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THE RÔLE OF OXYGEN IN GERMINATION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 181

CHARLES A. SHULL

A study of the respiration of Xanthium seeds was undertaken some time ago with the purpose of determining whether there was any change in the permeability of the seed coats to oxygen during the period following the normal ripening of the seeds. Some evidence was noted previously\(^1\) that there was either a change in permeability of the seed coat, or a change in oxygen need of the embryo during the early winter, and it was believed that a careful measurement of the oxygen used by the seeds with coats on and off at successive intervals during the year would show which of these changes occurred, and at what period of the ripening process.

Circumstances have prevented the carrying out of this series of tests; but the preliminary results are of sufficient interest in connection with the rôle of oxygen in germination behavior to warrant placing the data on record. The measurements were made with a respirometer of excellent type designed by Dr. William Crocker, to whom I am further indebted for suggestions regarding the problem. The respirometer was kept in a Freas thermostat at 25.25° C., and the volumes of oxygen used are reduced to standard conditions. Seeds of X. glabratum in dry storage for nine months were used.

First it was necessary to know what part of the oxygen was used by the coats under ordinary atmospheric germinative conditions. Two lower seeds were placed in one chamber of the respirometer, and the coats of two lowers in the other chamber. In 22.5 hours the two seeds used 0.475 cc. of oxygen, while the two coats used 0.098 cc. From the results of Becquerel’s work\(^2\) I had suggested that the coats were probably responsible for a part

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of the respiration of intact seeds. That part is now shown to be considerable, amounting in this instance to 20 per cent of the total.

The respiration of lower and upper seeds with coats intact under atmospheric conditions of germination was compared, with the result that two lowers used 0.687 cc. and the two uppers 0.509 cc. of oxygen in 42.3 hours, a ratio of lowers to uppers of 1.35 : 1. It should be said that upper seeds always weigh less on the average than the lowers; and in using equal numbers of seeds the weight of respiring substance is somewhat less in the uppers.

The respiration of the lowers with coats on and coats off in ordinary atmosphere is especially interesting (see table I).

**TABLE I**

<table>
<thead>
<tr>
<th>Time</th>
<th>Oxygen Used</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coats off</td>
<td>Coats on</td>
</tr>
<tr>
<td>10 hours</td>
<td>0.500 cc.</td>
<td>0.3615 cc.</td>
</tr>
<tr>
<td>10-15</td>
<td>0.478 cc.</td>
<td>0.1025 cc.</td>
</tr>
<tr>
<td>15-17.25</td>
<td>0.316 cc.</td>
<td>0.040 cc.</td>
</tr>
<tr>
<td>Total</td>
<td>1.294 cc.</td>
<td>0.504 cc.</td>
</tr>
</tbody>
</table>

**TABLE II**

<table>
<thead>
<tr>
<th>Time</th>
<th>Oxygen Used</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coats off</td>
<td>Coats on</td>
</tr>
<tr>
<td>5 hours</td>
<td>0.1609 cc.</td>
<td>0.075 cc.</td>
</tr>
<tr>
<td>5-15</td>
<td>0.618 cc.</td>
<td>0.1107 cc.</td>
</tr>
<tr>
<td>Total, 17.25 hours</td>
<td>0.9825 cc.</td>
<td>0.1947 cc.</td>
</tr>
</tbody>
</table>

A similar test with uppers is shown in table II. The coats were not placed in the chambers with the embryos where coats were off, so that the ratios in the tables are too low as regards actual embryo respiration. The rapid increase of use of oxygen by naked embryos as germination commences is well illustrated.

Finally, the oxygen used by uppers and lowers with coats on, in an atmosphere 96 per cent oxygen, was compared, with significant results. Two lower seeds used 1.007 cc. in 12.5 hours, while the
uppers used but 0.4406 cc., a ratio of 2.28:1. A repetition of this experiment resulted in the lowers using 1.257 cc. in 22 hours, the uppers 0.772 cc., a ratio of 1.63:1. Invisible defects in coats might cause some variation in these ratios, but they are believed to approximate average results.

It is interesting to note that two lowers in atmosphere used 2.687 cc. of oxygen in 42.3 hours, while the same number used 1.007 cc. in 12.5 hours in 96 per cent oxygen; and that uppers which used 0.509 cc. in 42.3 hours used 0.4406 cc. in 12.5 hours in 96 per cent oxygen. The increased oxygen pressure causes a large increase in the oxygen intake of both seeds with coats intact, but exerts the greater influence on the lowers. The relation between oxygen influence and respiration seems to be close. At least we may say that the conditions of the oxygen supply which lead to increased use of oxygen are just the conditions which bring about germination. The possibility that oxygen exerts its stimulative effect on germination by increasing respiration, thereby yielding more energy, is strongly suggested, without, however, precluding the possibility that other effects correlated with increased respiration might determine its influence in germination.

Becker3 recently tested the influence of oxygen on the germination of seeds of several plants. The fruits of Dimorphotheca pluvialis were found to germinate more readily in O2 than in air, the ray seeds especially showing the favorable influence. Short exposures to oxygen (15 hours) had no such effect, but if the time of exposure were lengthened to 30 hours, this exposure favored further germination under atmospheric conditions. The ray seeds again showed the effect more strongly than the disk seeds. When the fruit and seed coats were removed, 10 hours’ exposure to oxygen affected germination favorably, but 13 hours’ lengthened the germination time. The seeds of Calendula eriocarpa with coats intact were greatly favored by oxygen, while the yellow-brown vertical fruits of Atriplex hortensis and A. nitens showed an injurious effect from increased oxygen pressures. The relation of oxygen to germination in these cases seems to be irregular and inconstant.

BECKER draws a general conclusion from his results that oxygen acts as a stimulus, and takes particular exception to the idea advanced by CROCKER\(^4\) that the oxygen increases the respiration and in this way initiates germination. In reviewing BECKER's paper,\(^5\) I stated that there was no doubt that in *Xanthium* the oxygen was actually used in germination, and suggested that increased respiration might be identical with BECKER's stimulus. While it is entirely possible that the oxygen influence is exerted through some other process correlated with increased respiration, the data presented here give the ground upon which that suggestion was based. Unfortunately, BECKER's work gives us no data as to the respiration behavior of the seeds on which he worked, so that no comparison with the behavior of *Xanthium* seeds can be made at present.

LEHMANN,\(^6\) in discussing the possibility that O\(_2\) might act as a catalyst, accepts BECKER's idea that oxygen acts as a chemical stimulus, not merely by increasing respiration. Of course, the word "stimulus" is vague and indefinite. But it should not imply an additional absorption of oxygen, for this could not occur without involving oxidation of some kind, which would be respiration. Even if oxygen is conceived to be a catalyser, that conception does not involve increased use of O\(_2\), for catalysts are not used in the processes they carry on.

The biological rôle of oxygen is so complex that we may not say its effect is always due to increasing respiration or oxidation. The rôle, indeed, may be different in different seeds and plants. For instance, ÁRPÁD PAÁL\(^7\) claims that reduction of oxygen pressure even to 0.75 normal lengthens geo-presentation and geo-reaction time to a marked degree. This work of PAÁL's still awaits confirmation. And although the earlier work of STICH, JOHANNSEN, and others indicates that this amount of reduction


\(^5\) Bot. Gaz. 54:433. 1912.


should not affect the rate and nature of respiration, yet it would be very desirable to repeat Páál's work, studying the rate of respiration along with presentation time and reaction time to discover whether there is a parallel effect with that on the respiration rate and germination power of seeds.

Zaleski has noted the influence of oxygen on the rate of protein synthesis. Ivanoff has shown that oxygen is necessary for the transformation of zymogen into zymase, and, as is well known, there are a number of oxygen carriers and oxygen absorbers in the living cell. Xanthophyll and other pigments absorb oxygen, lecithin plays a similar rôle, and Palladin has now shown that his respiratory chromogens take up oxygen readily. All of these facts go to show how complex the oxygen rôle may be, and suggest some of the possibilities of even brief exposure of seeds to oxygen.

On the other hand, however, it would be strange if the oxygen effect in some cases were not due simply to its influence upon respiration. The influence of the amount of oxygen present on aerobic and anaerobic respiration, which differ so markedly in the amount of energy released, is well known. Anaerobic may change over to aerobic on access of oxygen, with a consequent rapid rise in energy release leading to germination.

With these Xanthium seeds it has been shown that when the oxygen supply is increased, it in some way brings about an immediate and rapid increase in the rate of oxygen absorption. At the same time, the increased oxygen supply brings about an immediate germination of the seeds. The two effects, increased absorption and germination, are closely correlated as regards their relation to the oxygen supply. This shows conclusively, I believe, that the assumption made by Becker and Lehmann, which led them to reject the idea that the influence was exerted through increased respiration, is not correct, so far as Xanthium is concerned. Nor does their work throw any light on this particular point, since they

did not measure the respiration of the seeds on which they worked. However, owing to the complexity of the oxygen rôle in physiological processes, it is very difficult to say just which function or functions are affected. It seems certain that the oxygen acts as a limiting factor on some function, whether by limiting the process of respiration or energy release, by limiting enzyme formation or the action of oxygen carriers, or in other still less definite ways. The exact method by which absence of oxygen delays germination can be determined only by further investigation. In the meantime theories may well await the facts which will make philosophical discussion of this question unnecessary.

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