STUDIES OF DORMANCY IN THE SEEDS OF SUBTERRANEAN CLOVER (*TRIFOLIUM SUBTERRANEUM* L.)

III.* DORMANCY BREAKING BY LOW CONCENTRATIONS OF OXYGEN

By L. A. T. BALLARD† and A. E. GRANT LIPP†

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Summary

When imbibed dormant subterranean clover seeds were exposed to low concentrations of oxygen for up to 6 days, and then transferred to either air or 100% oxygen atmospheres, germination was markedly increased above that of seeds held only in air. Stimulation of germination was similar whether the atmosphere of the second phase was air or 100% oxygen; it was maximal when that of the first phase contained no oxygen, and became insignificant above concentrations in the region of 5% oxygen. The additional germination was roughly proportional to the duration of exposure to low oxygen concentrations, and the effects of two separated exposures to low oxygen were additive. These effects could be produced only in those dormant samples whose seeds or embryos could also be made germinable by exposure to 2·5% carbon dioxide. At higher temperatures, anaerobic conditions were less effective in breaking dormancy, paralleling the reduced efficacy of carbon dioxide at these temperatures.

Treatment of dormant seeds with 0·1M ethanol also stimulated germination, as did treatment with acetaldehyde of similar concentration, although less regularly.

These findings suggest that a lowered oxygen concentration enhances glycolysis, and some product accumulates which later behaves similarly to those produced by carbon dioxide when it stimulates germination.

I. INTRODUCTION

The effects of oxygen on seed germination and dormancy have been extensively reviewed, particularly in relation to increased germination or decreased dormancy following treatment of seeds with atmospheres of greater oxygen concentration than that in air. These effects are held to result from the relief of oxygen deficiency caused by seed coat impermeability (Davis 1930; Brown 1940; Vose 1956, 1962) leading to increased or altered meristematic activity (Thornton 1945; Vegis 1963, 1964), to oxidative destruction of inhibitors (Wareing and Foda 1957; Black and Wareing 1959; Wareing 1965), or to the consummation of some non-respiration oxidation reaction (Roberts 1967; Major and Roberts 1968*a*, 1968*b*).

Concentrations of oxygen lower than that in air usually decrease the amount or rate of germination (Moyse 1952; Heydecker 1958; Tadmor and Hillel 1965). The seeds of many species retain some germinative capacity at concentrations of oxygen

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† Division of Plant Industry, CSIRO, P.O. Box 109, Canberra City, A.C.T. 2601.

as low as 1–2%, though very few appear to be able to germinate in the complete absence of oxygen (Edwards 1933; Siegel and Rosen 1962). There are few reports of enhanced germination at low concentrations of oxygen (Morinaga 1926; Ota 1956, cited by Koller *et al.* 1962; Fujii 1963).

The purpose of the present paper is to show that the dormancy of subterranean clover seeds, as judged by their germination in air, is reduced when they have previously been subjected to anaerobic conditions after imbibition.

II. Materials and Methods

Seeds of the following cultivars of subterranean clover: Mt. Barker, Geraldton, Dinninup, Daliak, CPI* 19465 (from Portugal), and CPI 15081 (from Turkey) were treated with gas mixtures having various proportions of O_2 and N_2, or with ethanol or acetaldehyde solutions.

Except where noted, experiments were started in one of two ways. In the first, scarified seeds were covered with 3–4 mm of distilled water or appropriate solution, and after 3 hr swollen or swelling seeds were transferred to Petri dishes or other containers holding filter paper moistened with water or solution. This is referred to as direct setting out. In the second method, referred to to as pre-incubation, scarified seeds were treated as above with water, and then incubated on filter paper moistened with water until germination had virtually ceased, which was usually within 5–8 days. Germinated seeds were discarded daily. Finally, the remaining dormant seeds were again set out on filter paper moistened with water, if for gas treatment, or with ethanol or acetaldehyde solutions. Germination is expressed as percentage of the remaining dormant seeds which were tested.

Two methods of gas treatment were used. In the first, the imbibed seeds (usually 50) were placed in tubes or bottles through which the required humidified gas was passed at a rate to give 20–30 changes per hour. In the second, the seeds in open dishes were held in sealed jars of 2·5 litres capacity containing gas of the required composition. After gas treatment, seeds were returned to air.

Ballard (1958) showed that dormancy of subterranean clover seeds could be broken by sealing them in small vessels, thus permitting accumulation of CO_2. The validity of the second method of gas treatment might therefore be queried. In the present experiments the volume of the container per seed was 15–25 times that in the earlier experiments, thus reducing the likelihood of CO_2 reaching a stimulatory level. We did, in fact, establish that the germination of dormant seeds held in 2·5-litre jars, initially containing air, was similar to that of seeds held in Petri dishes in the usual way.

Gas compositions are given in the appropriate section, expressed on a volume basis. Analysed gases were obtained commercially. They contained less than 50 p.p.m. CO_2 — a concentration without detectable effect on germination. The nitrogen had a maximum O_2 content of 10 p.p.m.

The experiments were done at 20°C, except where otherwise indicated, and generally as previously described (Ballard 1958; Ballard and Grant Lipp 1967). When CO_2 treatment was used, it was given in sealed vessels initially containing 2·5% CO_2. All treatments were replicated, usually four times, but twice only for some of the gas-flow experiments. Statistical analyses were carried out on values of percentage germination after angular transformation.

III. Results

(*a*) *Effect of Exposure to Nitrogen*

In general, after dormant seeds treated with N_2 were returned to air, more germination occurred than in control lots maintained in air throughout. Three types of response were observed.

* CPI = Commonwealth Plant Introduction.

The first type was shown by CPI 19465 and Mt. Barker and is exemplified in Figure 1. No, or few, seeds germinated while in N_2, but a flush of germination which quickly declined to the control rate occurred on transfer to air. If such a treatment did not promote full germination, a further exposure to N_2 could elicit further germination. In Figure 1 it can be seen that the combined effects of two separate N_2 treatments, each of 1 day, are similar to one single treatment of 2 days.

The equivalence of the effects of a given total exposure to N_2, whether given continuously in a single treatment or in two submaximal exposures, has been confirmed in three other experiments, the details of which are not cited here. In these, total exposures of up to 4 days and intervals between partial exposures of up to 3 days were employed.

Fig. 1

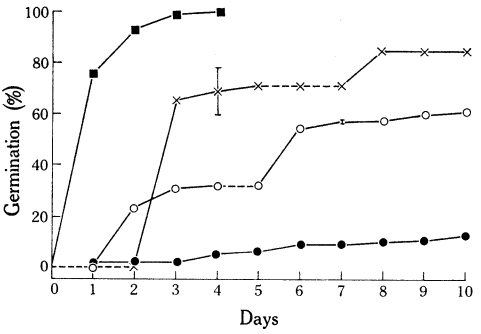

Fig. 2

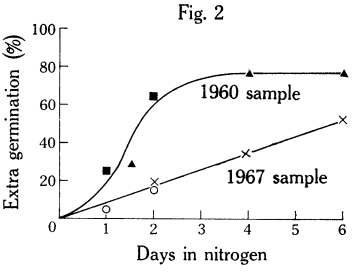

Fig. 1.—Stimulation of germination in subterranean clover, CPI 19465, following exposure to nitrogen by the gas-flow method. Seeds were pre-incubated for 7 days. ● Air (control). ■ 2·5% CO_2. ○ N_2 for two periods of 1 day each. × N_2 for two periods of 2 days each. Dotted lines indicate periods of nitrogen treatment. Bars indicate standard deviation of means at times 2 days after a total exposure to nitrogen of 2 days.

Fig. 2.—Relation between extra germination induced by nitrogen treatment over that of the control and duration of treatment in two samples of subterranean clover, CPI 19465. Different symbols on the two curves represent values from different experiments.

The form and extent of the response to N_2 vary, and, in addition to the duration of the treatment, they depend on such factors as cultivar, season in which the seed matured, and its dormancy status at the time of test. The simplest single measure of the response is the extra germination, beyond that of control lots, elicited by the treatment. The responses of two samples of CPI 19465 are shown in Figure 2. Broadly speaking, the magnitude of the response increases with the duration of treatment, though not necessarily linearly, at least up to 4–6 days.

Most of our experiments have been done with CPI 19465 using both methods of gas treatment, and on 11 occasions, using seeds from five different seasons, results conforming to the above picture were obtained and the magnitude of the effect mostly fell between the limits of the two curves of Figure 2. All these experiments showed this effect in some degree whether the seeds were used directly or after pre-incubation, though in the former case the germination response was somewhat more gradual and sustained than that in Figure 1. In each case germination was

markedly stimulated by CO_2, as in Figure 1, there being no occasion when this germination failed to reach 80% in 3 days. Mt. Barker, on the single occasion investigated, following pre-incubation, behaved similarly.

The second type of response was shown by Dinninup and Daliak. Results are available for seeds from only one season, grown in Western Australia. N_2 treatments were given in sealed 2·5-litre jars. When these cultivars were treated after pre-incubation no extra germination occurred on return to air, although two exposures to N_2 totalling 8 and 9 days respectively were given. In both cases the seeds were responsive to CO_2, and their viability at the end of the experiments was established (Table 1).

TABLE 1

ABSENCE OF STIMULATION OF GERMINATION BY NITROGEN TREATMENT

Days from Start of Treatment	Germination (%)			Days from Start of Treatment	Germination (%)		
	Air	N_2*	2·5% CO_2		Air	N_2*	2·5% CO_2
	Dinninup†				Daliak‡		
2	0	0	92	3	0	0	63
7	0	1	97	8	0	1	89
13	8	1	97	14	1	1	98
17§	19	2	97	16§	1	1	100
20	97	99	97	19	97	89	100

* Seeds in nitrogen for days 1 and 2 and 8–13 inclusive for Dinninup, and for days 1–3 and 9–14 inclusive for Daliak; otherwise in air.

† After 7 days pre-incubation, during which 46% germinated.

‡ After 5 days pre-incubation, during which 1% germinated.

§ All treatments transferred to 2·5% CO_2 to establish viability.

But if the seeds were set out directly, a substantial stimulation of germination occurred, with the response being more delayed and gradual than noted for CPI 19465 set out directly. This is shown in Figure 3 for Dinninup. For Daliak,

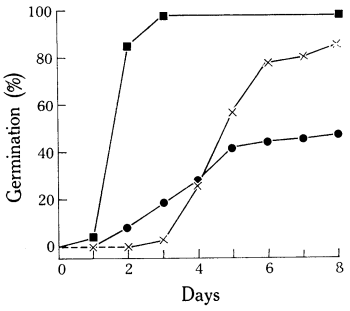

Fig. 3.—Stimulation of germination in subterranean clover, Dinninup, following nitrogen treatment in 2·5-litre jars. Seeds were not pre-incubated. ● Air (control). ■ 2·5% CO_2. × N_2 for 2 days (indicated by dotted line).

5 days after exposure to N_2 for 3 days, the percentage germinations were: air, 4·0±1·8; N_2, 37·5±5·9; CO_2, 100·0. The experiments with the different types of setting out were not done simultaneously; however, it is unlikely that the different

results are due to the shift in dormancy status which must occur with time, since, for Dinninup, the absence of stimulation after pre-incubation was established in experiments both earlier and later than that depicted in Figure 3.

The response of Geraldton, which was also grown in Western Australia, may be of this type. It was not tested after pre-incubation but, on direct setting out with 2 days in N_2, the subsequent germination was delayed and only gradually rose to 84% over the next 7 days (air control, 38%).

Whether this type of response is characteristic of these three cultivars, or a result of the different environmental conditions in Western Australia from those prevailing in Canberra, where all other samples were grown, is not known.

TABLE 2

EFFECT OF NITROGEN AND CARBON DIOXIDE ON THE GERMINATION OF SEEDS AND EMBRYOS OF SUBTERRANEAN CLOVER, CPI 15081

Seeds were imbibed on moist filter paper for 1 day before excising embryos. In experiment 1, gas treatments were then started. Experiment 2 was started 2 weeks later. The same seed sample was used, and the embryos were held on moist filter paper for 1 day in air after extraction before treatment. Nitrogen treatment was given in sealed 2·5-litre jars

Material	Treatment	Germination (%) on Indicated Day after Setting Out: 2	8	Material	Treatment	Germination (%) on Indicated Day after Setting Out: 2	8
	Experiment 1				Experiment 2		
Seed	Air	0	0	Embryos	Air	2	2
	2·5% CO_2	0	2		2·5% CO_2	100	100
	N_2*	0	2		N_2*	0	44
Embryos	Air	9	13				
	2·5% CO_2	99	100				

*Nitrogen treatment for days 1–4 inclusive; air thereafter.

The third type of response was shown by CPI 15081 which usually has a marked and long-lasting dormancy. As is shown in Table 2, the germination of intact seeds is stimulated neither by N_2 treatment of 4 days, nor by CO_2, nor by removal of seed coats. This complete lack of response to the last two treatments is very rare in subterranean clover. However, the embryos germinated promptly and fully on exposure to CO_2 and also showed a substantial stimulation of germination following exposure to N_2. The response of embryos to N_2 was investigated in only one experiment, but all the other features of Table 2 were confirmed using seed harvested in a different season.

(b) Effect of Temperature on Stimulation of Germination following Exposure to Nitrogen

Because exposure to N_2 was effective in stimulating germination only when exposure to CO_2 could also do so, we investigated the effect of temperature on the N_2 stimulation. Ballard (1967) has shown for subterranean clover that the dormancy

is more marked, and CO_2 is much less effective in breaking it, at 30 than at 20°C (see also Table 4).

Seeds of CPI 19465 imbibed on moist filter paper for 3 hr were exposed to N_2 for 3 days in sealed containers, and then transferred to air, at either 20 or 30°C.

TABLE 3

STIMULATION OF GERMINATION BY LOW OXYGEN CONCENTRATIONS COMPARED WITH THAT PRODUCED BY NITROGEN

Mt. Barker was used for experiment 1, and CPI 19465 for the others. Exposure to nitrogen was for 7 days in experiment 3, and 4 days in other experiments. In experiments 1 and 2, gas treatment was given in sealed jars, whilst the flow method was used in experiments 3 and 4. Values in parenthesis are the actual increases in percentage germination given by nitrogen treatment

Oxygen Concentration (%)	Experiment 1	Experiment 2	Experiment 3	Experiment 4
0 (N_2)	100 (54)	100 (65)	100 (66)	100 (71)
0·5	73	80	94	—
0·8	—	—	61	—
1·0	57	76	—	—
2·0	7	44	—	—
5·3	—	—	—	3
10·1	—	—	—	0

Other lots were exposed to N_2 for 3 days at either 20 or 30°C, and then transferred to air at the reversed temperatures. There were also parallel control lots without any N_2 treatment.

The results, presented in Figure 4, confirm the reduction in germination in air at 30°C. Other comparisons also show that the stimulation of germination following exposure to N_2 is much less at an exposure temperature of 30 than 20°C.

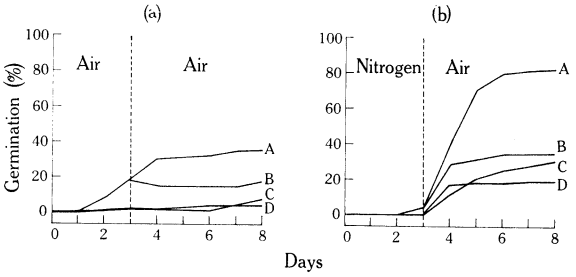

Fig. 4.—Effect of temperature on dormancy and on stimulation of germination induced by exposure to nitrogen. (*a*) Seeds in air throughout; (*b*) seeds in nitrogen for 3 days, then transferred to air. *A* 20, 20°C; *B* 20, 30°C; *C* 30, 20°C; *D* 30, 30°C. The first temperature denotes the temperature during the first 3 days and the second denotes that thereafter.

(*c*) *Effect of Exposure to Low Oxygen Concentrations*

So that these experiments could be of minimum duration and thus more accurate, being less influenced by drifting germination rates, they were all carried out on seeds giving the first type of response, and after pre-incubation. For reasons given earlier, the absolute values for different experiments are very different, and as a basis of comparison the extra germination given by any O_2 concentration over its

appropriate control is expressed as a percentage of that quantity given by N_2 (designated zero O_2).

Such values assembled in Table 3 indicate that the stimulation of germination by exposure to completely anaerobic conditions is sharply reduced in even low concentrations of O_2 and becomes negligible in the region of 5%.

(*d*) *Effect of Exposure to High Oxygen Concentrations*

Dormant imbibed seeds were exposed to various O_2 concentrations and to 2·5% CO_2 at 20 (or 22) and 30°C. Results presented in Table 4 confirm the ineffectiveness of CO_2 in breaking dormancy at 30°C, and also show that high O_2 concentrations will not stimulate germination at all, irrespective of temperature.

TABLE 4

EFFECTS OF TEMPERATURE, HIGH CONCENTRATIONS OF OXYGEN, AND 2·5% CARBON DIOXIDE ON GERMINATION

Different samples of CPI 19465 were used in the two experiments; seeds used in experiment 1 were pre-incubated, whilst those for experiment 2 were used after imbibing for 3 hr on moist filter paper. Only within-experiment comparisons are valid

Treatment	Germination (%) on Day 8 in:		
	Experiment 1 (22°C)	Experiment 2 (20°C)	Experiment 2 (30°C)
Air	7	18	8
50% O_2 in N_2	—	—	11
80% O_2 in N_2	—	—	6
100% O_2	5	—	7
2·5% CO_2 in air	83	95	8

The effect of high O_2 concentration following an exposure to anaerobic conditions was investigated in a single experiment. After being held in N_2 for 36 hr seeds were transferred either to air or to 100% O_2. After a further 48 hr the additional germination due to N_2 exposure was 29 ± 8% in air and 23 ± 6% in O_2. Apparently, any further metabolism of intermediates formed in the anaerobic phase is not limited by 21% O_2.

(*e*) *Effects of Ethanol and Acetaldehyde*

Ballard (1967) has previously reported that ethanol is without marked effect on dormancy, but at higher concentrations than were used then considerable stimulation of germination results, the optimum being in the range 0·05–0·1M (Table 5). Stimulation at only such high concentrations is unusual, and indeed some initial retardation possibly due to osmotic inhibition is apparent. Increase in germination was observed both in seeds treated directly and after pre-incubation.

The response to acetaldehyde was irregular both between and within experiments. Low concentrations were generally without effect; high concentrations killed some of the seeds, but others completed sufficient development to be scored as germinated. This led to high variability, so that the observed average increases had low statistical significance. Of four experiments, the increases in two were

insignificant ($P > 0{\cdot}05$), and significant in two ($P < 0{\cdot}01$). An example of each type of result is presented in Table 6. Both of the significant results were from pre-incubated seeds.

TABLE 5

STIMULATION OF GERMINATION BY ETHANOL

CPI 19465 was used, seeds being set out directly. Values in parenthesis are angular transformations

Concentration of Ethanol (M)	Germination (%) on: Day 3	Day 8
0 (H_2O)	21·0 (26·8)	27·0 (31·2)
0·01	25·5 (30·1)	39·5 (38·9)
0·02	19·5 (26·0)	49·0 (44·4)
0·05	9·0 (16·6)	71·0 (57·6)
0·10	7·5 (15·5)	63·5 (53·0)
Least significant difference, $P < 0{\cdot}05$	(7·5)	(7·9)
$P < 0{\cdot}01$	(10·4)	(11·0)

IV. DISCUSSION

Although there are differences in detail of the pattern of response, the generality of the stimulation of germination following a period of anaerobiosis seems well established in the above results, provided that the material is also responsive to

TABLE 6

GERMINATION RESPONSE TO ACETALDEHYDE

Experiment 1 was on directly treated seeds and experiment 2 on pre-incubated seeds of CPI 19465. Values in parenthesis are angular transformations

Concentration of Acetaldehyde (M)	Germination (%) on Day 8 in: Experiment 1	Experiment 2
0 (H_2O)	25·0 (29·9)	10·0 (18·2)
0·025	42·0 (40·3)	6·5 (14·8)
0·05	42·0 (40·1)	4·5 (12·0)
0·10	50·5 (45·1)	22·0 (27·8)
Least significant difference, $P < 0{\cdot}05$	n.s.†	(4·9)
$P < 0{\cdot}01$		(6·9)

† In experiment 1, the increase over the values for water of all aldehyde treatments taken together was significant at $P < 0{\cdot}05$.

carbon dioxide. This association is very strict—anaerobic stimulation is always noted in CO_2-sensitive material and never otherwise. While the causes for the

different patterns of response are not known, it is probable they have to do with differences in the conditions of growth and maturation and also of dormancy status between cultivars.

Germination may also be stimulated by high concentrations of ethanol and acetaldehyde. The facts that volatile products of fermentation can be smelled after the anaerobic phase and that a flush of germination usually occurs on restoration of aerobic conditions suggests that the accumulation of some product of glycolysis is an important feature. The capacity for glycolysis has been established in many plant tissues (Stumpf 1952), though specifically in seeds in fewer cases and with varying degrees of rigour (Taylor 1942; Appleman and Brown 1946; Hatch and Turner 1958; Doireau and Duperon 1966).

This suggestion is strengthened by the observed oxygen relations. James (1953) supposes "that anaerobic respiration, with formation of alcohol or other products, is not limited to complete absence of oxygen, but persists in low oxygen concentrations, and is gradually extinguished as the concentration rises. Its complete suppression would appear to need at least 3 per cent oxygen and considerably more in some tissues". Hatch and Turner (1959) observed increasing inhibition of glycolysis in their pea-seed extracts with oxygen levels above 2%. The results given in Table 3 are consistent with these findings.

The intermediate substance cannot be specified, but the similarities of stimulation of germination by anaerobic conditions and by carbon dioxide suggest that similar products are concerned in each case.

In the case of stimulation by low oxygen it appears that a compound formed later in the aerobic phase must reach a certain concentration to be effective in germination. This concentration varies for individual seeds, which explains the general increase in germination response with duration of treatment. The results of the fractional exposure experiments suggest that the compound is stable for periods of days.

The present experiments provide no evidence about which respiratory pathways may exist in subterranean clover seeds during their germination. However, the evidence provided by the low-oxygen experiments, in conjunction with the absence of effect of high oxygen concentrations, makes it unlikely that their passage out of dormancy follows from some non-respiration oxidation reaction, as has been suggested by Roberts (1967) and Major and Roberts (1968*a*, 1968*b*) to be the case for some cereals.

V. Acknowledgments

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