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

V. REVIEW OF LITERATURE. CHAPTER IV.

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(With Plate I.)

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CHAPTER IV

THE EFFECT OF CONDITIONS DURING GERMINATION AND IN
THE EARLY SEEDLING STAGE UPON SUBSEQUENT GROWTH
AND FINAL YIELD.

INTRODUCTION.

In the previous chapter of this review we (18) dealt with seed-treatments which could be classed as treatments affecting nutrition. The pre-determining effect of increased or decreased nutritional supply operating for a limited period during the critical stages of early development was demonstrated. The proportionality established between seedling weights due to differential nutrition is maintained when the nutritional supply

is subsequently equalised during the main period of growth, and it is directly reflected in the final yield.

In the light of evidence afforded by growth curves based on dry-weight measurements which were available in the literature, growth and development within the limits of hereditary potentialities were treated as fundamentally matters of physiological pre-determination. The general expression covering growth was described as the Compound Interest Law of Development. The operation of this law may be subject to a number of secondary modifications.

A few fundamental principles are necessary for the study of growth and development. These are conspicuous by their absence in existing text-books of plant physiology, which excel in the assemblage of interesting curiosities and of uncorrelated details. The phenomena of *normal growth* seem to call for further study and analysis and for the application of mathematical treatment. Even a clear grasp of the general conception of the compound interest law of development at once greatly simplifies the handling of problems of physiological pre-determination and of growth. One is able to formulate approximately the magnitude of effects that will be observed as the result of causes operating continuously or for a short time in relation to the stage of development at which the cause operates and the effect is desired.

In the cases with which we dealt in the preceding chapter the absolute magnitude of the final effects upon yield were out of all proportion to the absolute magnitude of the causes to which they were due. These causes operated for a short period during the early stages of development and initiated what we have termed physiological pre-determination. It is this fact which makes the phenomenon of physiological pre-determination of such importance from the economic point of view. Roughly speaking, the absolute value of the effect produced is proportional, not to the value of the initial cause (*i.e.* that which has to be supplied by the agriculturist), but to the value of the initial cause multiplied by the time-interval between the operation of the cause and the reaping of the result.

In the present chapter we deal with seed-treatments which we have classified for convenience under the following headings, viz.:

- (1) Physical treatments of the seed;
- (2) Chemical treatments of the seed, which do not obviously affect its nutrition¹.

¹ It should be pointed out that there are many papers which deal with the effect upon *germination* of various chemical treatments of seeds, but in which no mention is made of the pre-determining effects of the seed-treatments (cf. Bokorny (4); Sigmund (32)).

PHYSICAL TREATMENTS OF THE SEED.

(a) HIGH TEMPERATURES.

Experimental work in which seeds in the air-dry condition have been submitted to high temperatures falls into three categories.

It has been established that in the case of many seeds the capacity for germination, though low after the harvest, increases during storage to its full value, which is attained by the following spring. A typical example of the results obtained by Atterberg⁽²⁾ in the case of barley is given below (Table I).

TABLE I.

Barley reaped at four stages.

Stage of maturity of the seed when harvested at the end of September	Percentage of Moisture in the seed		Percentage of germination when sown on						
	When reaped at the end of September	On the 20th of October, after having been stored in a cold barn and then taken to the laboratory	Sept. 26th	Oct. 5th	Oct. 20th	Oct. 27th	Nov. 3rd	Nov. 19th	Dec. 2nd
Green	42	19.0	21	6	1	29	45	82	95
Green	39	18.6	17	3	2	31	36	85	94
Yellow ripe	35	18.3	17	2	0	21	30	90	98
Ripe	27	18.4	11	1	4	3	21	85	98

It has been shown by numerous workers (*e.g.* Hotter⁽¹⁶⁾; Velten⁽³⁶⁾; Atterberg⁽²⁾, and others) that if the seeds are exposed for a short time to relatively high temperatures during the period of low germination they at once attain their full capacity for germination (*cf.* Table II).

TABLE II (after Atterberg).

Kind of seed	Treatment of the seed		Result of germination test			
Barley	Dried for 2 days at 37° C.		Gave 22 % germination in 4 days			
	" 4	" "	" 50 %	" "	12	"
	" 6	" "	" 98 %	" "	10	"
	" 8	" "	" 99.5 %	" "	8	"
The control seed (untreated) gave only 4 % germination						

We have here a definite experimental result, but a full explanation of the underlying causes of the change which occurs during storage and which is accelerated by heat is as yet not forthcoming, neither, so far as we have been able to find, are there any records extant as to the influence, if any, this procedure exercises upon the development and final yield of the plants produced.

In the second category we have a large amount of experimental work which has been undertaken with the object of obtaining a simple method of sterilising seeds. In this work tests of the growth and yield of the plants from treated seeds as compared with that of the controls from untreated seeds have been carried out, but in considering the yields obtained the authors have not distinguished between the specific physiological effects of the heat-treatment and the effect of seed sterilisation.

Finally we have a category into which fall experiments carried out with the definite object of ascertaining the pre-determining effect upon growth and yield of exposing seeds to relatively high temperatures (cf. Sprengel (33); Ockel (25); Pietrusky (27); Krašan (21); Velten (36); and Wollny (43 & 44)). The results obtained are contradictory, and no definite conclusion can be drawn from them.

The most striking of the earlier results appear to have been obtained with flax by Pietrusky. A brief exposure of the air-dry seed to temperatures ranging from 30° to 50° C. increased the quality and yield of the fibre produced by the experimental plants.

Wollny (43 & 44) in the case of a number of cereals and other economic crops reached the conclusion that dry heating the seed generally increased the productivity of the plants produced. Some of the results obtained by Wollny are summarised in the following tables (Tables III and IV):

TABLE III (after Wollny).

Experiments carried out in 1876.

Kind of seed	Number of seeds	Weight of the experimental seeds		Percentage loss in weight during the drying-process	Weight of the untreated seeds	Temperature maintained during the drying-process
		on April 5th	on April 30th			
White lupins	200	82.49 gm.	80.07 gm.	2.93	83.30 gm.	30°-35° C.
Peas	200	68.23	64.75	5.10	67.80	30°-35° C.
Flax	—	100	96.95	3.05	99.30	30°-35° C.

Harvest Results.

Kind of seed	Condition of seed sown	Percentage of plants at the harvest	Yield from 100 plants	
			Seeds	Straw
Lupin	{ Dried at 30°-35° C.	87	371 gm.	406 gm.
	{ Untreated	95	264	347
Peas	{ Dried at 30°-35° C.	75	1381	1594
	{ Untreated	91	1143	1410

			Yield per 4 sq. m.	
			Seeds	Fibre
Flax	{ Dried at 30°-35° C.	—	290 gm.	1595 gm.
	{ Untreated	—	222	1208

The area allowed for each plant was 25 sq. cm. in the case of the lupins and peas. The flax seed was sown broadcast over an area of 4 sq. metres. All seed was sown on May 4th.

TABLE IV (after Wollny).

Experiments carried out in 1876-77.

Kind of seed	Number of seeds	Weight of the experimental seeds		Percentage loss in weight during the drying-process	Weight of the untreated seeds	Temperature maintained during the drying-process
		Before drying	After drying			
Winter rye	100	4.79 gm.	4.49 gm.	6.25	4.79 gm.	30°-35° C.
Maize	75	36.40	34.93	4.04	36.40	30°-35° C.
Peas	100	40.77	38.44	5.71	41.61	30°-35° C.
Lupin	100	44.51	42.25	5.08	45.08	30°-35° C.
Flax	—	80.00	76.39	4.52	79.85	30°-35° C.

Harvest Results.

Kind of seed	Condition of the seed sown	Percentage of plants at the harvest	Number of haulms per 100 plants	Yield from 100 plants	
				Seed	Straw
Winter rye	{ Dried at 30°-35° C.	82	693	1091 gm.	2378 gm.
	{ Untreated	85	497	808	1412
Peas	{ Dried at 30°-35° C.	50	—	1638	3125
	{ Untreated	99	—	1522	2714
Lupin	{ Dried at 30°-35° C.	83	—	1153	3172
	{ Untreated	91	—	1519	4304
Maize				Yield from 100 plants	
				Green	Air-dry
Maize	{ Dried at 30°-35° C.	38	111,250 gm.	74,166 gm.	
	{ Untreated	47	94,000	63,000	
Flax		Yield per 4 sq. metres			Weight of 500 of the harvested seeds
		Seeds	Total weight	Chaff	
Flax	{ Dried at 30°-35° C.	283 gm.	955 gm.	238 gm.	2.20 gm.
	{ Untreated	341	832	236	2.27

The area allowed for each plant was 20 sq. cm. in the case of the rye, and 25 sq. cm. in the case of the maize, peas, and lupins. The flax was sown broadcast. The seed was sown on May 4th, 1877, with the exception of the winter rye, which was sown on September 22nd, 1876.

An analysis of the effect of this treatment of the seed upon the development of the plant was carried out subsequently in considerable detail by Wollny (44), who showed that (1) the percentage of germination was decreased in some cases (*e.g.* peas, beans, rye), in others (*e.g.* wheat,

barley, oats) not appreciably; (2) the growth of the resulting plant was at first delayed; and (3) the experimental plants flowered earlier and more freely than the controls. He also found that seeds after dry heating were unusually sensitive to climatic and soil conditions during germination. As a result of this growth-analysis Wollny appears to have been doubtful as to the utility from the economic point of view of drying seeds.

(b) LOW TEMPERATURES.

Many authors have dealt with the effect upon germination of exposing seeds in the moist condition to low temperatures. This has been found to be a method of general application for stimulating the germination of dormant seeds (cf. Kinzel⁽²⁰⁾).

The question as to what effect exposure to low temperatures during the critical stages of germination may have upon the subsequent course of development has been investigated in the case of seeds of the so-called winter-cereals which normally germinate in late autumn, pass the winter in the vegetative condition, and flower during the following summer. If the seeds are sown in the spring, the plants produced do not complete their development during the ensuing summer and autumn but they flower and set seed only in the following summer.

This behaviour on the part of winter-annuals has attracted attention in relation to problems of rhythm and periodicity, the question at issue being whether rhythm and periodicity in plants are inherent properties of the protoplasm or the direct effects of external conditions. Without entering into a discussion of the theories put forward by various authors we may deal fully with the careful series of experiments recently carried out by Gassner⁽¹⁰⁾¹ at Hamburg, and published last year. Gassner planted several winter varieties of cereals² in the spring and investigated whether exposure of the seeds during germination or of the plants during the early stages of seedling growth to low temperatures would affect their subsequent development. In the only communication at present available this author confines his attention to the time of formation of the flowering stems (culms) of the cereals investigated.

In each experiment four lots of 50 seeds ("pure line") were germinated on moist sand in crystallising dishes, which were kept at tempera-

¹ Gassner gives a full list of references to previous work on this subject.

² For example, "Petkuser" winter rye; "Friedrichswerther Mammuth" winter barley; "Svalöfs Extra Squarehead" winter wheat, etc.

tures of 1° – 2° C., 5° – 6° C., 12° C., and 24° C. respectively. When germination was complete (*i.e.* when the cotyledon had attained a length of from 2 to 2.5 cms.) the seedlings were rinsed with water to remove sand, and the 20 most vigorous were forthwith planted out in four large flower-pots filled with good compost. After one day, during which they were kept in the shade, these flower-pots were sunk in the ground in a part of the Botanic Gardens where uniform illumination was assured, and from the time of germination onwards the plants were grown under similar external conditions.

Curves *A* and *B* in Fig. 1 give the temperatures obtaining at 1 p.m. and at 7 a.m. respectively from March 1st to September 30th. The time of flower-stem formation was reckoned from the day on which at least one flower-spike of a plant in a series had emerged at least half-way from its surrounding leaf-sheath.

His results may be briefly summarised as follows. Exposure of the seeds to low temperatures during germination or during the early seedling stage ensures that flowering shall occur during the first year (Plate I, Fig. 1; and cf. Appel and Gassner⁽¹⁾). He carried the analysis further and obtained the following quantitative results. Firstly, the lower the temperature (over a range of 0° – 25° C.) the shorter the interval between germination and culm-formation as is shown in Fig. 2, which we have constructed from Gassner's data. Secondly, the earlier in the development of the plant the exposure to the low temperature occurs, the more marked the result (see Tables V and VI; and cf. Gassner⁽⁹⁾).

TABLE V.

Effect of a low temperature at different stages in the development of "Petkuser" winter rye.

Date of sowing	Treatment following the sowing	Date on which the seedlings were planted out*	Result
March 18th	A. Kept at 24° C. for 30 hours	April 16th	Formed flowering-stems irregularly from the beginning of August
	B. Kept at 1° – 2° C. for 4 weeks		Formed flowering-stems regularly from June 25th onwards

* On April 16th the cotyledons of the plants belonging to series A were about 20 mm. in length whereas those belonging to series B were about 30 mm. in length.

Physiological Pre-determination

Fig. 1.

Fig. 2.

TABLE VI.

Effect of a low temperature at different stages in the development of "Uruguay" oats.

	Treatment	Result of treatment
Seeds kept at 6°-9° C. for 5 days	Followed by a temperature of 25° C. until germination was completed	Plants flowered during the same season
Seeds kept at 25° C. for 1-2 days	Followed by a temperature of 6°-9° C. for 5-7 days (i.e. until germination was completed)	Plants did not flower during the same season

If the exposure to the low temperature occurs 2-3 days after sowing at normal temperatures (e.g. 24° C.) it is necessary that the period of exposure to the low temperature be many times as long in order to obtain the same result as when the exposure is made during the first few hours after sowing (see Table VII).

TABLE VII.

Influence of low temperature on the time of culm-formation in "Petkuser" winter rye sown in the spring.

Treatment		Result of the treatment
Germination period at 24° C.	Followed by a period at 0° to -5° C.*	
3 days	25 days	Formed flowering-stems the same year after 68 days
3 "	3 "	} Did not form flowering-stems the same year
3 "	1 "	
3 "	0 "	

* The plants were subsequently grown under natural conditions.

In parallel experiments carried out with so-called summer-annuals of the same varieties it was found that exposure to low temperatures during germination did not appreciably influence the time at which culm-formation took place¹ (see Fig. 3).

(c) ELECTRICAL DISCHARGE.

Results of empirical experiments dealing with the effects of electrical discharge upon seeds during germination are on record. The interesting aspect of these experiments from our point of view lies in the fact that it is stated that brief exposure of seeds prior to and during germination

¹ Gassner and Grimme (11) have shown that plants which require a period of low temperature to bring about complete development, can withstand extreme cold, whereas plants which do not need a low temperature, are unable to withstand cold.

influences not only the vigour and percentage of germination, but also the whole course of subsequent growth and final yield. It is interesting in this connection to note the fact that from the records of experiments in which growing crops have been submitted to electrical discharge throughout their development there is reason to believe that beneficial results are most obvious during the initial stages of growth.

Fig. 3.

The following table (Table VIII) summarises certain recent results obtained at the Research Station for Plant Physiology at Dahlem, which were reported by Hösternann⁽¹⁵⁾ in the *Landwirtschaftliche Jahrbücher* for 1913. The main significance of these results, apart from the fact that effects were found to last throughout the life of the plant, seems to be that better results are obtained when the seeds are treated after swelling in water than when treated dry, and that injury can easily result from too powerful a discharge.

TABLE VIII.

A. *Experiments with Seeds as the Positive Electrode.*

Kind of seed used and its condition during experiment	Distance of discharging electrode from the seeds	Length of spark	Duration of discharge	Effect of treatments upon germination and subsequent growth
Dry seeds of <i>Phleum pratense</i> sown in germination dishes	5 cm.	22 mm.	1 min.	Has a <i>favourable</i> influence upon germination and also upon the subsequent growth
		32 mm.		Has an <i>unfavourable</i> influence upon the later growth
Swollen seeds of <i>Phleum pratense</i> sown in germination dishes	5 cm.	12 mm.	1 min.	The germination power is <i>greatly decreased</i> probably because the seeds were swollen for too long a period and because the discharge was too intense
Dry seed of SPRING RYE sown in germination dishes	5 cm.	12 mm.	1 min.	No effect
			2 mins.	These treatments have an initial <i>favourable</i> action upon germination and produce a <i>final small increase in growth</i>
			3 "	
			5 "	
			10 "	Causes injury and delay in growth

B. *Experiments with Seeds as the Negative Electrode.*

Kind of seed used and its condition during experiment	Distance of discharging electrode from the seeds	Length of spark	Duration of discharge	Effect of treatments upon germination and subsequent growth
Dry seeds of SPRING RYE sown in germination dishes	40-50 cm.	40 mm.	$\frac{1}{2}$ hour	Result in an <i>increase of germination</i> and of <i>ear-formation</i> , but a <i>decrease in growth</i>
			1 "	
			$1\frac{1}{2}$ hours	
			2 "	
Swollen seeds of BARLEY; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	32 mm.	2 mins.	The effect of these treatments is at first to increase growth considerably, but the difference disappears later
			10 "	
			30 "	
Swollen seeds of SPRING WHEAT; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	23 mm.	2 mins.	The effect of these treatments is to increase growth; this <i>increase in growth is maintained</i> . Ear-formation was doubled by the 10-minute treatment
			10 "	
			30 "	

Swollen seeds of SPRING WHEAT; these seeds had been previously soaked in water for 6 hours at 30° C. and were afterwards sown in the open	5 cm.	32 mm.	2 mins.	{ Increased growth was obtained particularly after the 2 minute and 10 minute periods * * This experiment was repeated with similar results
			10 "	
			30 "	
Swollen seeds of SPRING RYE; previously soaked in water at 30° C. for:	10 cm.	32 mm.	15 mins.	{ The best results upon subsequent growth were obtained with the seeds which had been soaked in water for 6, 7, and 8 hours respectively
1 hour				
3 hours				
5 "				
6 "				
7 "				
8 "				
Swollen seeds of SPRING RYE; soaked in water at 30° C. for 72 hours and then sown in the soil	40 cm.	40 mm.	30 mins.	Resulted in an increase in germinating power and in growth energy
Swollen seeds of SPRING WHEAT; previously soaked for 5 minutes	2 cm.	27 mm.	2 mins.	{ No acceleration in germination { Considerable delay in germination
Placed in germination dishes	"	"	5 "	
	"	"	10 "	
	"	"	20 "	{ Results: small acceleration at lower voltages; slight injury at moderate voltages; decided injury at high tensions (i.e. with spark lengths of 40 mm. and 50 mm.)
	"	"	30 "	
	"	"	"	
Swollen seeds of SPRING WHEAT; previously soaked for 5 minutes	2 cm.	12 mm.	10 mins.	{ Results: small acceleration at lower voltages; slight injury at moderate voltages; decided injury at high tensions (i.e. with spark lengths of 40 mm. and 50 mm.)
Placed in germination dishes	"	22 "	"	
	"	27 "	"	
	"	32 "	"	
	"	40 "	"	
	"	50 "	"	

According to Micheels and De Heen (23) the action of a high frequency alternating current upon wheat and pea seeds, which had previously been soaked in water for 24 hours, favourably affected the development of the seedlings, but unfortunately their observations extended over a few days only.

(d) X-RAYS.

Increased vigour of germination and increased growth of the resulting plant, so far as it has been followed, has been recorded by several authors as the result of brief treatment of the seeds to X-rays. An example may be quoted. Promsy and Drevon(31) found that exposure of swollen seeds for $\frac{1}{2}$ –1 hour to the influence of X-rays markedly increased the subsequent growth of the seedlings. This action of the X-rays occurred only when the seeds were kept at a relatively high temperature (40° C. *circa*) during the exposure. For details with regard to the rays used and the conditions of exposure, which were carefully recorded by the investigators, reference should be made to the original paper. The following table (Table IX) has been based upon the results obtained by Promsy and Drevon:

TABLE IX.

Experiment I.

White lupin seeds were soaked in water for 15 hours, after which the testas were removed. On the first 3 days the experimental seeds were exposed to the X-rays for 1 hour, $\frac{1}{2}$ hour, and $\frac{1}{2}$ hour respectively, the temperature being 40–45° C. On the 4th day the seeds were sown in damp sand together with the controls (untreated).

Results.

Results on	Treated*	Untreated
4th day	Average length of radicles = 16.7 mm.	Average length of radicles = 6.2 mm.
18th „	Shoots appeared	—
26th „	—	Shoots appeared
29th „	Average height of plants above level of sand = 9.9 cm.	Average height of plants above level of sand = 7.3 cm.

* The treatment also brought about certain anatomical modifications.

Experiment II.

Seeds of haricot beans were soaked in water for 2 hours after which they were exposed to X-rays for 1 hour (temp. 40° C.).

Results.

	Treated	Untreated
Average length of plants on the 15th day	10 cm.	5 cm.
Average dimensions of		
1. Cells of the cortex	55.0 μ	44.0 μ
2. Cells of the pith	48.0 μ	43.0 μ
3. Nuclei of the cortical cells ...	18.0 μ	11.1 μ
4. Nuclei of the pith cells	15.0 μ	13.2 μ

CHEMICAL TREATMENTS OF THE SEED.

(a) ACIDS.

A large number of workers (*e.g.* Fischer(8), Onodera(26), and others) have noted the stimulating effect of acids upon germination. We have only been able to find a few cases in which observation was extended to the subsequent course of development of the treated seeds, but whenever this has been done, it is interesting to find that the author has usually recorded favourable results of a more or less striking nature. A few examples may be quoted.

Promsy(30), having first established the fact that the effect upon germination of a continuously-acting acid medium was favourable in a

large number of trials, employed the method of soaking the seeds *for a short time* in the acid solutions and then sowing them in garden soil.

Seeds of a variety of *Cucurbita Pepo* were soaked for 48 hours in the following solutions, viz.:

0.5 % Tartaric acid	(<i>T</i>)
0.5 % Acetic acid	(<i>A</i>)
0.5 % Oxalic acid	(<i>O</i>)
Pure water	(<i>W</i>)

After this preliminary soaking treatment the seeds were washed in water and were then sown in sand in perforated dishes. *A* came up first, *T* next, followed by *O*, and several days later by *W*. Measurements taken sometime later (*i.e.* when the seedlings bore from 2–6 leaves) showed that the *A* plants had the largest number of leaves and also the greatest dry-weight, whereas the *W* plants had the smallest number of leaves and the smallest dry-weight. Forty days after sowing the perforated dishes were half buried in garden soil, but a single plant from each lot was transplanted. The final results in the case of those not transplanted were as follows. All the *W* plants died; of the others, flowers appeared first upon the *A* plants, and these plants also bore the largest and most numerous fruits. All the plants from the acid-treated seeds maintained their vigour throughout the experiment.

Of the transplanted plants, *A* produced three very large fruits, *O* produced two, *T* produced one, whilst *W* flowered, but did not fruit. Results of a similar nature were obtained by this author with Pepper seeds.

The main interest of these results lies in the fact that a brief treatment during the critical stage of germination was found to produce a beneficial effect on the whole course of subsequent development of the plants and also upon their final yields.

We may recall here the incidental observations of three other workers, namely, Goodspeed, Townsend, and Plate. Goodspeed⁽¹²⁾, when testing the effect of 80 per cent. H_2SO_4 upon the germination of tobacco seeds, found that treatment with this acid for a period not exceeding 10 to 12 minutes markedly increased the percentage of germination, and in some cases the rapidity of germination also. This result is in harmony with the results of many other investigators on the effect of strong acids upon the germination of hard-coated seeds. From our point of view, however, Goodspeed's most interesting contribution lies in a sentence hidden in the body of his paper—"Results at present at hand seem to leave no

doubt that the action of sulphuric acid is further strikingly effective in increasing the rate of growth during at least the first three months of the plant's life." This observation of Goodspeed's is supported by results recorded by F. Plate (29). Working with seeds of *Avena sativa* Plate noticed that after treatment with various inorganic acids the germination of the seeds was greatly accelerated, and that the plants produced from the treated seeds were more vigorous than the controls. He observed that the reserve materials were exhausted in the case of the acid-treated seeds in 10 days as against 15 days in the case of untreated seeds.

The effect of hydrocyanic acid gas upon dry and moist seeds respectively has been investigated by Townsend (34 and 35); the necessity for the investigation arose from the rapidly increasing use of this gas in the destruction of insect pests infesting stored grains and other seeds and also for the fumigation of greenhouses. Townsend found that *dry* seeds of corn, wheat, beans and clover might remain without injury to their germinating power for several weeks in an atmosphere containing a greater concentration of hydrocyanic acid gas than is required to kill quickly insect life. The germination of these seeds was found to be accelerated after this treatment and the rate of growth of the seedlings to be above the normal.

The action of boric acid upon the germination and subsequent development of seeds has been investigated by Morel (24). This author's results showed that brief treatment with boric acid at the time of germination produced a persistent deleterious effect upon haricot beans. The results noted about 7 weeks after sowing in ordinary soil are given in the following table:

TABLE X.

Treatment of the seeds previous to sowing in soil		Results noted in the plants after 7-8 weeks' growth
Strength of acid used	Period of soaking	
1 % boric acid	15 mins.	Showed no appreciable difference from the controls
1 % "	30 "	Differed from the controls only in the colour of their leaves which were of a less clear green
1 % "	60 "	The leaves of these plants were small and yellowish

It is seen that treatment of the *dry* seed with a 1 per cent. solution of boric acid even for $\frac{1}{2}$ hour has a clearly visible effect upon the resulting plant during its whole course of growth.

In a similar series of experiments with seeds which had been previously immersed for 6 hours in water in order to render them more permeable to the acid solution, the following results were obtained:

TABLE XI.

Treatment of the seeds subsequent to the 6 hours soaking in water, but previous to sowing*		Results noted in the plants after about	
Strength of acid used	Period of soaking	5 weeks' growth	7 weeks' growth
1 % solution of boric acid	1 hour	Plants poor, with small yellowish leaves	Growth of plants moderately vigorous, but their leaves remained yellowish and were much smaller than those of the controls
1 % "	2 hours	Plants poor, with small yellowish leaves	
1 % "	3 "	A very few plants came up and these were very feeble	
1 % "	6 "	Few very feeble etiolated plants produced, leaves very small and few in number	Growth very poor although showing a decided improvement

* The seeds were placed on damp sand for a few days at a favourable temperature and were then sown in garden soil. Only those treated for the shortest period (i.e. 1 hour) had germinated after an interval of 3 days.

Similar experiments carried out with wheat gave results analogous to those obtained with haricot beans.

The present authors, working with *Brassica alba*, have shown that concentrations of carbonic acid(19) and boric acid(41) which rapidly kill the growing root, have no injurious effect upon any part of the embryo in the ungerminated but fully swollen seed. We may distinguish three ranges of increasing concentration of these two acids, as follows. (1) A range of low concentration in which the seeds germinate, but suffer injury after germination. (2) A range of intermediate concentration in which the germination of the seeds is inhibited. No injury to any part of the embryo or seedling can be observed even after prolonged treatment with this concentration of acid when the seeds are finally brought to germination in an acid-free medium. In this region marked injury is shown, however, by seeds which are allowed to germinate before being placed in the acid medium. (3) A range of higher concentration in which the seeds suffer injury whether ungerminated or germinated. The concentration of acid used by Morel lies in this third region which causes injury to the ungerminated seed.

This difference between the effect of chemical solutions upon the growing plant and their effect upon the seed before germination is not confined to acids but appears to be general. For instance, Hicks (13 and 14), who tested the effect upon seeds of a number of chemical fertilisers,

reached the conclusion that the effect of treating seeds with various chemicals before sowing is no index of the action of these chemicals when applied to the soil. Injury to the young plant may result when the chemicals are applied to the soil although no injurious effect is shown when the seeds are treated before germination with the same solution. However, little can be said on this subject with certainty until it has been determined whether the solute under consideration penetrates the testa or not.

(b) CHEMICAL AGENTS OTHER THAN ACIDS.

(I) *Copper Sulphate* (= *Bluestone*).

We have previously dealt with the effect of soaking seeds in water (18), and have drawn attention to the distinction which must be made between seeds sown wet (*i.e.* immediately after the soaking treatment) and seeds sown after re-drying, with or without storage. It is necessary to bear these points in mind when dealing with the effect of treating seeds with chemical solutions in which they are immersed for various periods.

In 1904 Bréal and Giustiniani (6) published the results of an investigation on the effect of treating the seeds of various cereals with a solution of copper sulphate. Unfortunately, although they appear to have been aware of the distinction which must be made between the effect of soaking and the effect of the solute alone, their results, whilst demonstrating a considerable increase in yield as a result of the treatment they employed, do not allow us to draw any critical conclusion as to how far they are due to the soaking and how far they are due to any specific action of the copper.

Their line of thought appears to have been as follows: Seeds sown after being allowed to take up moisture are found to give a greater yield, but damp seeds are very susceptible to fungal attack. Copper sulphate, however, has frequently been employed as a fungicide in seed-treatments. Hence, can seeds be soaked in a solution of copper sulphate, not only without injury, but with a result beneficial to yield? Further, might it not be advantageous to make up the copper sulphate solution together with 2-3 per cent. of starch, on the grounds that by so doing the escape of soluble food-materials from the seed into the surrounding medium during the period of soaking would probably be decreased¹? They

¹ We have not found any published evidence to the effect that starch does decrease the exosmosis of soluble food-materials from the seed.

therefore adopted a Copper-Starch soaking treatment followed by liming and re-drying, and record results from which it appears that this treatment of the seeds renders them more resistant to fungal attack without affecting their germinating capacity. Moreover, seeds thus treated give rise to plants which are better developed and produce a larger yield than plants from untreated seeds. Bréal and Giustiniani drew attention to the fact that from the very beginning of their development the plants from the treated seeds gained on the controls, and that the superiority of the yield from the experimental plants over that from the controls was most marked in the case of the "heads." In the two following tables (Tables XII and XIII) the results of the authors' experiments are summarised, but these results, although of general economic interest, are unsatisfactory from our point of view because they do not show conclusively that the copper sulphate has any specific action on the seeds. Taken in conjunction with the beneficial results obtained by simply soaking cereal seeds in water, and in conjunction with the harmful effects of copper-treatments upon seeds recorded by other authors, it seems probable that the improvement of the plants following the copper-starch treatment of the seeds is to be attributed to the soaking alone.

TABLE XII.

Pot-culture experiment with equal weights of treated and untreated seed.

For details of the seed-treatments the original paper should be consulted.

Kind of seed	Duration of culture in days	Weight of the aerial parts of plants from treated seed, that of the control plants being taken as 100
Maize "Quarantain"	65	160
Wheat "Chiddam"	38	122
Barley "Chevalier"	36	120
Oats	35	110
White Lupin	33	119
Buckwheat	30	116

In a later investigation Bréal(5) confirmed his previous results and also conducted a number of water-culture experiments with treated and untreated seeds respectively of wheat, oats, barley and maize. These seeds were sown in vessels containing pure water, and the dry weight of the seedlings was taken after various short periods (*i.e.* 25-52 days). It was found (Table XIV) that in each case the total dry weight of the seedlings at the end of the experiment was less than that of the seeds originally sown, but that the plants from the treated seeds weighed considerably more than those from the untreated, this result

being due to the more vigorous stem and leaf development of the experimental plants. The results also show that the superiority of the plants from the treated seeds is evident from the beginning of their development.

TABLE XIII.

Experiments with equal weights of treated and untreated seeds sown "en pleine terre."

Maize seed used in each experiment.

No. of expt	Seeds	Fresh weight in kilograms after 100 days' growth		Weight of the aerial parts of the plants from treated seeds, that of the control plants being taken as 100	
		Entire yield	Heads	Entire yield	Heads
I	{Treated	0.765	0.270	137	146
	{Control	0.565	0.185		
II	{Treated	3.100	0.920	120	129
	{Control	2.500	0.710		
III	{Treated	4.200	1.295	107	148
	{Control	3.900	0.870		
IV	{Treated	2.000	0.615	74	112
	{Control	2.700	0.545		
V	{Treated	4.000	0.605	114	121
	{Control	3.500	0.500		

TABLE XIV.

Kind of seed	Duration of ex- periment in days	Dry weight in grams of the seeds sown	Dry weight in grams of yield from		% difference in yield in favour of the plants from treated seeds
			Untreated seeds	Treated seeds	
Wheat "Bordeaux"	25	88	60	72	20
" "	52	88	45	66	46
Wheat "Dattel"	20	87	77	81	5
" "	40	87	65	75	15
Wheat "Japhet"	20	89	77	80	4
" "	40	89	60	67	11
Wheat "Bordier"	23	87	74	76	2
" "	37	87	60	69	15
Wheat "Saumur"	20	88	75	83	10
Oats "Houdan"	27	87	70	78	11
Oats "Brie"	28	89	67	82	7
Barley	23	90	62	70	14
Maize "Gros jaune"	50	89	72	80	11
Maize "Dent de cheval"	32	89	73	81	10

Beyond the really important fact thus brought out that the final result can be forecasted at a very early stage in the development of the

seedling, it is impossible on the basis of the data given to determine the factors responsible for the results obtained. Bréal, however, is satisfied to conclude that the treatment ensures a better utilisation of the seed-reserves.

In view of the results obtained by Bréal and Giustiniani, which, as we have pointed out, cannot be attributed in the absence of further evidence to the specific action of the copper, the recent critical work of Jungelson (17), who worked with maize, is of interest. Jungelson used simple solutions of various copper salts and obtained similar results whatever the nature of the anion, thus definitely indicating that copper is the main factor in producing the results. He also showed that the results varied with the concentration of the salt.

The effects of the copper treatment on the seeds showed themselves throughout the whole course of development and were even carried over into succeeding generations. These effects, however, although very distinct and characteristic, were altogether harmful from the point of view of vigour and yield. Firstly, the copper treatment of the seeds decreases their power of germination, and secondly, there is both a retardation of the vegetative development and a delay in the flowering of the plants produced. Thirdly, a tendency towards variation, which manifests itself in the appearance of abnormal "heads" and seeds, is shown by the plants from the treated seeds; but these new characters do not appear to be handed on to the next generation. Lastly, plants from seeds treated in identically the same way exhibit totally different abnormalities.

Jungelson's results are especially important from two points of view; firstly, they demonstrate the persistence of the effect of the copper treatment of the seeds, and secondly they prove that the results of treating seeds with copper are distinctly unsatisfactory. Jungelson himself suggests that the degeneration of local races of cereals, which has become so marked of late years, may in a certain measure be due to the general use of seed-treatments in which copper is employed for the purpose of preventing the development of smut.

(II) *Other salts.*

We have already indicated the possibility that such results as those obtained by Bréal and Giustiniani (6) may be due to the soaking involved in their treatment of the seed rather than to the action of the copper. This possibility must be borne in mind when the question of other seed-treatments which involve soaking for certain periods in solutions of various salts is under consideration.

Accounts of the treatment of seeds with solutions of various salts with the object of testing the effect upon final yield are to be found scattered through the literature, but although sweeping conclusions are occasionally drawn, the experimental data upon which these conclusions are based are in the majority of cases completely inadequate. Two or three examples may be given.

In discussing the results of a long series of pot-culture experiments extending over a number of years, carried out at the Woburn Experiment Station with the primary object of testing the manurial value of small quantities of the so-called rarer constituents of ash, Voelcker⁽⁴⁰⁾ observes (p. 325) that "certain metallic salts have either a toxic or a stimulating effect upon vegetation, the particular effect depending upon the quantity of the metal present. At what stage of the plant's life are these influences exerted? The evidence so far adduced, leads strongly to the belief that it is during the germination of the seed, rather than at the later stages of the plant's growth, that these influences are exercised."

The substances tested by Voelcker were in most cases applied to the soil, but in a few experiments the only application of the substances was to the seeds, which were soaked in solutions for a short time before sowing. It was found that in some cases this treatment gave very favourable results, and in other cases it produced a moderately good result, whereas when the same substances were applied to the soil in various amounts, the results obtained were always negative. Some of the results obtained by Voelcker^(37, 38, 39, and 40) are collected together in the following table (Table XV).

TABLE XV.

Kind of seed used	Treatment*		Yield result expressed as % increase or decrease as compared with the control	
	Solution used	Period of soaking	Grain	Straw
Winter Wheat (White Chaff Browick)	1 % NaI	10 mins.	+16.5	+30.1
	1 % NaBr	10 "	+ 8.7	+10.0
Wheat	10 % MnI	15 "	-30.9	- 4.5
	5 % MnI	15 "	- 0.4	+ 3.4
	1 % MnI	15 "	+ 3.1	+13.3
	10 % NaBr	10 "	+13.8	+19.6
Barley	10 % MnI	15 "	+12.7	+14.2
	5 % MnI	15 "	+ 5.6	+ 8.5
	1 % MnI	15 "	+14.2	+13.0

N.B. In a later series of experiments it was found that soaking the seed for 20 mins. in NaI or NaBr (1, 10, and 20 % solutions) did not give beneficial results.

* All the seeds were steeped in hot water for 10-15 minutes before treatment in order to kill smut.

These results should be accepted with considerable reserve since the pot-culture experiments were conducted with relatively few plants and the probable errors of the experiments were not determined.

A regular increase in yield with increased strength of the solution employed was reported by J. Craig (7) as the result of soaking pea seeds for one hour in solutions of NaNO_3 of the following concentrations, viz. 1 oz., 2 oz. and 3 oz. of the salt to one gallon of water.

One more instance may be noted. An increase in the tillering of several varieties of wheat to the extent of 12.8 per cent. and 20.6 per cent. respectively as the result of treating the seed with $(\text{NH}_4)_2\text{SO}_4$ (3 per cent. solution) and NH_4NO_3 (3 per cent. solution) was recorded by Wild (42) in the *Agricultural Journal of New Zealand*, 1914. In order to estimate the tillering 20 plants were taken at random from the various experimental plots, and in the case of each variety tested it was found that the effect of the treatment upon the tillering of the plants was a positive one. But here again the experimental data upon which the conclusions were based appear to be totally inadequate.

(III) *Hydrogen peroxide.*

Several workers have recorded observations on the effect of hydrogen peroxide treatments of seeds upon germination and upon the seedlings produced from the treated seeds. It would appear that in some cases hydrogen peroxide in certain concentrations may stimulate germination (cf. Pinoy and Magrou (28)), but the usual effect recorded is a retardation of the germination of the seeds.

Massee (22) when testing the effect of hydrogen peroxide upon seeds with a view to its possible utilisation in seed-sterilisation found that although germination was retarded, the growth of the seedlings eventually produced was rapid so that in many cases at the end of three weeks the plants from the treated seeds were distinctly larger than those from untreated seeds used as controls. But unfortunately the records of investigations with hydrogen peroxide are usually completely unsatisfactory for the reason that the strength of the solution employed is not determined.

CONCLUSIONS.

In concluding this review of the literature bearing upon what we have termed physiological pre-determination we may briefly summarise the available evidence. The evidence, as a whole, seems to show that

the factors which influence the plant during its earliest stages of development, have a more or less pronounced effect upon the whole of its subsequent life-history.

In the first chapter of this review we dealt with the factors which acted upon the plant whilst still a seed upon the parent. The most useful criterion here was found to be the size of the seed. A large amount of work bearing upon the effect of the size of the seed upon the growth and yield of the plant produced was reviewed, and an endeavour was made to distinguish critically between genetic and physiological factors. A certain amount of evidence was found indicating that the effects of the parental environment of a seed were sometimes only visible in the resulting plant.

In chapter II we dealt with the influence of the degree of maturity of the seed at the time of harvesting upon its "potentiality," and came to the conclusion that all comparisons made between mature and immature seeds were vitiated by the fact that immature seeds deteriorate more rapidly under storage conditions than mature seeds. In many cases it was found that the yield per plant from immature seed was at least equal to that from mature seed.

In the third and present chapters we have dealt with the aspect of the subject which is probably of most interest to the practical man, namely, the effect of the conditions during germination and in the early seedling stage upon subsequent growth and final yield. The work dealing with the soaking of the seed in water or salt solutions was critically reviewed in chapter III. In the present chapter the most interesting group of facts which have come under review appear to be those brought out by the work of Gassner and others on the effect of low temperatures in pre-determining the time of flowering of spring-sown winter cereals. This effect of exposure to low temperatures is a very clear and distinct phenomenon. While it still remains unexplained, it nevertheless bears out the general thesis based on the evidence which we have collected from various sources, namely, that the external conditions which obtain during the early stages of the development of the plant have a very pronounced effect upon its subsequent development. The results of Gassner's investigations show clearly that it is during the first few hours of germination that the "pre-determination phenomenon" can be most easily and quickly brought about by exposure to cold. As the seedling develops, the duration of the exposure to cold and the degree of cold necessary to ensure flowering in the same year rapidly increase.

While much is known with regard to the effect upon germination of

various chemical treatments of seeds, very little experimental work is on record with regard to the subsequent growth and yield of the plants produced from the treated seeds. All the available evidence, however, supports the conclusion that where germination and early seedling growth are stimulated by chemical treatments of the seed the subsequent growth and final yield are favourably influenced in proportion.

One of the most interesting outcomes of the present review of literature has been to emphasize the fact that normal plant-growth falls into line with a "compound interest" law of development. The data obtained by various workers from growth experiments with plants from seeds which had been deprived of part of their original food-reserves show that, broadly speaking, the growth and yield of the resulting plants are proportional to their initial "food-capital," and thus provide an illuminating demonstration of this "compound interest" law.

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I.

Germinated at 12° 24° 5° 12° 24° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5°
 Germinated on 10. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28.

April

March

II.

Germinated at 12° 24° 5° 12° 24° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5°
 Germinated on 10. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28.

April

March

May

III.

Germinated at 12° 24° 5° 12° 24° 5° 12° 5° 24° 1° 12° 24° 1° 1° 12° 5° 24° 12° 5° 1° 24° 5°
 Germinated on 10. 20. 10. 16. 17. 17. 23. 23. 30. 30. 3. 5. 7. 10. 13. 13. 13. 14. 20. 20. 25. 25. 28.

March

April

May

June

The development of "Petkuser" Winter Rye in relation to the germination temperature and the time of germination (after Gassner).

Fig. I was photographed on June 8th.

Fig. II was photographed on June 27th.

Fig. III was photographed on July 26th.