONASPIS manni, caroli.  
 HEMICHIONASPIS separata, theae,  
 aspidistrae.  
 HOWARDIA biclavis.  
 FIORINIA fioriniae, theae.  
 ASPIDIOTUS camelliae, cyanophylli,  
 destructor, dietyospermi, theae,  
 lataniae, orientalis, duplex, poe-  
 oniae, transparentis.  
 LEPIDOSAPHES newsteadi.
- PARLATORIA theae, mytilaspiformis,  
 sylvaticus.
- THEOBROMA (Sterculiaceae) 'Cacao.'  
 PALAEOCOCCUS theobromae.  
 ASTEROLECANIUM pustulans.  
 TACHARDIA albizziae.  
 PSEUDOCOCCUS theobromae, cro-  
 tonis, citri, tayabanus, virgatus.  
 STICTOCOCCUS sjostedti, dimorphus,  
 gowdeyi, intermedius.  
 HEMILECANIUM theobromae.  
 PULVINARIA jacksoni.  
 CEROPLASTES bussei, theobromae.  
 CEROPLASTODES virescens.  
 INGLISIA conchiformis, theobromae.  
 PHILEPHEDRA broadwayi.  
 ASPIDIOTUS trilobitiformis, palmar,  
 articulatus.  
 PSEUDOPARLATORIA pusilla.
- THEOPHRASTA (Myrsinaceae).  
 PULVINARIA psidii.
- THESIUM (Santalaceae).  
 ASTEROLECANIUM fimbriatum, thesii.
- THESPESIA (Malvaceae).  
 PALAEOCOCCUS bicolor.  
 WALKERIANA eincrea.  
 ASTEROLECANIUM thespesiace.  
 LECANIUM nigrum.  
 PULVINARIA thespesiace.  
 INGLISIA bivalvata.  
 PSEUDOCOCCUS corymbatus.  
 PHENACOCCUS glomeratus.
- THRINAX (Palmaceae).  
 DIASPIS trinacis, boisduvali.  
 CHIONASPIS unilateralis.  
 PINNASPIS buxi.  
 ASPIDIOTUS destructor.
- THUJA (Coniferae).  
 PSEUDOCOCCUS ryani.  
 LECANIUM fletcheri, arion.  
 DIASPIS carueli, minima, visci.  
 CHIONASPIS striata.  
 ASPIDIOTUS lataniae, hederac.  
 PARLATORIA chinensis.
- THUNBERGIA (Acanthaceae).  
 ORTHEZIA insignis.  
 PSEUDOCOCCUS virgatus.  
 CEROPUTO barberi.  
 HEMICHIONASPIS minor.

- THUNBERGIA (Acanthaceae)—*cont.*  
   ASPIDIOTUS dictyospermi, lataniae.  
   PARLATORIA pergandei.  
 THYMELAEAE (Thymelaeaceae).  
   ERIOCOCCUS thymelaeae.  
   ASPIDIOTUS privignus, labiatarum,  
     hederae, niger.  
 THYMUS (Labiatae).  
   ERIOCOCCUS ericae.  
   LECANIUM oleae.  
 TILIA (Tiliaceae) 'Lime.'  
   XYLOCOCCUS filiferus.  
   PHENACOCCLUS aceris, aericola.  
   LECANIUM nigrofasciatum, tulipi-  
     ferae, coryli.  
   PULVINARIA innumerabilis, tiliac, vitis.  
   CHIONASPIS salicis.  
   ASPIDIOTUS ancyclus, diffinis, os-  
     treaeformis, perniciosus.  
   LEPIDOSAPHES ulmi.  
 TILLANDSIA (Bromeliaceae).  
   ASPIDIOTUS personatus.  
 TOLPIS (Compositae).  
   ASPIDIOTUS rapax.  
 TORREYA (Coniferae).  
   PUTO cupressi.  
   POLIASPIS pini.  
 TOWNSENDIA (Compositae).  
   PALAEOCOCCUS townsendi.  
 TRACHYCARPUS (Palmaceae).  
   LECANIUM tessellatum.  
   ASPIDIOTUS persearum, hederac.  
   PARLATORIA pergandei.  
 TRACHYMENA (Umbelliferae).  
   ERIOCOCCUS buxi-australis.  
 TRECULIA (Artocarpaceae).  
   LECANIUM longulum.  
 TREMA (Urticaceae).  
   ANOMALOCOCCUS cremastogastris.  
   LECANIUM tremac.  
   DIASPIS pentagona.  
 TRIBULUS (Zygophyllaceae).  
   PSEUDOCOCCUS virgatus-humilis.  
 TRICALYSIA (Cinchonaceae).  
   ASPIDIOTUS gracilis.  
 TRICHILIA (Meliaceae).  
   PSEUDOCOCCUS trichiliae.  
 TRICHOGONIA (Compositae).  
   TECTOPULVINARIA albata.
- TRICHOMANES (Filices).  
   RIPERSIA filicicola.  
 TRICYCLA (Nyctaginaceae).  
   CEROCOCCUS andinus.  
 TRIFOLIUM (Leguminaceae).  
   GUERINIELLA sciratulac.  
   ORTHEZIA urticae.  
   ASTEROLECANIUM fimbriatum.  
   PSEUDOCOCCUS trifolii, aridorum.  
   LECANIUM tulipiferae.  
   ASPIDIOTUS hederac.  
 TRIPLARIS (Polygonaceae).  
   CEROPLASTES floridensis.  
 TRISTANIA (Myrtaceae).  
   ASPIDIOTUS subrubescens.  
 TRITICUM (Gramineae).  
   ERIOCOCCUS insignis.  
   PHENACOCCLUS cholodkovskyi, gra-  
     minis.  
   MICROCOCCUS similis.  
 TRIUMFETTA (Tiliaceae).  
   HEMICHIONASPIS minor.  
 TROPHIS (Artocarpaceae).  
   ASPIDIOTUS tesseratus.  
 TSUGA (Coniferae).  
   PHYSOKERMES taxifoliae.  
   LEUCASPIS kelloggi.  
   ASPIDIOTUS tsugae, ehrhorni, abietis.  
 TULIPA (Liliaceae).  
   PSEUDOCOCCUS hibernicus.  
 TUNICA (Caryophyllaceae).  
   ORTHEZIA urticae.  
 TUPIDANTHUS (Araliaceae).  
   PSEUDOCOCCUS adonidum.  
 TURPINIA (Sapindaceae).  
   AONIDIA columnifera.  
   FIORINIA fiorinia.  
 TURRAEA (Meliaceae).  
   HEMICHIONASPIS chionaspiformis.  
 TYLOPHORA (Aselepiadaceae).  
   DIASPIS pentagona.
- ULEX (Leguminosae) 'Gorse.'  
   ICERYA purchasi.  
   ERIOCOCCUS insignis.  
   PHENACOCCLUS aceris.  
   LECANIUM mori, pulchrum.  
   ASPIDIOTUS camelliae, hederac.  
   LEPIDOSAPHES ulmi-ulicis.

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- ULMUS (Ulmaceae) 'Ehm.'  
   GUERINIELLA serratulae.  
   LECANODIASPIS pruinosa.  
   GOSSYPARIA spuria.  
   PSEUDOCOCCUS adonidum, citri,  
     longispinus.  
   PHENACOCCLUS ulmi, aceris.  
   RIPERSIA pupifera.  
   LECANIUM aceris, canadense, caryae,  
     cockerelli, quercitronis, corni,  
     rugosum, tiliae, nigrofasciatum,  
     coryli, capreae.  
   PULVINARIA innumerabilis, pruni.vitis.  
   DIASPIS pentagona.  
   CHIONASPIS americana, furfura, salicis.  
   ASPIDIOTUS perniciosus, ulmi, os-  
     treaeformis, camelliae, cydoniae,  
     hederae.  
   LEPIDOSAPHES ulmi, ficifoliae-ulmi-  
     cola.  
 UNCARIA (Rubiaceae).  
   HEMICHIONASPIS aspidistrac.  
 URENA (Malvaceae).  
   DIASPIS pentagona.  
   HEMICHIONASPIS minor.  
 URERA (Urticaceae).  
   PHYLLOCOCCUS oahuensis.  
 URTICA (Urticaceae) 'Nettle.'  
   ICERYA purchasi.  
   ORTHEZIA urticae.  
   PSEUDOCOCCUS citri.  
   DIASPIS pentagona.  
 UVARIA (Anonaceae).  
   CEROPLASTES uvariae.  
   HEMICHIONASPIS uvariae.  
 VACCINIUM (Ericaceae).  
   ERIOCOCCUS quercus, costaricensis.  
   LECANIUM distinguendum, kingi,  
     nigrofasciatum, websteri, coryli.  
   PULVINARIA ericae.  
   CHIONASPIS salicis.  
   ASPIDIOTUS oxycoccus.  
   LEPIDOSAPHES ulmi.  
 VALERIANODES (Verbenaceae).  
   HEMICHIONASPIS minor.  
 VANDA (Orchidaceae).  
   PARLATORIA pseudaspidotus, proteus.  
   LEPIDOSAPHES vandae.  
 VANILLA (Orchidaceae).  
   ASPIDIOTUS aurantii.  
 VATERIA (Dipterocarpaceae).  
   AONIDIA tentaculata.  
   PARLATORIA vateriae.  
 VATICA (Dipterocarpaceae).  
   ISCHINASPIS spathulata.  
 VERBENA (Verbenaceae).  
   PALAEOCOCCUS nudatus.  
   ICERYA purchasi.  
   PSEUDOCOCCUS adonidum.  
 VERNONIA (Compositae).  
   ORTHEZIA insignis.  
   TECTOPULVINARIA albata.  
   CEROPLASTES novaesi.  
   INGLISIA castilloae.  
   HOWARDIA biclavis.  
 VERONICA (Serophulariaceae).  
   ASTEROLECANIUM fimbriatum.  
   PSEUDOCOCCUS alpinus.  
   LECANIUM pulchrum.  
   ASPIDIOTUS hederae.  
   POLIASPIS media.  
 VERSCHAFFELTIA (Palmaceae).  
   AONIDIA simplex.  
 VIBURNUM (Caprifoliaceae).  
   CEROCOCCUS muratae.  
   PSEUDOCOCCUS viburni, citri.  
   PHENACOCCLUS aceris.  
   LECANIUM eorylifex, corni.  
   PULVINARIA innumerabilis, viburni,  
     vitis.  
   LICHTENSIA viburni.  
   FILIPPIA oleae.  
   CHIONASPIS lintneri, eugeniae, salicis.  
   ASPIDIOTUS perniciosus, britanni-  
     cus, hederae, spinosus, perseae.  
   PARLATORIA myrtus.  
   LEPIDOSAPHES ulmi.  
 VICIA (Leguminosae).  
   GUERINIELLA serratulae.  
   ASTEROLECANIUM fimbriatum.  
 VIMINARIA (Leguminosae).  
   PULVINARIA maskelli-viminariae.  
 VINCA (Apocynaceae).  
   ORTHEZIA urticae.  
   LECANIUM hesperidum, corni, oleae  
   ASPIDIOTUS rapax, hederae, britan-  
     nicus.

- VIOLA (Violaceae).  
   PSEUDOCOCCUS virgatus, eriogoni.  
   PHENACOCCUS wilmattae.
- VISCUM (Loranthaceae) 'Mistletoe.'  
   GOSSYPARIA spuria.  
   POROCOCCUS pergandei, tinctorius.  
   LECANIUM hesperidum.  
   PULVINARIA betulae.  
   CEROPLASTES rusei.  
   DIASPIS phoradendri, visci.  
   LEPIDOSAPHES ulmi.
- VISNEA (Ternstroemiaeae).  
   LECANIUM hemisphaericum.  
   ASPIDIOTUS lauretorum.
- VITEX (Verbenaceae).  
   ASPIDIOTUS hederac.
- VITIS (Vitaceae).  
   GUERINIELLA serratulac.  
   ICERYA purchasi, palmeri.  
   MARGARODES vitium, capensis,  
     greeni.  
   PSEUDOCOCCUS subterraneus, longi-  
     spinus, bakeri, capensis, citri,  
     adonidum, vitis.  
   PHENACOCCUS aceris.  
   RHIZOECUS falcifer.  
   LECANIUM armeniacum, berberidis,  
     vini, oleae, fukayi, magnoliarum,  
     nigrofasciatum, persicae, longu-  
     lum, corni, corni-robiniarum.  
   PULVINARIA innumerabilis, simplex,  
     vinifera, vitis, betulac.  
   LICHTENSIA viburni.  
   CRYPTINGLISIA lounsburyi.  
   DIASPIS pentagona.  
   CHIONASPIS vitis.  
   HEMICHIONASPIS minor.  
   ASPIDIOTUS cydoniac, uvac, tesse-  
     rata, aurantii, obscurus, vitis,  
     fossor, convexus, pedroniformis,  
     perniciosus, rapax, ficus, labia-  
     tarum, pectinatus, hederac.  
   LEPIDOSAPHES ulmi, ulmi-vitis, buz-  
     ensis.  
   PARLATORIA proteus, oleac, per-  
     gandei-camelliac.
- VOACANGA (Apocynaceae).  
   PROTOPULVINARIA longivalvata-  
     bakeri.
- VRIESIA (Bromeliaceae).  
   ASPIDIOTUS hederac.
- WACHENDORFIA (Liliaceae).  
   PSEUDOCOCCUS wachendorfiac.
- WALSURA (Meliaceae).  
   AONIDIA dentata.  
   FIORINIA fioriniac.
- WARNERIA (Rubiaceae).  
   PULVINARIA psidii.  
   PROTOPULVINARIA pyriformis.
- WASHINGTONIA (Palmaceae).  
   LECANIUM hesperidum.  
   DIASPIS boisduvali.  
   COMSTOCKIELLA sabalis.  
   ASPIDIOTUS ficus.  
   PARLATORIA pergandei.
- WENDLANDIA (Rubiaceae).  
   PHENACOCCUS iceryoides.
- WENDTIA (Geraniaceae).  
   CEROCOCCUS badius.
- WIGANDIA (Hydroleaceae).  
   ASPIDIOTUS lataniae.  
   LEPIDOSAPHES pinnaeformis.
- WILLUGHBEIA (Apocynaceae).  
   ASPIDIOTUS javanensis.
- WISTERIA (Leguminosae).  
   CONCHASPIS angracii.  
   PSEUDOCOCCUS kraunhiac.  
   CHIONASPIS wisteriac.
- ASPIDIOTUS perniciosus.
- WITHAMIA (Solanaceae).  
   LECANIUM nigrum.
- XANTHOPHYLLUM (Polygalaceae).  
   CRYPTOPARLATORIA parlatorioides.
- XANTHORRHOEA (Liliaceae).  
   CHIONASPIS xanthorrhoeac.  
   ASPIDIOTUS rossi.  
   LEPIDOSAPHES pallens.
- XANTHOSOMA (Araceae).  
   PSEUDOCOCCUS virgatus.
- XANTHOXYLUM (Rutaceae).  
   LECANIUM quercitronis, infrequens,  
     xanthoxylum.  
   CEROPLASTES grandis.
- XEROTES (Juncaceae).  
   CHIONASPIS xerotidis.  
   ASPIDIOTUS cladii.

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- XIMENIA (Olacaceae).  
 CHIONASPIS nigerensis.  
 XYLIA (Leguminosae).  
 TACHARDIA lacca.  
 XYLOCARPUS (Meliaceae).  
 CHIONASPIS usambarica.  
 ASPIDIOTUS articulatus.  
 XYLOPHYLLA (Euphorbiaceae).  
 ASPIDIOTUS lataniae.  
  
 YUCCA (Liliaceae).  
 LECANODIASPIS yuccae.  
 PSEUDOCOCCUS olivaceus.  
 CEROPUTO yuccae.  
 LECANIUM oleae, hesperidum.  
 CEROPLASTES rusci.  
 CONCHASPIS angracei.  
 HEMICHIONASPIS minor.  
 ASPIDIOTUS hederæ, yuccae, yuccae-neomexicana, yuccarum, lataniae, biformis, alienus.  
 LEPIDOSAPHES nigra, philococcus, ulmi.  
  
 ZALACCA (Palmaceae).  
 ISCHNASPIS filiformis.  
 ZAMIA (Cycadaceae).  
  
 PSEUDOCOCCUS zamiae.  
 LECANIUM hemisphaericum.  
 DIASPIS zamiae, pentagona.  
 HEMICHIONASPIS minor.  
 ASPIDIOTUS ficus.  
 ZANTEDESCHIA (Araceae).  
 PULVINARIA psidii.  
 ZEA (Gramineae) 'Maize.'  
 CEROPLASTES rusci.  
 ASPIDIOTUS dictyospermi.  
 ZILLA (Cruciferae).  
 ASPIDIOTUS seurati.  
 ZINGIBER (Zingiberaceae).  
 CEROPLASTES rubens.  
 ZIZYPHUS (Rhamnaceae).  
 TACHARDIA lacca.  
 PSEUDOCOCCUS perniciosus, filamentosus.  
 CEROPLASTODES cajani.  
 PULVINARIA burkilli.  
 DIASPIS pentagona.  
 CHIONASPIS megaloba.  
 ASPIDIOTUS lataniae.  
 PARLATORIA zizyphi, chinensis.  
 ZUCCAGNIA (Leguminosae).  
 ERIOCOCCUS diversispinus.  
 LECANIUM silvestrii.

(*Note.* The names in the foregoing list have, in most cases, been entered in the exact form in which they have been recorded by the various observers. Consequently, the same species may sometimes appear under different aliases: e.g. *Pseudococcus adonidum* and *longispinus*; *Lecanium persicae*, *coryli* and *corni*; etc. I have left them as they are, partly because the synonymy is not yet universally accepted and, also, for the convenience of observers who would recognise the species more readily by the names to which they are accustomed.)

Some interesting observations on the host-affinities of *Coccidae* may be gathered from these lists. It will be noticed, for instance, that the GRAMINEAE (including the Bamboos) have a special Coccid fauna comprising such genera as *Antonina*, *Aclerda*, *Eriopeltis*, *Lecanopsis* and *Odonaspis*. The CONIFERAE have a monopoly of the genus *Physokermes* and support twelve out of the eighteen named species of *Leucaspis*. The genus *Kermes* is dependent upon species of Oak; while most of the gall-making Coccidae—including the genera *Opisthoscelis*, *Ascelis* and *Apiomorpha*—occur only upon various species of *Eucalyptus*.

The grasses can probably claim to support the largest number of species, with the total of 243, out of which number 63 must be credited to the Bamboos. Of individual genera, *Eucalyptus* heads the list, with 133 separate species; but is run very close by *Acacia* with 130 and *Quercus* with 124. If the *Acacias* and *Mimosas* were to be counted together, they would take the first place with a sum total of 149. The only other genus that exceeds the century is *Ficus*, with 102; though it is closely approached by *Citrus*, with 99. After these, the figures drop very steeply, *Pyrus* coming next with 59 species to its credit, followed by *Vitis* with 54, *Thea* and *Pinus* with 52 apiece, and *Cocos* with 48. The rest tail off very rapidly.

It would be interesting to ascertain the species of *Coccidae* that have the largest number of host-plants, but this would entail more labour than I should care to expend upon the work. I think, however, that *Pseudococcus citri*, *Lecanium hesperidum*, *Lepidosaphes ulmi* and *Aspidiotus hederæ* would come somewhere near the top of the list.

## THE USE OF SCIENTIFIC AND POPULAR NAMES IN ECONOMIC BIOLOGY.

BY S. A. NEAVE, M.A., D.Sc. (OXON.).

BIOLOGICAL SCIENCE in its economic aspects is a comparatively modern study, and since it necessarily appeals to a far wider public than does the purely scientific side of the subject, it is perhaps not unnatural, and to some extent inevitable, that popular names for plants and animals should be widely used in preference to scientific ones by writers on the subject. At the same time it must be recognised that the work of the systematist is necessarily the foundation on which economic workers must build. Without the accurate identification and nomenclature of plants or animals, no important study of their biology or distribution can be rendered available to others and no comparison of results can be made between those who speak different languages.

It is obvious however that much of the work of the economic biologist is published for the benefit of agriculturists and others who have little or no scientific training. It is therefore essential that to convey anything to such a public the popular names of the plants and animals concerned must be used. This does not however justify the *omission* of scientific names, a practice that is only too frequent at the present time. If the use of these in the text is objected to, they can always be added as a footnote—as is done in many of the bulletins of the United States Department of Agriculture.

One objection—and that not an unreasonable one—that has been raised to the use of scientific names is the unfortunate change in nomenclature that continually arises, even in the case of the commonest species and most widely known pests. The recent change of the name of the brown-tail moth—known for so long as *Euproctis chrysorrhoea* and now called *Nygmia phaeorrhoea*—is a good example of this. Though this objection is sound so far as it goes, the remedy lies, not in the disuse of scientific names, but in the cooperation on the part of workers in the economic field to put pressure on the International Committee on Zoological Nomenclature to bring about with the minimum of delay some final decision as to the names of the principal animals and plants of economic importance.

Somewhat similar objections may also be raised to popular names. These are frequently of very local application and may vary considerably within the same country, or the same name may be used in widely separated parts of the English-speaking world for entirely distinct animals or plants. Since it is clear that the use of popular names must be continued under present conditions, some uniformity is highly desirable. This can only be obtained by the formation of a central body to which lists of local names both of plants and animals in use throughout the English-speaking world could be sent. It would be the duty of such a body to collect data as to all the recognised names, to reduce their number to a minimum and to compile a list that authors should agree to use as far as possible. The names selected should, where practicable, be informative and have some educational value for the layman.

In this respect much advantage might be gained in the entomological field if some agreement could be come to as to the popular names to be applied to the larval stages of different orders of insects: *e.g.* the restriction of "caterpillar" to the Lepidopterous larva, of "maggot" to the Dipterous and of "grub" to the Coleopterous. The term "worm," though objectionable as having a precise zoological significance, is in very general use especially in connection with Lepidopterous larvae infesting cotton-bolls and might be retained in this restricted sense, but limited to it. The use of misleading names such as "white ants" for "termites" should be avoided altogether. Names such as "Imported Cabbage Worm" used in North America for *Pieris rapae* are unsatisfactory as being only applicable to one part of the English-speaking world, and "European Cabbage Caterpillar" would be better. Similar adjustments of popular names among plants are advisable in the botanical field, and many cases will at once occur to the economic botanist.

To recapitulate, the weight of evidence goes to show that the use of *both* scientific and popular names is necessary under present conditions; there are difficulties inherent in the use of either, but these arise from the same cause, *i.e.* lack of uniformity and agreement on the subject among workers throughout the world; these difficulties can and should be remedied to a considerable extent.

## LAWS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS

1. The Association shall be named "The Association of Economic Biologists."

2. The objects of the Association shall be to promote the study of Economic Biology.

3. The Association shall consist of Honorary and Ordinary Members.

4. Each candidate for ordinary membership shall be nominated by two members. Such nomination shall be approved by the Council and confirmed by a vote of two-thirds of the members present and voting at the next General Meeting.

Every member elected shall receive notice from the Secretary and shall continue a member until his written resignation shall be received by the Secretary, or until membership be forfeited under the Laws.

Ordinary Members shall pay an annual subscription of One Guinea, due on January 1st of each year, or may compound for their subscription with a sum of fifteen guineas.

All Ordinary Members on first election shall pay an entrance fee of half-a-guinea.

5. Ordinary Members shall be entitled to admission to all the meetings of the Association, to vote thereat, to present papers, to take part in discussions and to receive a copy of the Association's publications.

Each member shall be entitled to introduce personally non-members to the Association's meetings.

6. Honorary Members shall be persons, *not subjects of the British Crown*, who have contributed in an eminent degree to the advancement of the science of Economic Biology. They shall be recommended by a majority of the whole Council and elected in the same manner as Ordinary Members.

The number of Honorary Members shall not at any time exceed *twelve* and not more than *two* shall be elected in any one year.

Honorary Members shall not be liable to any payments and shall each receive a copy of the Association's publications.

Their privileges shall be the same as those of Ordinary Members, but they shall not be entitled to vote at the meetings.

7. The Council shall have power, at any of their meetings, by two-thirds of the votes of those present and voting, to terminate the membership of any member whose subscription shall be one year or more in arrears, or whose membership shall, from any other cause, be undesirable. No member whose subscription is in arrears shall be entitled to vote at a General Meeting or to receive the Association's publications, nor shall any publication be sent to a new member until his entrance fee and subscription shall have been received.

8. All meetings shall be announced by circular addressed to all Members resident in the United Kingdom. The place and time of the meetings shall be decided by the Council; ten shall be a quorum at such a meeting.

9. An Annual General Meeting shall be held and shall ordinarily be the General Meeting falling nearest to the end of the year or as the Council shall decide.

At this meeting the order of business shall be:

1. The reading of the minutes of the previous meeting.
2. The reading of a report of the Council on the work of the past year.
3. The statement of the Treasurer.
4. The election of members.
5. The election of Officers and other members of the Council.
6. Other business.

10. The business of the Association shall be conducted by a Council consisting of a President, not more than five Honorary Vice-Presidents, a Treasurer, one or more Secretaries, and twelve other members.

11. The Council shall nominate the Officers and other Members of the Council for the ensuing year. A list of such nominations shall be sent to all members resident in the United Kingdom at least three weeks before the Annual General Meeting. The President shall designate two Members of Council to act as Vice-Presidents.

Any Member proposing an addition to, or an alteration in the list must inform the Honorary Secretary by letter at least ten days before the Annual General Meeting.

The nominations shall be confirmed by the members present at the Annual General Meeting and a ballot shall be taken in the event of any additions or alterations being proposed.

12. The Council may fill up any vacancy that may occur in the list of Officers and Council.

13. The Council shall meet at such times as they may determine; six members shall form a quorum.

The Council shall purchase such books, instruments, specimens, furniture and other necessaries as may be required, pass the accounts and authorise their payment, and generally manage the affairs and administer the funds of the Association.

14. The Council shall appoint from the Members of the Association an Editorial Committee who shall be responsible for the publications.

15. At a Council Meeting, prior to the Annual General Meeting, the Council shall appoint one or more Auditors to audit the Treasurer's Accounts.

16. All properties of the Association, both present and future, shall be deemed to be vested in the Council of the Association for the time being, in conformity with the provisions of the Literary and Scientific Institutions Act, 1854.

17. No new Law shall be made nor any Law altered except on the proposition of the Council or the requisition of at least ten members addressed to the Honorary Secretary. The new Laws or alterations of Laws shall be proposed in writing, signed by the requisitionists and delivered to the Honorary Secretary a month before an Extraordinary General Meeting, which shall be called for the purpose.

Such proposed new Laws or alterations in the Laws shall be printed in the circular convening the Meeting, and sent to all members resident in the United Kingdom at least two weeks before the date of such Meeting.

No new laws, alterations or amendments shall be passed except by a two-thirds majority, when not less than fifteen members are present and voting.

## LIST OF MEMBERS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS

1914. ADAIR, E. W., *Department of Agriculture, Cairo.*
1908. ALCOCK, Col. A. W., C.I.E., M.B., LL.D., F.R.S., *Heathlands, Belvedere, Kent.*
1914. ANSTEAD, R. D., *United Planters' Association, Bangalore, Southern India.*
1908. ASHWORTH, J. H., D.Sc., F.Z.S., 69, *Braid Avenue, Edinburgh.*
1914. BAILEY, M. A., 491, *Alleyn Park, Dubwich.*
1905. BALFOUR, Andrew, C.M.G., M.D., *c/o Messrs Burroughs and Wellcome, Snow Hill Buildings, London, W.C.*
1914. BALLARD, E., F.E.S., *Government Entomologist, Coimbatore, Madras.*
1914. BARBER, Dr C. A., *Coimbatore, India.*
1914. BARKER, Prof. B. T. P., *National Fruit and Cider Institute, Long Ashton, Bristol.*
1919. BEER, R., *Westwood, Bickley, Kent.*
1914. BEESON, C. F. C., *Forest Research Institute, Dehra Dun, India.*
- Hon. BERLESE, Prof. Dr Antonio, *R. Staz. di Entomologia Agraria, Firenze, Italy.*
1915. BIJL, P. A. van der, M.A., F.L.S., *Natal Herbarium, Berea, Durban.*
1914. BILLINGHURST, H. G., 76, *Lebanon Gardens, Wandsworth, S.W. 18.*
1919. BLACKMAN, Prof. V. H., F.R.S., *Imperial College of Science, S.W. 7.*
- Hon. BLANCHARD, Prof. Dr Raphael, 15, *Rue de l'École de Médecine, Paris, France.*
1909. BLES, E. J., D.Sc., *Elterholm, Madingley Road, Cambridge.*
1916. BOCOCK, C. H., F.E.S., *The Elms, Ashley, Newmarket.*
- Hon. BOS, Prof. Dr J. Ritzema, *Willie Commelin Scholten, Amsterdam, Netherlands.*
1907. BOURNE, Prof. G. C., M.A., D.Sc., F.R.S., *Savile House, Oxford.*
1914. BRIERLEY, W. B., *Rothamsted Experimental Station, Harpenden.*
1914. BROOKS, F. T., M.A., *The Botany School, Cambridge.*
1907. BURDON, E. R., M.A., F.L.S., *Ikenhilde, Royston, Herts.*
1914. BURNS, W., *Office of Economic Botanist, Agricultural College, Poona, India.*
1914. BURT, B. C., *Agricultural College, Cawnpore, India.*
1917. CAMERON, A. E., M.A., D.Sc., *Entomological Laboratory, Agassiz, British Columbia.*
- Orig. CARPENTER, Prof. G. H., B.A., B.Sc., *Royal College of Science, Dublin, Ireland.*
1914. CAYLEY, Miss D. M., *Fairlands, Fairmile, Cobham.*
1905. CHANDLER, S. E., D.Sc., 59, *Anerley Park, Penge, S.E.*
1908. CHITTENDEN, F. J., F.L.S., V.M.H., *The Laboratory, R.H.S. Gardens, Wisley, Surrey.*
- Hon. CHOLODKOVSKY, Prof. Dr, M.A., *Institut Forestier, Petrograd, Russia.*
1914. COOPER, W. F., *The Research Laboratory, Watford.*
1914. CORBETT, G. H., *The Greta, Troubridge, Wilts.*
- †1905. CORNWALLIS, F. S. W., *Linton Park, Maidstone, Kent.*
1915. COTTON, A. D., *Pathological Laboratory, Royal Gardens, Kew.*

1918. CRAGG, P. A., *Merivale Nurseries, Heston, Middlesex.*  
 Hon. CUBONI, Prof. Guiseppa, *Phytopathological Station, Rome.*
1915. DAVIDSON, J., *Highfield House, Neston, Cheshire.*
1914. DEAKIN, R. H., 38, *Jakman Road, Belsall Heath, Birmingham.*
1915. DOIDGE, Miss E. M., M.A., F.L.S., *Division of Botany, Dept. of Agriculture, Pretoria, South Africa.*
1918. DOWNES, Dr H., F.L.S., F.G.S., F.R.M.S., *Dilton Lea, Ilminster.*
1917. ELTRINGHAM, H., M.A., D.Sc., F.E.S., 6, *Museum Road, Oxford.*
1914. EMPTAGE, W. F., 1, *Ullswater Road, West Norwood, S.E. 27.*
1916. EYRE, J. A. Vargas, *S.E. Agricultural College, Wye.*
1909. FARMER, Prof. J. B., D.Sc., F.R.S., *Imperial College of Science, South Kensington, S.W. 7.*
1905. FREEMAN, W. G., A.R.C.S., B.Sc., *Agricultural Station, Trinidad.*
1913. FRYER, J. C. F., M.A., F.E.S., *Board of Agriculture, 4, Whitehall Place, S.W. 1.*
1918. GAHAN, C. J., M.A., D.Sc., F.E.S., *British Museum (Natural History), Cromwell Road, S.W. 7.*
1914. GAMBLE, Prof. F. W., F.R.S., *The University, Edmund Street, Birmingham.*
1914. GARDINER, Prof. J. S., F.R.S., *Bredon House, Selwyn Gardens, Cambridge.*
1908. GARNSEY, Major E., *Board of Agriculture and Fisheries, S.W. 1.*
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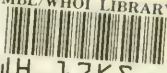
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