PHYSIOLOGICAL PRE-DETERMINATION¹: 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.

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(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

¹ 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 development¹.

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.

¹ 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	
				stem	
				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>				Dry weight (tops only)	
	0	50	50	0.555 g.	
	8	50	50	0.510	
	24	50	44	0.455	
	48	50	50	0.435	
	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. These 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		Seed soaked previous to sowing				
			0 hours	6 hours	24 hours	48 hours	72 hours
Wheat	100	Germination results	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.
$\frac{1}{2}$	6	92	2.065
1	24	96	2.119
2	48	95	2.369
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	1.075
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	0.657
24	93	0.577
48	77	0.571
72	100	0.479

Dwarf Beans (Phaseolus). These plants were harvested $4\frac{1}{2}$ 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°		
- Thermostat

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) 22.17	(20) 21.74
24	(9) 20.05	(12) 21.04	(18) 20.33	(16) 19.18
48	(8) 13.92	(15) 17.93	(20) 16.28	(13) 11.54
72	(15) 17.80	(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 ($\frac{1}{2}$), 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 ($\frac{1}{2}$), 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