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THE MANIPULATION OF WEED SEED DORMANCY

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ABSTRACT

Aspects of primary and secondary dormancy in weed seeds are discussed, particularly in relation to plant growth regulators. The possibilities of utilising this knowledge to manipulate seed dormancy in the field is assessed.

INTRODUCTION

It is commonplace to point out that the soil seed bank is a major source of weed infestation; equally, it is glaringly obvious to suggest that could this seed bank be successfully manipulated then many of our problems would be solved. However, most workers in the area of seed dormancy, whether of cultivated plants or of weeds, would agree that almost the only observable common factor is that the mechanisms of dormancy control appear to be almost as diverse as the species themselves. A number of hypotheses have been proposed suggesting the possibility that there exists some common feature or process which might be susceptible to manipulation. For example, Roberts (1972) came forward with an attractive suggestion that the breaking of seed dormancy involved a switch in metabolism from the Embden-Meyerhof-Parnas (EMP) pathway to the pentose phosphate pathway (PPP). With those species examined, the hypothesis fitted the known facts. However, it became clear on further investigation that not all seeds behaved as expected (e.g. Jones & Hall, 1981).

It would nevertheless be a counsel of despair to say that the problem is intractable, since to do so would imply a knowledge of the mechanisms of seed dormancy far greater than that which we possess. Furthermore, since the fashion, at least in herbicide research, is to look for substances capable of affecting specific key processes - for example glyphosate and the shikimate pathway - it would be moving against the trend not to assess the feasibility of such an approach with seeds.

PRIMARY DORMANCY

It is unnecessary to rehearse in detail the effects of environmental factors upon seed dormancy except to point out that the array of responses is clearly related to survival value, as for example in chilling or light requirements. The question which needs to be asked is whether there is any common feature of responses to environmental factors or some common process which can be identified and manipulated. As mentioned above, one of the most attractive of these was that of Roberts (1972) concerning switches between respiratory pathways. This had the attractions of simplicity, of dealing with a set of basic processes and of explaining the peculiar dormancy breaking characteristics of such substances as cyanide. We ourselves who were working at that time on the involvement of ethylene in seed dormancy were most interested by the theory's possibilities, since ethylene is well known to affect respiratory pathways in tissue such as fruits (e.g. Hobson *et al.* 1984). However, although the seed we were concerned with, i.e. *Spergula arvensis*, showed the predicted responses to applied substances (see Table 1), examination of the behaviour of this seed under dormancy-breaking conditions indicated that the expected respiratory switch did not occur -

TABLE 1

Response of dormant *Spergula arvensis* seed to applied chemicals

Compound Concentration	Germination (%)*
None	10
Ethylene (100 µl l^{-1})	57
Potassium cyanide (0.15mM)	81
Hydroxylamine (5mM)	64
Thiourea (1mM)	38
Potassium nitrate (25mM)	52
Potassium nitrite (25mM)	51
Hydrazine (0.2M)	67
Gibberellic acid (10^{-4}M)	80
Glutamate (0.2M)	54
β-chloroalanine (5mM)	63

* Incubations in the light

quite the reverse in fact (Jones & Hall, 1979). Of course the essence of Roberts' hypothesis was that by inhibiting the EMP pathway some oxidative reaction was promoted and this could well be something other than the PPP.

In part, the situation is clouded because many of the substances capable of breaking dormancy which fit in with the respiratory switch hypothesis are not of themselves specific and their effects are susceptible of different explanations. Thus, the effect of cyanide has been explained by the suggestion that the cyanoalanine formed from cyanide and cysteine contributes to the asparagine pool. The hypothesis is supported by the fact that β-cyanoalanine can break dormancy in some species (Taylorson & Hendricks, 1973), although of course the whole idea does depend on the assumption that asparagine or its derivatives are limiting.

Some of our own work also suggests that amino acid metabolism may be involved, at least in *Spergula*. Thus β-chloroalanine, a known inhibitor of glutamate-oxalacetate aminotransferase (GOT), promotes germination markedly. Equally, hydroxylamine severely inhibits the activity of both GOT and glutamate-pyruvate transaminase (GPT). It is unclear why the inhibition of such enzymes and the resultant build up of glutamate should break dormancy although application of glutamate to *Spergula* seeds is effective in breaking dormancy (Table 1). The situation is further complicated in the case of treatments with hydroxylamine which reacts with glutamate to form γ-glutamohydroxamate, a reaction catalysed by glutamine synthetase. Furthermore, hydroxylamine prevents a decrease in glutamate-oxoglutarate aminotransferase (GOGAT) in imbibing *Spergula* seeds.

In much the same way Hendricks and Taylorson (1975) have suggested that thicurea, nitrite and hydroxylamine may act by inhibiting catalase, thus permitting a more rapid operation of PPP.

One last aspect of promoters and inhibitors concerns growth regulators. All of the known natural plant growth regulators have been shown to affect

seed germination, but most attention has been focussed on gibberellins (GA), ethylene (ETH) and abscisic acid (ABA). Although the role and significance of natural growth regulators has been called into question in recent years (e.g. Trewavas, 1981), recent elegant work with monogenic mutants differing from wild type in endogenous hormone content has disposed of any doubts in this connection, as for example in the ABA deficient mutants of *Arabidopsis* (Koorneef *et al.* 1984). Similar work is now ongoing with gibberellins and ethylene (Karssen, pers. comm.).

It must be admitted, however, that the certainty that growth regulators are involved in maintaining and/or breaking dormancy does not of itself help us in assessing their role. As with the substances mentioned above, there are a multitude of hypotheses to account for the means whereby growth regulators break or impose dormancy. Only in one system, namely barley aleurone, are the roles of gibberellins and abscisic acid beginning to be clarified (e.g. Jacobsen *et al.* 1982).

In one case, namely that of ethylene, the situation is further complicated by the fact that the growth regulator is not only produced naturally by the seed but is a normal component of the soil atmosphere at physiologically active concentrations.

There is one aspect of the involvement of growth regulators in seed dormancy which, while almost wholly speculative at this juncture, is nevertheless something to be considered for the future. It is a *sine qua non* of developmental physiology that plants, like animals, must possess receptors for natural growth regulators. These receptors must have the ability to perceive the growth regulator and, by interacting with it transduce a particular biochemical effect leading to a developmental response. Although no receptor for a plant growth regulator has as yet been unambiguously identified as such, several candidate proteins have now been purified to homogeneity (see Venis 1985), including one from a seed (Williams *et al.* 1987). If these are indeed receptors and are involved in the transduction of responses necessary for the breaking of dormancy, then another possible tool for manipulating the process presents itself. Thus, provided the environment of the binding domain for the growth regulator can be mapped - something which we ourselves are undertaking for the ethylene binding site from *Phaseolus vulgaris* - it becomes realistic to construct structural analogues which will block such a site and hence presumably any response. Such an approach is proving fruitful in animal systems, and there is no reason to suppose that this cannot be achieved in plants.

SECONDARY DORMANCY

A major complication when assessing seed dormancy in the field is the well-known fact that dormancy characteristics may change as a result of burial - for example by the acquisition of a light requirement (Wesson & Wareing 1969). This is a much less well investigated area than primary dormancy, although many of the treatments which break primary dormancy also do so in secondarily dormant seeds. The type of response observed is shown in Table 2 for *Spergula arvensis*, although this is typical of many other species.

While the induction of a light requirement as a result of burial is observable, this feature is lost in the long term and is followed by a period where light is inhibitory. Equally, the magnitude of the response to ethylene is very variable ranging from an almost absolute requirement to a marginal effect. Figures such as these cannot take into account whether the

TABLE 2

Changes in dormancy characteristics of seed of *Spergula arvensis* with time and treatment

	Germination (%)			
	Light		Dark	
	- Ethylene	+ Ethylene	- Ethylene	+ Ethylene
Freshly shed seed	15	52	7	17
5 months at 20°C	68	95	59	85
1 year at 20°C	35	60	75	80
After burial for 3 months in the field*	78	93	58	45
After burial for 12 months in the field*	25	38	49	30

* Burial commenced on January 1st. Figures given are for remaining ungerminated seeds; approximately 5% of the buried seeds had germinated *in situ* by 3 months and 35% by 12 months.

same seeds or group of seeds are being affected in the same way; it is rarely possible to obtain effectively total germination and yet >95% of the seeds are viable - at least as evidenced by tetrazolium staining.

If one restricts consideration only to the effects of burial, what are the factors responsible? It is clear both from our work and that of others (e.g. Karssen, 1981) that the water content of the medium is important and this appears to relate at least in part to the oxygen tension in the soil. Wesson and Wareing (1969) suggested that a volatile inhibitor, either from the soil or from the seeds, was responsible for the changed dormancy characteristics. We have investigated this problem with *Spergula* and identified by GCMS the volatile products produced.

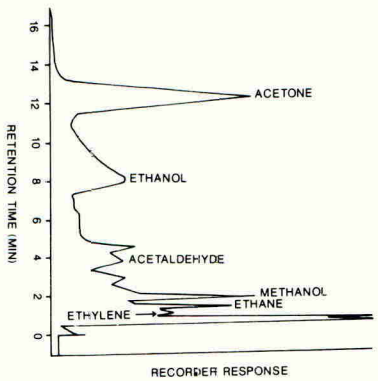

Fig. 1. Total ion current scan of a gas sample collected from seeds of *Spergula arvensis* L. buried in sand at 60% moisture content. Sample taken after four weeks incubation at 20°C.

A total ion current scan of the products released by *Spergula* seed after four weeks burial in sand is shown in Fig. 1. All but one of the products were characterised unequivocally. Ethanol and acetaldehyde are characteristic products of anaerobic metabolism, the production of acetone is somewhat harder to explain but it may arise from acetoacetyl CoA during fatty acid biosynthesis. These various components had differing effects upon dormant and non-dormant seeds. However, ethanol, acetone and acetaldehyde did inhibit germination at concentrations exceeding 10^{-8}M and at least in the case of acetone such inhibition could be overcome by light treatment. Whether, however, one or all of these volatiles are involved in the induction of the light requirement is both unclear and problematical.

CONCLUSIONS

This paper has presented a very selective overview of aspects of the manipulation of seed dormancy. A comprehensive review would not only have been encyclopaedic but would not, I believe, have shed greater light on the problem. The question remains, is there any prospect of developing a realistic strategy from the known data? The answer must be yes, but not yet. It has to be admitted that our knowledge remains fragmentary and there is no unifying hypothesis which can account for all the observed effects.

The authors doubt if indeed there is any unifying hypothesis. For example developmental physiologists long ago rejected the idea that growth regulators affected a single key reaction in any given system and all the evidence suggests that a multiplicity of primary events are involved (e.g. Zeroni & Hall, 1979). There is no reason to suppose that seeds are in any sense unique in this respect.

It seems likely, therefore, that any solution is likely to take one of two possible forms, namely treatments designed to promote or suppress the germination of a single species or a defined range of species or a treatment designed to affect a single process central to metabolism.

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VARIATION IN GERMINATION WITHIN U.K. POPULATIONS OF PHALARIS PARADOXA.

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ABSTRACT

Germination requirements have been studied for seed of several U.K. populations of Phalaris paradoxa using seed from plants grown in uniform spaced conditions at Reading. Seed were harvested by hand and stored at 4°C until used. Populations exhibited quite large variations in germination behaviour. Caryopses germinated well in most instances providing temperatures below 15°C were used, but some populations germinated at faster rates than others. At temperatures between 15 and 20°C some populations did not germinate while others had good germination. Slow germination rate was correlated with inability to germinate at warmer temperatures. The presence of glumes decreased dark germination in all populations and this effect could not be replaced by NO_3^- or alternating temperatures. Only the most dormant caryopses samples responded to light at 15°C but this could be replaced by alternating temperatures of 10°/20°.

Establishment of seed on the soil surface was poor but generally establishment was good from 3-7 cm planting depth and still possible from 10cm depth for rapid germinating samples. No evidence was found for growth inhibitory substances in glumes. It is concluded that these variations in germination characteristics and those from flowering observations confirm that several distinct populations of P. paradoxa exist in U.K. some of which demonstrated quite well-developed dormancy behaviour in storage and in soil.

INTRODUCTION

Phalaris paradoxa (awned canary grass) is an annual grass weed widespread through the Mediterranean region and Middle East. It has been recorded as an occasional alien at several locations in Britain for over 100 years in urban areas, docks and waste tips.

Between 1981 and 1983 there were reports of severe infestations from several locations in England in field crops of winter cereals which suggested that it might become a major weed if unchecked. In 1984 a survey was carried out by Thurley and Chancellor (1985) which confirmed 68 infestations of which the largest concentration was in Essex. With infestation as far west as Somerset and Gloucester and as far north as Lincolnshire the weed was already widespread. It is possible that these infestations had been present for some time but were mistaken for other grass species which show a superficial similarity to it, e.g. Timothy (Phleum pratense) Crested Dogtail (Cynosurus cristatus) or Blackgrass (Alopecurus myosuroides). It is not readily controlled by chlortoluron or isoproturon which controls Blackgrass.

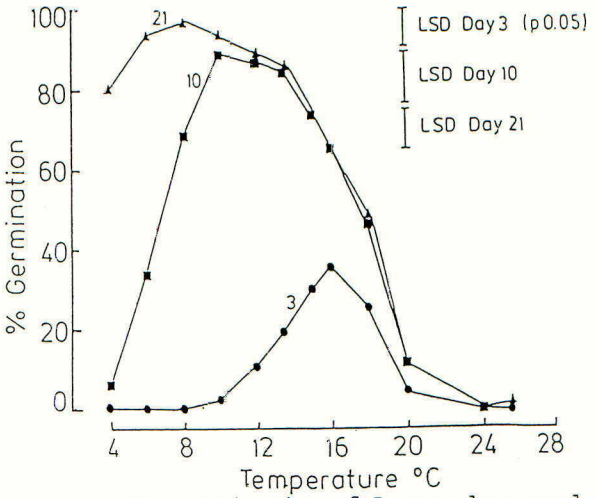

Fig. 1. The germination of P. paradoxa seed at constant temperatures counted at 3, 10 and 21 days

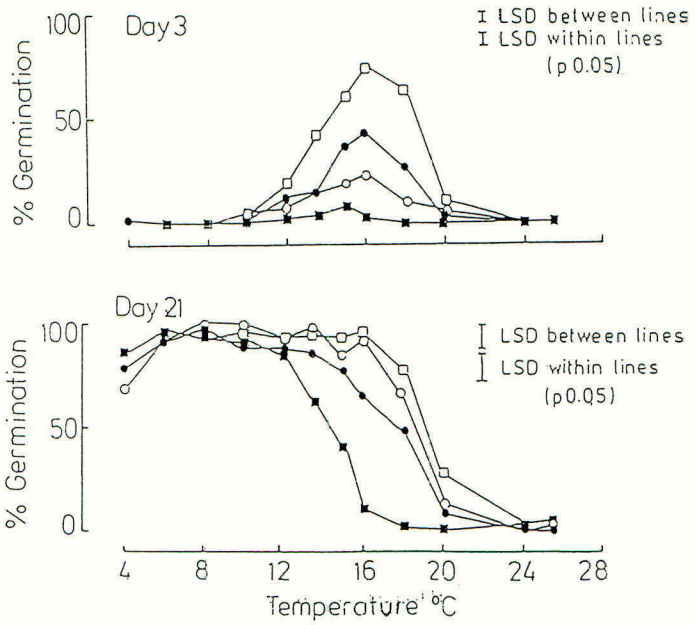

Fig. 2. The germination of P. paradoxa seed at constant temperatures counted at 3 and 21 days for P(25) (North Essex ●, P(34) Kent ■ , P(55) (South Essex) O, and P(68) (Worcestershire) □.

Viable seed were obtained from 32 of the arable populations collected by Thurley and Chancellor and these were grown in the experimental grounds of the Plant Science Laboratories during 1985. The seed were hand-harvested in August-September 1985, air-dried and stored dry at 4°C until used. When mature the seed are shed enclosed in persistent glumes and sterile spikelets. These can be removed to leave caryopses by gently rubbing between two layers of ribbed rubber sheeting and blowing off the detached glumes on a sieve.

RESULTS

Germination at constant temperatures

3 samples of 50 caryopses from 4 populations of P. paradoxa were germinated 2 months after being in storage at 4°C in perspex boxes (37 x 25 x 12 mm) on 2 layers of cellulose filter paper with 5cm^3 of distilled water added. These were placed on a linear thermogradient plate (Fox & Thompson, 1971) with temperatures between 4°C and 24-5°C. Four 40 watt white fluorescent tubes were suspended above the plate. Averaged over the 4 populations the response to temperature varied during the germination period. Those seed which could germinate rapidly did so at temperatures around 14-18°C in the first few days but later at cooler temperatures more complete germination was evident between 6°-16°C and few seed germinated above 20°C. Ungerminated seed from the warmer temperatures germinated rapidly when transferred to 10°C for a short period confirming that the "dormancy" was temperature enforced and lacked persistence.

Variability between the 4 populations was considerable. A population from Kent (P34) germinated most slowly and had a lower maximum germination temperature (about 16°C) than the other 3 populations. These differed from each other in rate of germination more than the temperature range at which germination could occur.

Germination at alternating temperatures

Seed of the most and least dormant samples from the 4 populations examined above were germinated in all 25 factorial combinations of day (8 hours) and night (16 hours) temperatures of 5°,10°,15°,20° and 25° on a thermogradient plate. The results broadly support the earlier results. Germination occurs rapidly over a wider temperature range in the least dormant Worcestershire population but is restricted to temperatures close to 15° in the Kent population at 5 days. Maximum germination is evident at combinations below 25° in the Worcestershire population (P68) but at temperatures above 20° germination was poor in the Kent population and full germination was restricted to temperatures below 15°C.

Combined effects of temperature, light and nitrate on germination

Samples of 50 caryopses or seeds with glumes were germinated in petri dishes on two 9 cm cellulose filter papers with either 6cm^3 water or 0.2% KNO_3. Germination conditions were a constant temperature of 15°C or alternating 10°/20°C for 16/8h, either in the light or dark (wrapped in layers of black polythene). There were 3 replicates of each factorial combination. Dark-germinated seed were examined under a safelight made from a Primary Green Cinemoid filter over a white fluorescent tube (Hilton, pers. comm.). Four populations were examined but only the

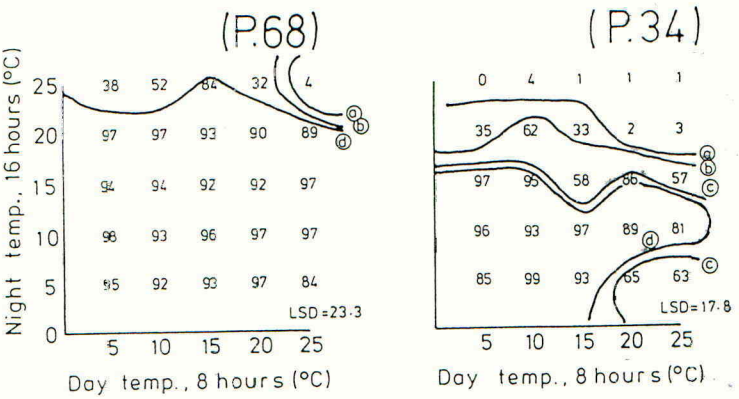

Fig. 3. Germination of seed of P(68) (Worcestershire) and P(34) (Kent) populations of P. paradoxa after 30 days at alternating temperatures in the light

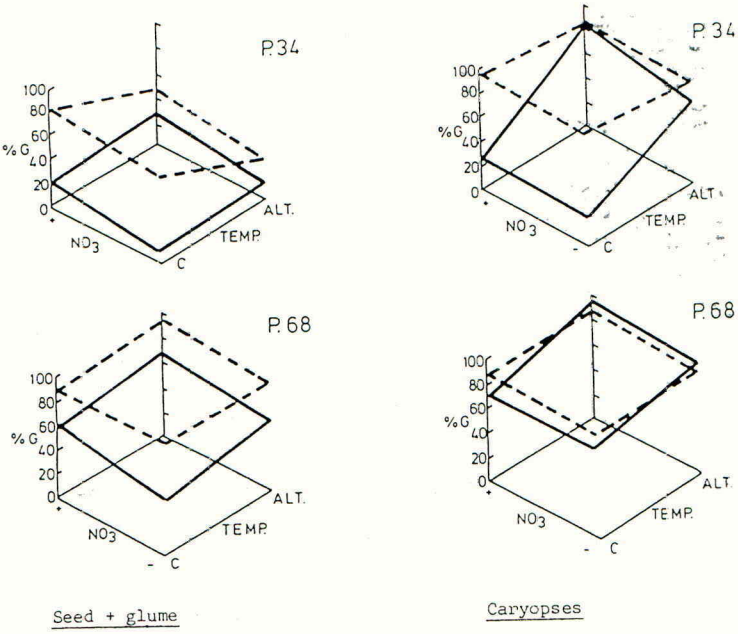

Fig. 4. Germination of seed of P(34) (Kent) and P(68) (Worcestershire populations of P. paradoxa in all combinations of water or 0.2% KNO_3, 15°C or 10/12°C, light (broken line) or dark (solid line) for 30 days

results for two which differed to the greatest extent are shown. For caryopses germination of Worcestershire population (P68) was good in all conditions but was slightly improved by alternating temperatures. In a Kent population (P34) germination at 15°C constant was small but was increased to almost 100% by light and to close to this by alternating temperature. For seed with glumes, alternating temperatures or nitrate had little effect on germination but light treatments increased germination in every population examined. Nitrate effects were generally small in all situations but there was a small response to nitrate at alternating temperatures in caryopses germinated in the dark. The presence of glumes inhibited germination appreciably, 52% compared with 78% without glumes averaged over all other treatments and all 4 populations.

Emergence from different depths in soil.

8 replicate samples of 100 fertile seed with glumes from the 4 populations used in earlier studies were planted in 20 x 15 cm pots of sandy loam soil on a layer of nylon mesh placed at depths of 0, 1, 2, 3, 4, 5, 7 and 10 cm. The pots were sunk into the soil to within 2 cm of the rim in late October and covered with a net to keep out birds. All the seedlings that emerged did so in one single flush starting in mid-December, while mean air temperature still remained above 5°C. The pots were left undisturbed until the seed were recovered from 2 replicates after 8 months. Few seedlings emerged throughout the following summer period but seed taken back into the laboratory for germination tests were still viable after 8 months, except for those on the surface which had been predated or decayed.

Emergence was best from depths of 3-7 cm. Surface sown seed established poorly and planting at 10 cm also gave poorer emergence. All 4 populations showed a similar response to planting depth but more seedlings emerged from the Worcester (P68) and least from the Kent (P34) population with 2 Essex populations (P55 & P25) intermediate.

The same experiment was repeated in March in a growth room at a constant temperature of 15°C. As found outdoors, there was one flush of seedling emergence 20-30 days after planting with little additional emergence up to 150 days. There was again poor emergence from surface sown seed but germination at 1 & 2 cm depths was very much improved compared to that in the outdoor experiment.

The poor germination of surface sown seed contrasts strikingly with the improvement of germination of seed with glumes in the light compared with the dark in the laboratory studies.

It was not possible to demonstrate any germination inhibitory substances in the glumes of several populations, or when glumes were separated but added back with caryopses in germination tests.

CONCLUSIONS

Others working with P. paradoxa have observed the inhibitory effect of the enclosing glumes on germination and that freshly harvested samples may show considerable levels of seed dormancy (Horowitz, 1964; Palti, 1964; Wilson, 1981; R.J. Chancellor & E.N. Flack, pers. communication). The response to light by seeds with glumes was also noted by Chancellor & Flack, but was not observed by Yadaraju et al (1984) with caryopses. As seen here however the caryopses response is only evident in the more dormant samples and at temperatures above 15°C. The poor germination at 20°C or more exhibited here has also been noted by others and conforms with its field germination pattern as an autumn germinating species in Mediterranean areas (Calizone & Viggiani, 1980). The role of the glumes in limiting germination does not appear in these studies to be associated with inhibitors as suggested by Palti (1964) but is more likely to be associated with impeded gas exchange.

Emergence in soil down to 10cm with best emergence from 3-7 cm depths for seed with glumes suggests little role of light in such conditions. Poor establishment for surface sown seed might indicate susceptibility to small predators or poor tolerance of desiccation during germination. Ungerminated seed in soil were still viable after 8 months which indicates a carry-over capacity from one crop season to another.

Observations taken during the seed production year showed a considerable variation in first flowering date between populations with a range from 6th June to 27th June.

There appeared to be little association between area of collection and flowering date. Four of the 5 earliest flowering populations came from Essex but, 3 of the latest flowering strains also came from the same county. The most dormant strain, P34 from Kent was only a few days later in flowering than the least dormant strain P64 from Worcestershire.

These observations on flowering and germination behaviour in the U.K. populations of Phalaris paradoxa do not support the view that its recent build-up resulted from one or multiple introductions from a single populations source but that several different sources have contributed to present U.K. stocks.

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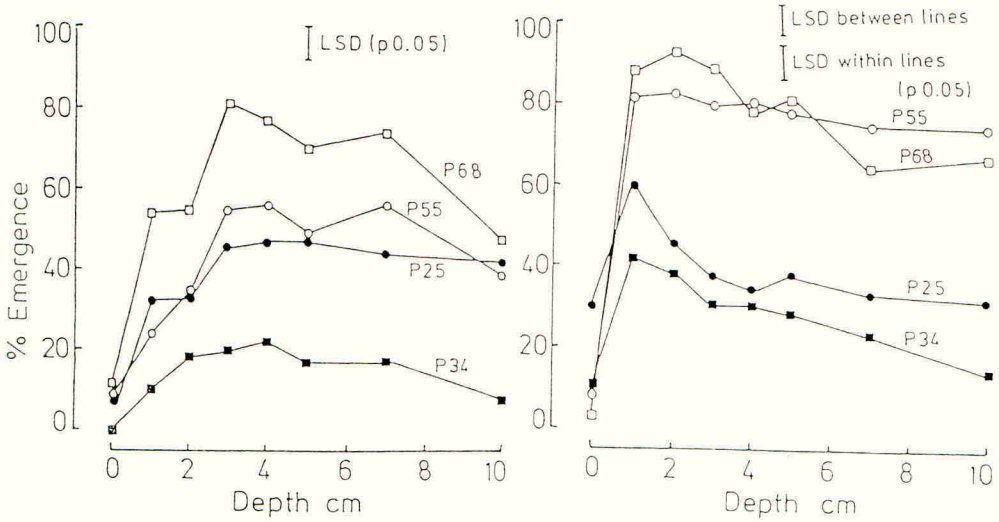

Fig. 5. Final emergence percentage of seed with glumes of P. paradoxa sown in soil at depths to 10cm outdoors (left) or at 15°C in a controlled environment room. The populations are those of figure 2.

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