

The Rôle of the Seed-coat in Relation to the Germination of Immature Seed.

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With six Tables and one Chart in the Text.

IN previous papers (9 and 10) it has been shown that the germination of seeds of *Brassica alba*, sown in the presence of certain percentages of carbon dioxide, can be completely inhibited, and that this inhibition of germination is often maintained indefinitely after the removal of the seeds to air. This is a remarkable phenomenon, and it is the more striking in that seeds rendered dormant by carbon dioxide show no signs of injury when finally brought to germination even after the lapse of twelve months. So far the authors have found only two certain methods of destroying the dormant condition into which the seeds are thrown by the carbon dioxide treatment. One method is to redry the seed, the other method is to remove the testa without drying.

In the present paper results are recorded which show that a condition of dormancy, similar in many ways to that produced when dry mature seeds of *Brassica alba* are sown in the presence of carbon dioxide, may be observed when immature seeds of this plant are sown immediately after removal from the parent and before the natural drying process has begun.

EXPERIMENTS WITH *BRASSICA ALBA*.

The seeds in the following experiments were obtained from plants grown in the Botanic Gardens, Cambridge. The different degrees of ripeness of the seeds were as follows:

- A. *Green-ripe*: Seeds fully swollen; still quite green; 50 per cent. to 80 per cent. of the dry weight of ripe seeds. Siliques bright green.
- B. *Yellow-ripe*: Seeds fully swollen; yellow in colour; of practically the same dry weight as fully ripe seeds. Siliques still moist; beginning to turn yellow.

The germination results are set forth in the following tables (Tables I-IV) and chart. Yellow-ripe seeds with the testa intact, when sown

immediately after removal from the parent, remained in a dormant condition or showed a long delay in germination. On the other hand, yellow-ripe seeds with the testa removed, or dried in the laboratory for twenty-four hours with the testa intact, germinated immediately (100 per cent.), even more rapidly than a sample of the previous year's seed used as a control.

Green-ripe seeds sown after the removal of the testa germinated completely (100 per cent.), but after a delay of a few days. When sown with the testa on they mostly died, and in the case of the few seeds which did germinate, it was noticed that germination was always preceded by a change in the colour of the radicle from green to yellow. If dried for forty-eight hours before sowing practically all the seeds were killed.

TABLE I.

Germination of White Mustard Seeds at different stages of maturity.

- Lot A. Twenty **yellow-ripe seeds** gathered and removed from the siliques on Sept. 8, 1918. **Dried** in the laboratory for one day.
- Lot B. Twenty **yellow-ripe seeds** gathered on Sept. 8 and removed from the siliques on Sept. 9. **Sown immediately** (i. e. not dried).
- Lot C. Twenty **green seeds** gathered and removed from the siliques on Sept. 8. **Sown immediately** (i. e. not dried).
- Lot D. Twenty **green seeds** gathered and removed from the siliques on Sept. 8. **Testas removed** before sowing.

All the seeds were sown on moist silica sand in a glass thermostat at 20° C.

| | <i>Germinations after:</i> | | | | | | | | | |
|-------|----------------------------|--------------|--------------|--------------|------------|------------|------------|------------|-------------|-------------|
| | 16 hours. | 40 hours. | 45 hours. | 65 hours. | 4 days. | 5 days. | 7 days. | 9 days. | 12 days. | 21 days. |
| Lot A | 1 | 16 | 18 | 20 | — | — | — | — | — | — |
| „ B | 0 | 0 | 4 | 9 | 10 | 13 | 13 | 14 | 15 | 20 |
| „ C | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 8 | 10 | 14* |
| „ D | 0 | 0 | 0 | 0 | 2 | 3 | 20 | — | — | — |

* The 6 ungerminated seeds were dead.

TABLE II.

Germination of White Mustard Seeds at different stages of maturity.

All the seeds were sown on moist silica sand in a thermostat at 20° C.

| <i>Kind of Seed sown (sown on Sept. 11).</i> | <i>Number of Seeds sown.</i> | <i>Germinations after:</i> | | | | | | | |
|---|--------------------------------------|----------------------------|--------------|--------------|--------------|------------|------------|-------------|-------------|
| | | 18 hours. | 24 hours. | 41 hours. | 65 hours. | 5 days. | 7 days. | 10 days. | 19 days. |
| Green-ripe, testas off | 10 | 0 | 0 | 0 | 0 | 7 | 10 | — | — |
| „ „ „ on | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1* |
| Yellow-ripe, testas off | 10 | 9 | 10 | — | — | — | — | — | — |
| „ „ „ on | 10 | 0 | 0 | 3 | 5 | 5 | 6 | 6 | 7† |
| Dry mature seed (1917) | 10 | 0 | 6 | 10 | — | — | — | — | — |
| Yellow-ripe, dried in the laboratory air for 3 days | 10 | 3 | 10 | — | — | — | — | — | — |

* The nine ungerminated seeds were dead. † The three ungerminated seeds were not dead.

TABLE III.

Germination of White Mustard Seeds at different stages of maturity.

All the seeds were sown on moist sand in a thermostat at 20° C.

| Kind of Seed sown (sown on Sept. 11). | Number of Seeds sown. | Germinations after: | | | | |
|--|-----------------------------|---------------------|------------|------------|------------|-------------|
| | | 1 day. | 3 days. | 5 days. | 8 days. | 17 days. |
| Yellow-ripe, testas off, dried in the laboratory air for 2 days | 10 | 8 | 10 | — | — | — |
| Green-ripe, testas off, dried in the laboratory air for 2 days | 10 | 0 | 1 | 2 | 2 | 2* |
| Green-ripe, testas on, dried in the laboratory air for 2 days | 10 | 0 | 0 | 0 | 0 | 0* |

* The ungerminated seeds were dead.

TABLE IV.

Germination of White Mustard Seeds at different stages of maturity.

Lot A consisted of ten green-ripe seeds.

Lot B consisted of ten bare embryos from similar seeds.

Sown on moist sand, July 14.

| | 2 days. | 4 days. | 6 days. | 7 days. | 12 days. | 18 days. |
|-------|---------|---------|---------|---------|----------|----------|
| Lot A | 0 | 0 | 0 | 0 | 1 | 2* |
| „ B | 0 | 0 | 5 | 10† | — | — |

* The 8 ungerminated seeds finally died.

† Healthy plants.

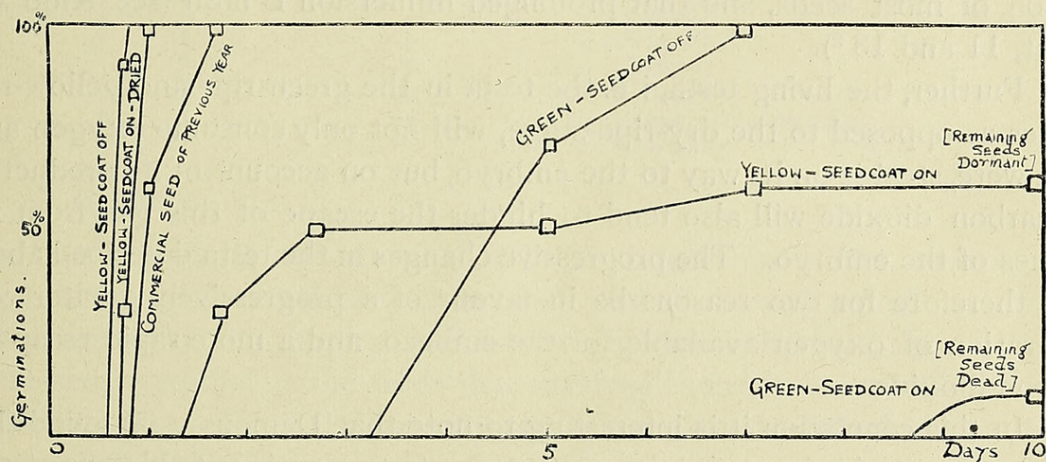


CHART. Germination of White Mustard seeds at different stages of maturity as affected by the seed-coat and by drying the seed (see Table II).

From the above experiments on the germination of immature White Mustard seeds it appears that the presence of the testa is fatal so long as the seeds are still green and have not reached their full dry weight. If they are sown without the testa they germinate in a healthy manner, but if sown with the testa on they perish. As the seed ripens, however, and

turns yellow, the effect of the presence of the seed-coats is markedly reduced. The presence of the seed-coats in the yellow-ripe stage only causes dormancy or delayed germination. Finally, when the testa is completely yellow and the seed is dry, the testa no longer has any appreciable effect upon germination.

Since the embryos will germinate freely at all three stages if the seed-coats are removed, there does not seem to be any ground for seeking an explanation of the above differences in behaviour between green-ripe, yellow-ripe, and dry-ripe seeds in progressive changes occurring in the embryo itself.

The progressive changes which occur in the testa, to which we must therefore look for an explanation, may be described as follows. In the green-ripe seed the embryo is enclosed in a relatively thick green coat consisting of actively functioning tissue, while between this coat and the embryo a considerable quantity of liquid is usually found. In the yellow-ripe seed the testa is relatively thinner and presumably less active, but is still living. The liquid between the embryo and the seed-coats has by this time disappeared. In the dry-ripe seed the testa is a thin membrane and presumably dead.¹

Considered as an obstacle to the gaseous exchange of the embryo the testa probably behaves in relation to its thickness in the same way as a film of water; in other words, the thicker the testa the more slowly do gases pass through.

It is a well-known fact that immersion in water does inhibit the germination of most seeds, and that prolonged immersion is fatal (see Kidd and West, 11 and 13²).

Further, the living testa, i. e. the testa in the green-ripe and yellow-ripe stages as opposed to the dry-ripe stage, will not only consume oxygen and, as it were, steal it on its way to the embryo, but on account of its production of carbon dioxide will also tend to hinder the escape of this gas from the tissues of the embryo. The progressive changes in the testa described above will therefore for two reasons be in favour of a progressively greater concentration of oxygen available for the embryo, and a more rapid escape of carbon dioxide.

In this connexion it is interesting to note that Demoussy (5) found that hydrogen peroxide increased the percentage of germination of old Cress seeds. Hydrogen peroxide has a lethal action upon the saprophytic flora of the dead seed-coats. He suggested that non-germination in these old seeds was to some extent due to the respiratory action of moulds or bacteria present in

¹ For details as to the histological and microchemical characters of the testa in the case of the genus *Brassica*, the reader is referred to papers by Schroeder (21), Sempelowski (22), Holfert (8), Burchard (3), Gram (7), Kinzel (14), Pieters and Charles (20), Kondo (16), and Kidd and West (10).

² In this paper the literature dealing with the effect of soaking seeds in water is critically reviewed.

the seed-coat, attributing to them a rôle in causing dormancy similar to that which we are here attributing to the respiratory activity of the living testa.

EXPERIMENTS WITH *PISUM SATIVUM*.

The results of certain experiments with immature seeds of *Pisum sativum* are recorded in Table V, and appear to be essentially similar to those obtained with *Brassica alba*.

TABLE V.

Germination of seeds and bare embryos of Pisum sativum at different stages of maturity.

- A. { Lot I. Twenty immature seeds. These had attained their full size
(the funicle comes away with the pea when taken from the pod).
Lot II. Twenty bare embryos from similar seeds.
- B. { Lot I. Twenty less immature seeds (peas break from the funicle when
taken from the pod).
Lot II. Twenty bare embryos from similar seeds.
- C. { Lot I. Twenty seeds picked ten days later.
Lot II. Twenty bare embryos from similar seeds.
- D. Twenty seeds picked at a still later stage.
- E. Controls = Twenty mature seeds gathered during previous season.
- Seeds sown in garden soil. Temperature 15°–20° C.

Number of Germinations after:

| | | 5 days. | 10 days. | 14 days. |
|---|------------|---------|---------------------------|----------|
| A | { Lot I | 0 | 1 (19 dead) | — |
| | { „ II | 20 | 20 (18 healthy) | — |
| B | { „ I | 0 | 0 (all dead) | — |
| | { „ II | 20 | 20 (all healthy) | — |
| C | { „ I | — | 10 (10 ungerminated dead) | — |
| | { „ II | — | 20 (all healthy) | — |
| D | | — | — | 18 |
| E | [Controls] | 20 | — | — |

If the testa is not removed a large proportion of the seeds perish when sown. The most immature seeds tested showed a high mortality, but as maturity was approached so the injurious effect of the testa was decreased, nevertheless the seeds that survived showed an appreciable delay in germination. No real dormancy similar to that described above in the case of *Brassica alba* was observed.¹

In order to test our hypothesis that the effect of the testa, as shown in the experiments above, is to be attributed to its property in limiting the gaseous exchange of the embryo, further experiments were carried out in

¹ It is interesting to note here that this is the same relation between seeds of *Brassica alba* and those of *Pisum sativum* in regard to dormancy as that found when the germination of these seeds was inhibited by atmospheres containing certain percentages of carbon dioxide (cf. Kidd, 9). Seeds of White Mustard exhibit secondary dormancy when removed to air. No such phenomenon can be obtained with peas.

the following way. It was argued that, assuming the hypothesis to be correct, these immature seeds, when sown under germinating conditions, must either be in a condition in which the limitation of the gaseous exchange of the embryo is so great as to become actually harmful (e.g. in the cases where sowing on damp sand is followed by death), or at any rate must be near the point at which any further limitation will cause injury. It follows that if we impose even for a short period a condition which further limits the gaseous exchange of the embryo we should, if our hypothesis is correct, obtain a pronounced result. In order to further limit the gaseous exchange, the seeds were immersed in water for short periods before sowing. The result, as Table VI shows, is striking and bears out our hypothesis. Whereas fully ripe dry pea seeds will endure immersion in water for several hours without showing any obvious decrease in the percentage of germination (Kidd and West, 11), the unripe pea seeds suffer heavily even after a few hours' immersion. The amount of injury shown is more or less proportional to the period of soaking. On the other hand, soaking *per se* for the periods used in this experiment is in no way harmful to the embryo, as is shown by the results of a parallel series of experiments with the bare embryos from unripe pea seeds.

TABLE VI.

The seeds used in this experiment were similar to those of category C in Table V. Twelve seeds were used in each experiment. They were sown in garden soil. Temperature 15°–20° C.

| Condition of the Seed. | Treatment. | Results observed 11 days after sowing : | | |
|-----------------------------|---|---|--------------------------------------|-------------------------------------|
| | | Percentage of seeds dead. | Percentage of vigorous plants. | Average length of the shoots. |
| Immature. With testas | Dried in air for 15 hours before sowing | 20 | 58 | 2 cm. |
| | Sown immediately after removal from parent plant | 33 | 50 | 2 „ |
| | Soaked in tap-water for 1½ hours before sowing | 50 | 42 | 3 „ |
| | Soaked in tap-water for 5 hours before sowing | 58 | 33 | 2 „ |
| Immature. Without testas | Dried in air for 15 hours before sowing | 0 | 50 | 2.5 „ |
| | Sown immediately after removal from parent plant | 0 | 92 | 3 „ |
| | Soaked in tap-water for 1½ hours before sowing | 0 | 100 | 4.5 „ |
| | Soaked in tap-water for 5 hours before sowing | 0 | 100 | 4.5 „ |
| Mature intact seeds | Soaked for 24 hours | 0 | 100 | 8.5 „ |

The above table also shows results which were obtained with bare embryos and with intact seeds which were dried in the air for fifteen hours before sowing. The germination of the bare embryos is reduced from 100 per cent. to 50 per cent. by the drying process, which is thus shown to be injurious to unripe pea seeds. A similar reduction in the percentage of

germination occurs when the testa is allowed to remain *in situ* whether the seeds are dried previous to sowing or not. When the seeds are not subjected to the drying process before sowing, the living testa is responsible for the 50 per cent. mortality observed. When the seeds are sown after having been dried the testa is presumably a dead membrane, and it is now the drying of the seed which causes the 50 per cent. mortality observed, just as in the case of the bare embryos which had been allowed to dry.

Experiments conducted by Dr. F. F. Blackman and Miss N. Darwin (4), of which an abbreviated account was read at the British Association Meeting held at Sheffield in 1910, but of which no published record is at present available, are significant in relation to the hypothesis put forward above to the effect that the living testa of unripe seeds limits the gaseous exchange of the embryo in the same way as a continuous film of water. They worked with barley grains, the vitality of which had been reduced (by age or by immersion in the swollen condition in hot water at 50° C. (*circa*) for twenty minutes), but which still showed a full percentage of germination when sown under ideal conditions. It was found that slight films of water greatly delayed the germination, reduced the germination percentage, and resulted in the death of a large proportion of such seeds. The results obtained were more or less proportional to the thickness of the water films.

CONCLUSIONS.

Many authors (see especially Nobbe (19), Mazé (18), Windisch (23), Eberhart (6), Atterberg (1), Babcock (2), Kinzel (15), and Kondo (17)) have described experiments dealing with the dormancy or delayed germination observed when certain seeds, which, although immature and with a relatively high moisture content, have nevertheless attained their full size, are sown immediately after removal from the parent plant. The process of drying has generally been found to terminate the dormant condition of such seeds. Different theories have been put forward to account for the dormancy of unripe seeds sown in the moist condition immediately after removal from the parent plant (see Kidd and West, 12). In the present paper it has been shown that in the case of *Brassica alba* and *Pisum sativum* the removal of the testa not only accelerated the germination and terminated the dormant condition of unripe seeds, but also increased the germination percentage. It is clear that the rest period observed when attempts are made to germinate unripe seeds fresh from the parent plant may be largely attributed to the presence of the testa, and there are strong indications that under these conditions the *living* testa limits the gaseous exchange of the embryo. A fact which should always be borne in mind in this connexion is that the testa, considered as a membrane through which the gaseous exchange of the embryo must occur, undergoes great modifications during the ripening and drying off of the seed.

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