SESSION 7C

BIOLOGY OF WEED SEED

CHAIRMAN	DR R. W. SNAYDON
SESSION ORGANISER	DR P. D. PUTWAIN

INVITED PAPERS 7C-1 to 7C-4

THE INTERACTION OF ENVIRONMENTAL FACTORS ON SEED DORMANCY

E.H. ROBERTS, A.J. MURDOCH, R.H. ELLIS

Department of Agriculture, University of Reading, Earley Gate,
P O Box 236, Reading RG6 2AT, UK

ABSTRACT

The main environmental factors which trigger the germination of small weed seeds are light, alternating temperatures and, in some cases, chilling (stratification) and nitrate ions. Frequently there are strong positive interactions, especially between light and alternating temperatures so that most seeds in a population may require both. White light is usually promotory at photon doses up to about 10^{-1} mol m^{-2} d^{-1}, but inhibitory above this level. Any light filtered through a leaf canopy tends to be inhibitory because of the high far-red/red ratio. The stimulation of alternating temperatures generally increases with increase in amplitude, decrease in mean temperature, and increase in number of cycles (days). These properties of light, temperature, and their interactions largely explain seed responses with respect to position (in relation to soil profile and the vegetation cover) and season.

INTRODUCTION

Many weeds are opportunists: most of the individuals in a field at any one time are dormant seeds waiting for conditions to arise when they can germinate with some probability of developing into mature plants capable of producing more seeds. To this end seeds need to germinate at the right time in the right place. The right time usually means germinating when growth of vulnerable young seedlings would not occur under stressful conditions (e.g. in the winter in cool temperate latitudes or in the dry season in Mediterranean climates and the tropics). Since many weed seeds are small, the right place usually means at or near the soil surface, otherwise food reserves would run out before emergence. But germination at the soil surface could still be inappropriate if the ground already supports a luxuriant vegetation which would provide more shade and competition than might be healthy for a young seedling. Germination at the soil surface could also be inappropriate if the seed is exposed to bright sunshine which could rapidly dry the surface.

The main purpose of this paper is to identify the main environmental factors which determine that seeds respond appropriately, to characterize these factors in more detail, and to illustrate the importance of interactions between them.

ENVIRONMENTAL STIMULI AND THEIR CHARACTERISTICS

Although the gaseous composition of the soil atmosphere may have some influence in the deeper layers of the soil or under water-logged conditions, the main factors affecting germination in the upper layers of agricultural soils appear to be temperature and light (Roberts, 1972).

Temperature

The effect of temperature differs depending on whether the seed is wet or dry. Under dry conditions seeds tend to lose dormancy at a rate which increases semi-logarithmically with increase in temperature (Roberts, 1988);

such responses may be important during hot dry seasons although, of course, the seeds would not be able to germinate until the soil is subsequently re-moistened. However 'dry after-ripening', as it is called, has not yet been adequately studied in weed species.

When seeds are moist, as most buried seeds are for most of the time in many climates, the responses to temperature are quite different. Either excessively warm or excessively cool conditions may induce dormancy (Bewley & Black, 1982). On the other hand, many temperate species show a stratification response in which cool temperatures (typically -5 to 15°C) stimulate germination, providing the seeds subsequently experience warmer temperatures. An example is shown in Fig. 1 for *Rumex obtusifolius* which also shows that the ability to germinate depends on the duration of the treatment. Furthermore in this species, and probably others, the proportion of the population able to germinate may decrease after prolonged treatment because of the induction of secondary dormancy at a rate which increases with increase in temperature.

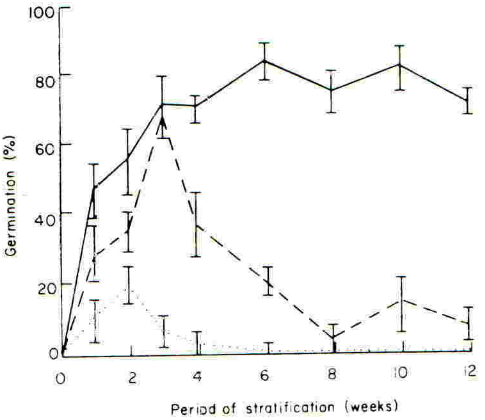


Fig. 1. Germination of *Rumex obtusifolius* after 4 weeks at 25°C in the light following stratification for various periods in the dark at 1.5°C ——, 10°C – – –, or 15°C ······. (From Totterdell & Roberts 1979.)

Another common factor affecting the germination of small seeds is the stimulatory effect of alternating temperatures. The stimulation could, conceivably, be due to a number of characteristics. Any of these may be classified as primary if it can be altered independently within an experiment. A secondary characteristic is determined by more than one primary characteristic and cannot be altered, therefore, without altering a primary characteristic. If it is intended to hold a secondary characteristic constant within an experiment, then if one of the primary characteristics which determines its value is altered, this has to be compensated by confounding it with a change in another determining characteristic. This is made clear in Fig. 2 which shows, for example, that amplitude is a secondary characteristic dependent on the primary characteristics of minimum and maximum temperature. It is only possible to alter minimum temperature, while holding amplitude constant, by confounding it with a compensating alteration in maximum temperature. For reasons such as this it is impossible to design experiments which unequivocally determine which characteristics of alternating temperatures are controlling germination responses.

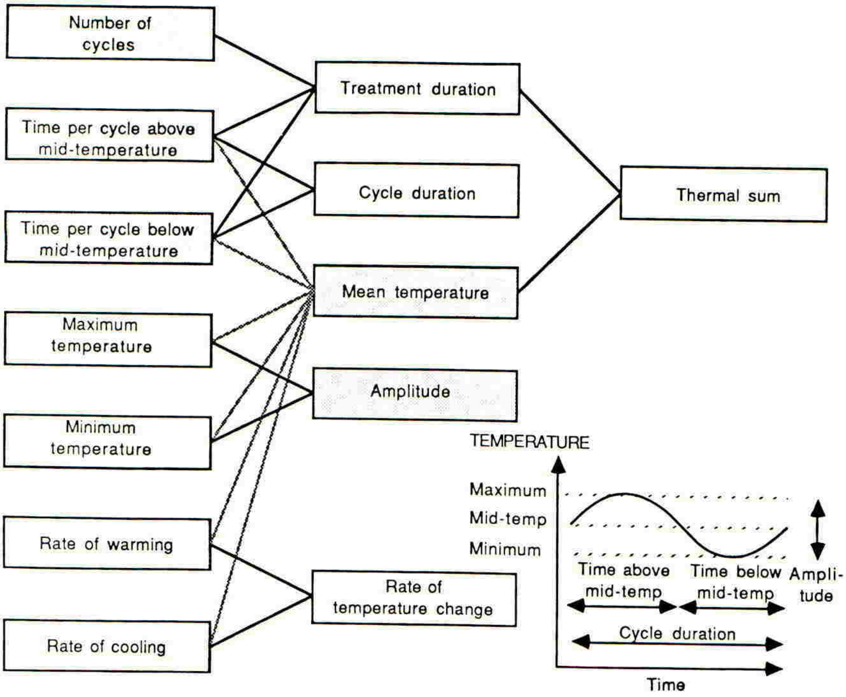


Fig. 2. Characteristics of alternating temperatures which might stimulate germination. Those characteristics thought to be important are shaded. Primary characteristics are shown in the left-hand column.

We believe the best solution to the problem is to carry out large experiments which include variations in many of the characteristics and to search for the simplest model which explains the results. Fig. 3 shows an interim stage in the process using experimental data on *Chenopodium album* obtained from a two-way thermogradient plate. Many responses are normally distributed amongst the seeds of a population and accordingly it is usually helpful to transform germination percentages to probit (or present the data on a probability scale, as has been done in Fig. 3). It then emerges that in constant temperatures there is a positive linear relation between temperature and probit percentage germination up to an optimum value, above which there is a negative linear relation. It is only at mean temperatures less than this constant-temperature optimum that alternating temperatures are stimulatory. In this region the stimulatory effect of alternating temperatures increases with increase in amplitude, nd the optimum mean temperature of alternating temperature regimes decreases with increase in amplitude. Thermoperiod (the relative time spent in the warmer and cooler

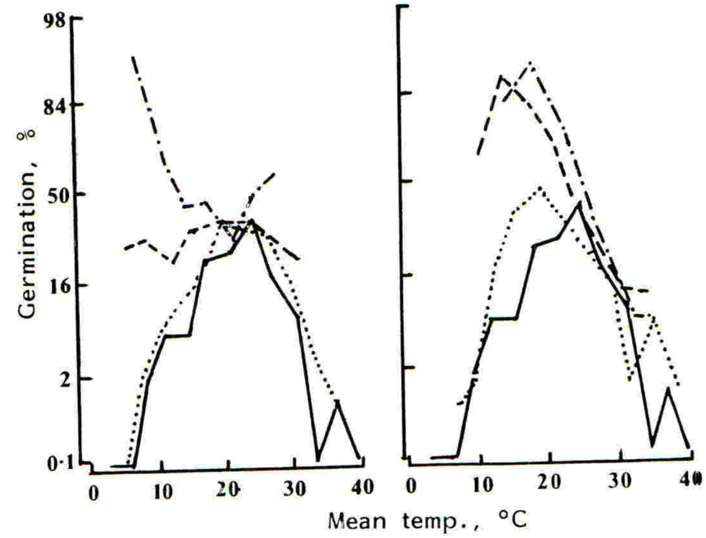


Fig. 3. Germination of *Chenopodium album* after 28 d of alternating temperature in thermoperiods when either 8 h in each day was spent at the warmer temperature (left) or 16 h (right). Temperature amplitude: —— 0° (constant temperatures); ······ 6.2°C; — — — 12.3°C; —·—· 18.5°C. (Murdoch & Roberts, previously unpublished.)

parts of the cycle) is also important: in *C. album*, for example (Fig. 3), it is clear that cycles with the longer period spent at the warmer temperature are generally more stimulatory at any given mean temperature and amplitude. But in *Chenopodium polyspermum* and *Rumex crispus* (Figs 5 and 6) it is clear that the converse is true. Apart from these differences in preferred thermoperiod, however, the general response pattern illustrated by Fig. 3 appears to be of wide application and, for example, applies equally well to the tropical grass *Panicum maximum* (unpublished data).

Light

It is now well established that the phytochrome system provides a mechanism which not only allows seeds to respond positively to light of appropriate quality (daylight) but also negatively to light filtered through a leaf canopy (Frankland & Taylorson 1983). This is controlled by the equilibrium ratio between the active and inactive forms of phytochrome, commonly referred to as the Low Energy Reaction. Thus most small seeds are provided with a sensor which contributes to their ability to germinate at or near the soil surface providing it is not covered by a dense leaf canopy.

In addition to this response, however, is the so-called High Irradiance Reaction in which light of almost any quality inhibits germination if applied at high irradiances for sustained periods. This may be due, at least in part, to rapid cycling of the alternative forms of the phytochrome pigment, but it is also possible that an additional pigment is involved (Frankland & Taylorson 1983). Recent work on several species of Gramineae has shown that there is an increase in germination with increase in daily photon dose of white light up to about 10^{-1} mol m^{-2} (Ellis *et al.* 1986*a*). The response is linear if the probit of percentage germination is plotted as a function of the logarithm of photon dose. As an example, the results for *Echinochloa turnerana* are shown (Fig. 4) in which it can be seen that

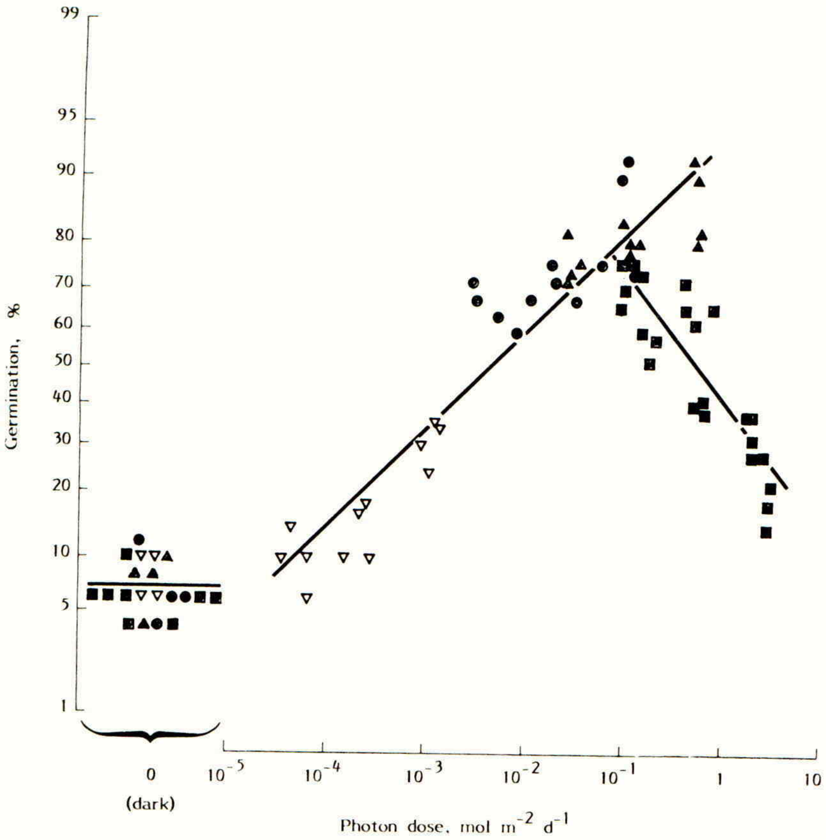


Fig. 4. Germination of *Echinochloa turnerana* after 7 d in alternating temperatures of 30 C (8 h)/20 (16 h) in response to photon dose in different photoperiods: ■ 24 h d^{-1}; ▲8 h d^{-1}; ● 1 h d^{-1}; ▽1 min d^{-1}. (From Ellis *et al.* 1986.)

a few seeds are stimulated to germinate at doses as low as 10^{-5} mol m^{-2} d^{-1}, but some require a minimum of 10^{-1} mol m^{-2} d^{-1}. Above this dose, however, some seeds are inhibited; the number inhibited increases with dose and a few require more than 10 mol m^{-2} d^{-1} to prevent germination. The negative response at doses above 10^{-1} mol m^{-2} d^{-1} is common in other species. Although in Fig. 4 the inhibitory effect is only shown in continuous light, data from other species suggests that normal photoperiods (≥8 h d^{-1}) are sufficient to inhibit germination when doses are of this magnitude (Ellis *et al.* 1986*a*, 1986*b*). If this is the case, then typical summer days in UK, when photon doses vary between $10^{2.2}$ and $10^{2.7}$ mol m^{-2} d^{-1}, are certainly sufficient to inhibit seeds exposed on the surface of the soil. The ecological significance of the High Irradiance Reaction has not been studied in any detail, but it may bestow an advantage in preventing seeds from germinating when bright sunshine could lead to rapid drying of the soil surface.

7C—1

INTERACTION OF ENVIRONMENTAL STIMULI

Laboratory experiments suggest that seeds seldom rely on a single environmental signal to stimulate germination. For example, light on its own seldom stimulates the germination of many seeds, but only does so in combination with alternating temperature or after stratification.

Figs 5 and 6 illustrate responses typical of many weed seeds to the effects of light, alternating temperatures, and nitrate ions investigated in 2^3 factorial experiments. Nitrate was included in these experiments because it is the only common inorganic ion in soil water which affects the germination of a wide range of species and, because of its distribution in the soil profile and in time, it could conceivably have some ecological significance. Its concentration is normally greater near the soil surface and at the beginning of the normal growing season - i.e. in spring in temperate climates and at the beginning of the rainy season in the tropics. Although nitrate frequently interacts with the other stimulatory factors, it generally has less influence than light or alternating temperatures, and its ecological significance is still a matter of speculation.

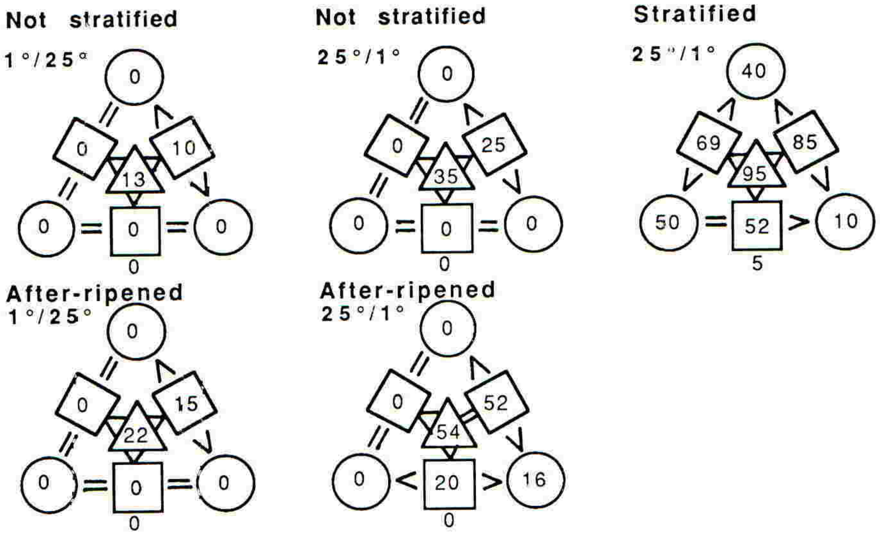


Fig. 5. Germination of *Chenopodium polyspermum* after 28 d in the presence or absence of light, 10^{-2} M KNO_3, and alternating temperatures (8 h/16 h thermoperiods; temperatures indicated on diagrams) in 2^3 factorial combination, before and after stratification (1°C for 4 weeks) or dry after-ripening at 1°C for 1 year). Results of single-factor treatments are shown in circles: light (top); alternating temperature (right); nitrate (left). Two-factor combinations are shown in rectangles between contributing single factors, and the three-factor combination in a triangle. Results of control treatment (dark, constant temperature, no nitrate) are shown below. (From Vincent & Roberts 1977.)

Fig. 5 shows that in *C. polyspermum* there is considerable variation in dormancy within a seed population and that there are a number of alternative routes to loss of dormancy. For example no seeds germinated in the presence of only one potentially stimulatory factor but, in the absence of stratification or after-ripening, some seeds responded to light + alternating temperatures and a few more responded when nitrate was added to this combination. Either stratification or dry after ripening markedly increased these responses but also enabled light, nitrate or alternating temperatures on their own to be stimulatory under some circumstances. Similar features are shown by *Rumex crispus* but with even more extreme first and second-order interactions (Fig. 6).

The results of these 2^3 factorial experiments show the importance of interactions but are of limited value since only one level of each potentially stimulatory factor is included. The next problem is to quantify the effects of interacting factors so that laboratory responses can be used to explain and predict field behaviour. A good start in this direction has been made in *Dactylis glomerata* (Probert *et al.*, 1985*a*, 1985*b*, 1986).

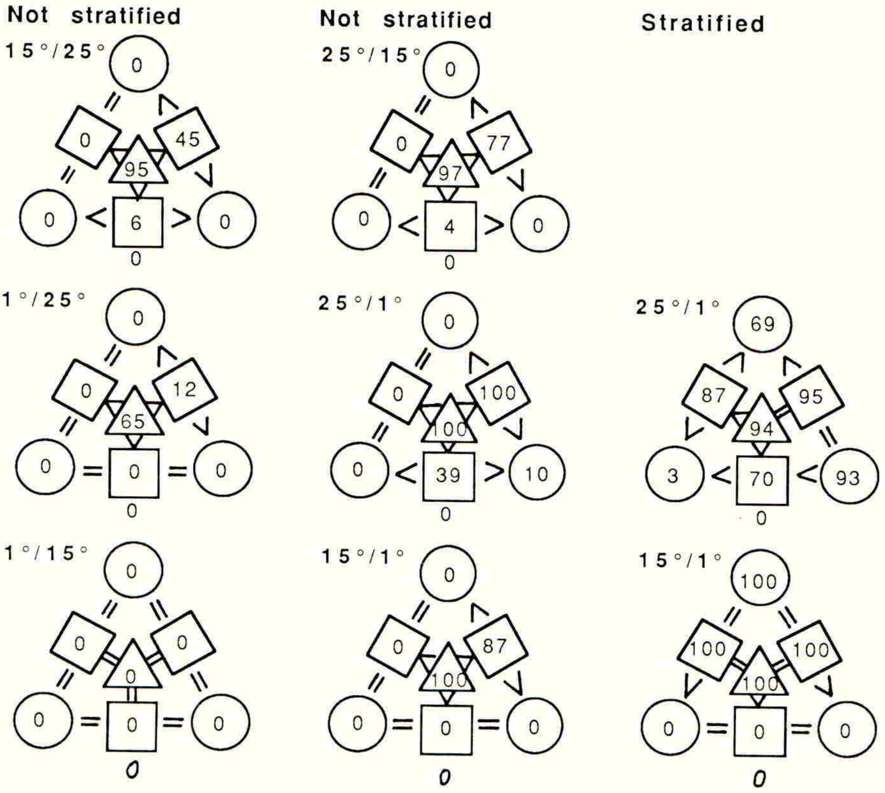


Fig. 6. Germination of *Rumex crispus* after 28 d before and after stratification. Further explanation as for Fig. 5. (From Vincent & Roberts, 1977.)

REFERENCES

Bewley, J.D.; Black, M. (1982) *Physiology and Biochemistry of Seeds in Relation to Germination*, Vol. 2, Berlin: Springer-Verlag, 375 pp.

Ellis, R.H.; Hong, T.D.; Roberts, E.H. (1986*a*) Quantal response of seed germination in *Brachiaria humidicola*, *Echinochloa turnerana*, *Eragrostis tef* and *Panicum maximum* to photon dose for the Low Energy Reaction and the High Irradiance Reaction. *Journal of Experimental Botany* 37, 742-753.

Ellis, R.H.; Hong, T.D.; Roberts, E.H. (1986*b*) The response of seeds of *Bromus sterilis* L. and *Bromus mollis* L. to white light of varying photon flux density and photoperiod. *New Phytologist* 104, 485-496.

Frankland, B.; Taylorson, R. (1983) Light control of seed germination. In: *Encyclopaedia of Plant Physiology, Vol. 16* W. Shropshire Jr and H. Mohr (Eds), Heidelberg: Springer-Verlag, pp. 428-456.

Probert, R.J.; Smith, R.D.; Birch, P. (1985) Germination responses to light and alternating temperatures in European population of *Dactylis glomerata* L. II. The genetic and environmental components of germination. *New Phytologist* 99, 317-322.

Probert, R.J.; Smith, R.D.; Birch, P. (1985*a*) Germination responses to light and alternating temperatures in European populations of *Dactylis glomerata* L. IV. The effects of storage. *New Phytologist* 101, 521-529.

Probert, R.J.; Smith, R.D.; Birch, P. (1985*b*) Germination responses to light and alternating temperatures in European populations of *Dactylis glomerata* L. V. The principle components of the alternating temperature requirement. *New Phytologist* 102, 133-142.

Roberts, E.H. (1972) Dormancy: a factor affecting survival in the soil. In: *Viability of Seeds* E.H. Roberts (Ed.), London: Chapman and Hall, pp. 321-359.

Roberts, E.H. (1988) Temperature and seed germination. In: *Plants and Temperature.* Society of Experimental Biology Symposium 42 (in press).

Totterdell, S.; Roberts, E.H. (1979) Effects of low temperatures on the innate dormancy and development of induced dormancy in seeds of *Rumex obtusifolius* L. and *Rumex crispus* L. *Plant, Cell and Environment* 2, 131-137.

Vincent, E.M.; Roberts, E.H. (1977) The interaction of light, nitrate and alternating temperature in promoting the germination of dormant seeds of common weed species. *Seed Science and Technology* 5, 659-670.

ENVIRONMENTALLY INDUCED CHANGES IN THE DORMANCY STATES OF BURIED WEED SEEDS

JERRY M. BASKIN, CAROL C. BASKIN

School of Biological Sciences, University of Kentucky

Lexington, KY 40506-0225, U.S.A.

ABSTRACT

Seeds of many species in the buried seed pool undergo changes in dormancy states. Conditions and factors of the soil environment that cause these changes include high and low temperatures, darkness, low levels of oxygen, high levels of carbon dioxide, low water potentials, nitrate, nitrite and ethylene. Vegetation effects changes in the dormancy states of seeds by altering light quality (decreased R/FR ratio) and decreasing the amplitude of diurnal temperature fluctuations on or near the soil surface, and through its influence on the soil chemical environment. Of the environmental factors that cause changes in the dormancy states of buried seeds in temperate regions, temperature is the most important one. A knowledge of the dormancy states in seeds may be useful in planning a strategy for weed control by chemicals that stimulate germination of buried seeds.

INTRODUCTION

According to Roberts (1981), "seed bank" means the reserves of viable seeds in the soil and on the soil surface. In cultivated fields, the numbers of buried seeds may be as high as 70,000 to 90,000 per m^2 in the upper 15 to 25 cm of soil (Roberts, 1981). Thus, from the agriculturalist's point of view, the need to understand the ecology of dormancy and germination of seeds in the soil seed bank is obvious.

A significant contribution to seed bank ecology was the demonstration that many buried seeds exhibit periodicities in their germination requirements, i.e., they are not in a continuous "germination-ready" state, even when exposed to light (Courtney, 1968; Schafer and Chilcote, 1970; Taylorson, 1970). The fact that buried seeds can change from endogenous to exogenous dormancy and back was included by Schafer and Chilcote (1969, 1970) in their conceptual model of the factors involved in the persistence and depletion of buried seeds. When Roberts (1972) modified the Schafer-Chilcote model, he recognized the three types of dormancy (innate, enforced, induced) suggested by Harper (1957).

It is important to realize that the model developed by Schafer and Chilcote (1969, 1970), and as modified by Roberts (1972), is for seeds that exhibit physiological dormancy. Physiological dormancy is one of the five types of seed dormancy recognized by Nikolaeva (1977), and it is due to low growth potential of the fully developed embryo. Seeds with physiological dormancy undergo changes in their dormancy state, and a high percentage of weed seeds exhibit this type of dormancy. Thus, many buried weed seeds undergo changes in their dormancy states. In some weedy species (e.g., those of the Leguminosae, Malvaceae and Geraniaceae), dormancy is due to the presence of an impermeable seed coat (physical dormancy), and hard seeds of a few species also have a physiologically dormant embryo (combination dormancy). Relatively few species (e.g., those of the Ranunculaceae and Umbelliferae) of arable land have morphological dormancy (i.e., an underdeveloped embryo that is not physiologically dormant) or morphophysiological dormancy (i.e., an underdeveloped embryo that is physiologically dormant).

To look at the changes in dormancy states that can occur in seeds with physiological dormancy, let us start with a freshly matured seed that is fully dormant (D)-i.e., one which will not germinate under any set of normal environmental conditions. As the dormant seed comes out of dormancy (afterripens), it exhibits a continuum of germination responses (Baskin and Baskin, 1985a), gradually acquiring the capacity to germinate over a wider and wider range of conditions until it becomes fully nondormant (ND), in which state it can germinate over the widest range of conditions possible for that seed. This transitional state between dormancy and nondormancy is known as conditional dormancy (CD), and there are many phases of it. If the afterripened, nondormant seed is prevented from germinating, it may re-enter dormancy. During re-entrance into dormancy, the seed will exhibit a continuum of germination responses in the opposite direction to those of afterripening. In addition to the annual D/CD/ND/CD/D cycle described above, seeds of some species have D/CD/ND/CD/ND, CD/ND/CD/D/CD/D or perhaps other cycles. Seeds of still other species are dormant or conditionally dormant at maturity, and they become nondormant and remain nondormant; they do not cycle (Baskin and Baskin, 1985b).

The purpose of this paper is to examine the environmental factors that cause changes in dormancy states in seeds with physiological dormancy. We will deal primarily with seeds buried in the soil because the majority of seeds in persistent seed banks are buried (Thompson and Grime, 1979).

ENVIRONMENTAL FACTORS CAUSING CHANGES IN DORMANCY STATES

Temperature

Some of the best examples of temperature-induced changes in dormancy states are found in buried seeds of annuals. Dormant and conditionally dormant seeds of obligate (germinate only in autumn) and facultative (germinate in autumn and in spring) winter annuals afterripen fully at high (25/15, 30/15, 35/20 C) summer temperatures, but they do not afterripen or only partially afterripen at low (5, 15/6 C) winter temperatures (Baskin and Baskin, 1986). In obligate winter annuals such as Lamium purpureum L. (Baskin and Baskin, 1984a), low winter temperatures induced nondormant seeds into dormancy, while spring and autumn (15/6, 20/10 C) temperatures did not. Nondormant seeds of facultative winter annuals such as *Lamium amplexicaule* L. (Baskin and Baskin, 1984b) are induced into conditional dormancy by low winter temperatures, but not by spring and autumn temperatures. However, exposing nondormant seeds of the facultative winter annual *Capsella bursa-pastoris* (L.) Medic. sequentially to simulated March (15/6), April (20/10) and May (30/15 C) thermoperiods caused them to enter into a deeper phase of conditional dormancy than seeds kept continuously at 5 C. Seeds kept at 30/15 C did not enter conditional dormancy at all (Baskin and Baskin, unpubl.).

Dormant seeds of summer annuals such as *Ambrosia artemisiifolia* L. and *Polygonum pensylvanicum* L. that germinate in spring afterripen fully at low (5, 15/6) winter temperatures but little, or none, at high (25/15, 30/15, 35/20 C) summer temperatures (Baskin and Baskin, in press). The same requirements for afterripening of dormant seeds are found in *Panicum dichotomiflorum* Michx. (Baskin and Baskin, unpubl.), which retains the capacity to germinate throughout the growing season (Baskin and Baskin, 1983). A portion of the fresh seeds of some spring- and summer-germinating summer annuals such as *Chenopodium album* L. and *Amaranthus hybridus* L. exhibit conditional dormancy, germinating at 25/15, 30/15 and/or 35/20 C. While seeds of these two species afterripen best at low (5 and/or 15/6 C) temperatures, they also afterripen some at high temperatures. At high temperatures, the seeds rapidly gain the ability to germinate to high percentages at high, but not at low temperatures.

The temperatures that induce seeds of summer annuals into dormancy are correlated with germination phenology of the species. Nondormant seeds of spring-germinating summer annuals such as *Ambrosia artemisiifolia* (Baskin and Baskin, 1980) are induced into dormancy by increasing temperatures in the field in late spring-early summer. In some spring/summer germinating summer annuals such as *Panicum dichotomiflorum* (Table 1), seeds begin to enter conditional dormancy in early to mid summer (8 weeks at 30/15 C), and the depth of conditional dormancy increases as seeds are exposed to October (20/10) and November (15/6 C) temperatures during autumn. However, the depth of conditional dormancy in seeds kept at 30/15 for 20 weeks does not differ from that in seeds exposed sequentially to 30/15 for 12 weeks, 20/10 for 4 weeks and 15/6 C for 4 weeks. In seeds of other summer annuals such as *Amaranthus hybridus* that retain the capacity to germinate throughout the growing season, neither summer (30/15) nor autumn (20/10, 15/6 C) temperatures induce nondormant seeds into conditional dormancy (Baskin and Baskin, unpubl.).

TABLE 1

Germination percentages (mean ± SE) of nondormant buried seeds of <u>Panicum dichotomiflorum</u> exposed sequentially to September (30/15), October (20/10) and November (15/6 C) thermoperiods.

	Test temperatures (C)			
Treatment	20/10	25/15	30/15	35/20
Nondormant seeds	100	100	100	100
Placed at 30/15 C				
4 weeks	99±1	87±1	100	100
8	47±2	99±1	100	100
12	7±3	85±5	100	100
16	0	32±3	96±2	88±2
20	1±1	8±5	66±4	77±2
30/15 C (12 w) → 20/10 C				
4	1±1	45±2	98±2	95±2
8	0	16±3	61±3	77±2
30/15 C (12 w) → 20/10 (4 w) → 15/6 C				
4	1±1	12±1	83±7	99±1

Buried seeds of biennials and of monocarpic and polycarpic perennials have not received the same amount of attention as those of annuals; thus, we do not know much about changes in their dormancy states. Buried seeds of the monocarpic perennials <u>Verbascum thapsus</u> L. and <u>V</u>. <u>blattaria</u> L. undergo an annual CD/ND/CD cycle (Baskin and Baskin, 1981). Vanlerberghe and Van Assche (1986) demonstrated that seeds of <u>V</u>. <u>thapsus</u> show increases and decreases in degree of dormancy when incubated at high (20 C) and low (4 C) temperatures, respectively. They showed conclusively that the changes in dormancy states were due to temperature and not to some other factor(s) associated with the burial environment. Seeds of various monocarpic and polycarpic perennials sown in soil that was plowed regularly exhibited periodicity of germination (<u>e</u>.<u>g</u>., Roberts, 1979; Roberts and Chancellor, 1979), implying that seeds undergo changes in their dormancy states.

<u>Other factors of the soil environment</u>

Although temperature is the major environmental factor causing changes in the dormancy state of buried seeds in temperate regions, it does not operate independently, and it is not the only factor that can cause changes in dormancy states. Temperature frequently interacts with other environmental factors in the induction of dormancy. Inhibition of germination during the season(s) when temperatures are favorable for germination of nondormant seeds is a prerequisite for dormancy induction. Many nondormant seeds in the seed bank have a light requirement for germination (Wesson and Wareing, 1969). Thus, since soil attenuates light very effectively (Tester and Morris, 1987), seeds buried more than a few millimeters deep are in complete darkness and can not germinate. Although the red/far-red photon flux ratio is lowered as light passes through soil, soil-filtered light has been shown to stimulate rather than inhibit germination (Tester and Morris, 1987). Other factors that may prevent germination of buried seeds until they are induced into dormancy by temperature are oxygen and carbon dioxide levels in the soil (Popay and Roberts, 1970a), volatile metabolites from the seeds themselves (Holm, 1972), low soil water potential, (Oomes and Elberse, 1976), flooding (Pons, 1982), allelopathic influences of vegetation (Jackson and Willemsen, 1976) and a low amplitude of diurnal temperature fluctuations (Thompson and Grime, 1983).

Darkness is a factor associated with the burial environment that has been shown to cause a change in the dormancy state of seeds; however, its effects are temperature dependent (*e*.*g*., Arnold, 1973). Imbibed seeds of *Lactuca sativa* L. (Powell *et al*., 1983), *Rumex crispus* L. (Samimy and Khan, 1983a), *Kalanchoe blossfeldiana* v. Poelln. (Rethy *et al*., 1983) and *Lamium amplexicaule* (Taylorson and Hendricks, 1976) held in darkness were induced into conditional dormancy -*i*.*e*., made light-requiring for germination. In *R*. *crispus*, the degree and rate of dormancy development increased with temperature, with the maximum speed of induction occurring around 25 C, and in *L*. *amplexicaule* seeds held in darkness at 15 and 25 C showed a greater loss of sensitivity to the plant hormone gibberellic acid than those held at 5 C. Nondormant buried seeds of *Ambrosia artemisiifolia* subjected sequentially to increasing temperature regimes of 5, 15/6, 20/10 and 30/15 C entered secondary dormancy, whereas those held continuously at 5 C did not enter secondary dormancy (Baskin and Baskin, 1980).

It generally is agreed that oxygen is required for the breaking and induction of dormancy in seeds. Nondormant seeds of *Ambrosia trifida* L. embedded in agar, which restricted oxygen supply, developed dormancy slower than seeds exposed to air (Davis, 1930). Oxygen also is required for dormancy induction in seeds of *Lactuca sativa* (Vidaver and Hsiao, 1975) and *Rumex crispus* (Le Deunff, 1973). Seeds have been shown to require oxygen to afterripen. For example, seeds of. *A*. *artemisiifolia* stratified at 5 C in nitrogen failed to afterripen, whereas those stratified in air afterripened normally (Brennan *et al*., 1978). In the aquatic species *Scirpus juncoides* Roxb. (Pons and Schroder, 1986) and *Zizania aquatica* L. (Simpson, 1966), low oxygen tensions promoted afterripening. Germination of dormant seeds of *Trifolium subterraneum* L. (seeds have a hard seed coat and a physiologically dormant embryo) is greatly improved if imbibed seeds are stored at low oxygen concentrations for several days and then transferred to either normal air or 100% oxygen (Ballard and Grant Lipp, 1969).

Evidence that levels of carbon dioxide in the soil influence changes in dormancy states of seeds is limited. Embryo dormancy in imbibed seeds of *Trifolium subterraneum* was broken by 0.3 to 5.0% (by volume) carbon dioxide (Ballard, 1958), and an increase in carbon dioxide concentration promoted afterripening of dormant seeds of *Polygonum scandens* L. (Justice, 1941). The levels of carbon dioxide in the soil may play a secondary role in overcoming dormancy of some seeds. In seeds of *Lactuca sativa* (Negm *et al*., 1973), *Xanthium pensylvanicum* Wallr. (Katoh and Esashi, 1975) and *Spergula arvensis* L. (Jones and Hall, 1979), dormancy is broken by ethylene only if carbon dioxide is present.

Soil water potential *via* its effects on tissue water potential can cause changes in dormancy states of some seeds. Seeds of *Corylus avellana* L. are only partially dormant at maturity but become completely dormant during dry storage of intact fruits (Shannon *et al*., 1983). Drying partially reimposed dormancy in stratified seeds of *Pyrus* spp. (Westwood and Bjornstad, 1968), and stratified seeds of *Polygonum* spp. entered dormancy when stored dry at room temperature (Justice, 1941). However, air drying stratified seeds of *Ambrosia artemisiifolia* did not cause them to become dormant (Bazzaz, 1970). Low water potentials obtained with solutions of polyethylene glycol 6000 have been used to induce dormancy in seeds of *Chenopodium bonus-henricus* L. (-8.6 bars) (Khan and Karssen, 1980) and *Rumex crispus* (-15.7 bars) (Samimy and Khan, 1983a). Alternate wetting and drying at alternating temperatures broke dormancy in seeds of *R. crispus*, while the same treatments at constant temperatures were ineffective (Vincent and Cavers, 1978). Depth of dormancy was reduced in seeds of *Lactuca sativa* and *Phacelia tanacetifolia* Benth. when substrate hydration level was low during exposure of seeds to environmental conditions that normally induce dormancy (McDonough, 1968). In *Sisymbrium officinale* (L.) Scop., a higher percentage of the seeds entered dormancy at high than at low soil moisture (Karssen, 1980/81a).

Nitrate and nitrite ions are present in the soil and have been shown to break dormancy and stimulate germination in seeds of many species (*e.g.*, Hendricks and Taylorson, 1974). In *Sisymbrium officinale* nitrate is required for afterripening of seeds even at low (2 C) temperatures, and in both *S. officinale* and *Polygonum persicaria* L. the presence of nitrate prevents induction of nondormant seeds into dormancy at 2 C (Karssen, 1980/81b). Nitrate promoted germination of dormant seeds of *Avena fatua* L. in darkness, but the stimulatory action decreased with increases in temperature (Saini *et al*., 1985a). In dormant seeds of *Chenopodium album*, the dormancy breaking action of ethylene was dependent on the availability of nitrate (Saini *et al*., 1986); however, the presence of nitrate masked the interaction between light and ethylene (Saini, 1985b). Popay and Roberts (1970b) observed a seasonal increase in the level of nitrate in the soil which was correlated with a peak of germination in *Capsella bursa-pastoris*. However, applications of nitrates to the soil have been shown to stimulate germination in seeds of some species (Sexsmith and Pittman, 1963) but not in others (Hurtt and Taylorson, 1986). In seeds of some species, nitrite is more effective than nitrate in breaking dormancy (Cohn *et al*., 1983).

VEGETATION EFFECTS ON CHANGES IN DORMANCY STATES

Sunlight filtered through leaves has a low red/far-red photon flux ratio (R/FR) (Smith, 1982), and thus it inhibits the germination of seeds of many species (*e.g.*, Gorski, 1975; Gorski *et al.*, 1977; Fenner, 1980a,b). Significantly, Gorski (1975) showed that dark-germinating *Lactuca sativa* seeds exposed to leaf-filtered light for a few days became light requiring in the usual phytochrome mediated manner, and Fenner (1980b) showed the same thing for seeds of *Bidens pilosa* L. In *Cirsium palustre* (L.) Scop. (Pons, 1983) and *Plantago major* L. ssp. *major* (Pons, 1986), however, a low R/FR ratio was much less effective in inhibiting stratified than nonstratified seeds, and in *Plantago major* ssp. *major* the effectiveness of a low R/FR ratio in inhibiting germination was dependent upon other environmental factors, including temperature, nitrate and osmotic potential (Pons, 1986). Germination of the seeds of some species is not inhibited by a low R/FR ratio (Gorski *et al.*, 1977; Fenner, 1980a). In fact, in seeds of some species FR has been shown to promote germination (Downs, 1964) and R to inhibit it (Hilton, 1984).

In addition to altering the quality of sunlight, vegetation can play other, often indirect, roles in causing dormancy changes in seeds in the seed bank. The amplitude of daily temperature fluctuations in the surface layer of soil is considerably less under plant canopies than in adjacent openings (Vazquez-Yanes and Orozco-Segovia, 1982), and thus germination of seeds with impermeable coats may be prevented. High daily fluctuations of temperature can overcome dormancy by rupturing the seed coat in many hard seeded species (Quinlivan, 1971; Vazquez-Yanes and Orozco-Segovia, 1982). It was noted above that nitrate and nitrite break dormancy in seeds of many species. Thus, since the activities of plant roots and soil microbes help determine the concentrations of these ions in the soil, vegetation may directly or indirectly cause a change in the dormancy states of buried seeds. Plants produce ethylene (Smith, 1976) which alone (Schonbeck and Egley, 1980) or in combination with carbon dioxide (Negm *et al.*, 1973) or nitrate (Saini *et al.*, 1986) stimulates breaking of dormancy in seeds of some species. The plant root exudate strigol stimulates germination of the obligate root parasitic weed *Striga asiatica* (L.) Ktze. (Cook *et al.*, 1966). Respiration of plant roots undoubtedly contributes to decreased oxygen and increased carbon dioxide concentration in the soil atmosphere, and these changes may cause dormancy break in some seeds (*e.g.*, Justice, 1941; Ballard and Grant Lipp, 1969).

SIGNIFICANCE FOR WEED POPULATION MANAGEMENT

Since (1) there is a large reserve of viable seeds in most agricultural soils, only a fraction of which may germinate in any one year, and (2) conventional weed control practices do not kill ungerminated seeds, lack of germination of buried dormant, conditionally dormant and nondormant seeds is a major reason that weeds are so difficult to control. Learning how to break dormancy and to stimulate germination of these buried seeds by application of chemicals to the soil would be a major technological advancement for weed control (Chancellor, 1981).

It has been demonstrated that the sensitivity of seeds to light and plant growth regulators gradually decreases as they enter dormancy (Bewley, 1980), and it is supposed that the seeds' sensitivity to these factors gradually increases as they come out of dormancy. Thus, information on the dormancy states of seeds in the soil seed pool would allow one to apply chemicals to the soil when they would be most efficient in stimulating seeds to germinate, or when entrance into dormancy would be prevented. A good example of using chemicals to control the dormancy state of weed seeds, and thereby causing a reduction in the number of buried seeds in the soil, is the study by Samimy and Khan (1983b) on Ambrosia artemisiifolia. Application of a mixture of the plant growth regulators kinetin, ethephon (ethylene releasing) and gibberellin A_4 + A_7 to soil containing seeds of A. artemisiifolia prevented nondormant seeds from entering dormancy in spring. By the second spring, only 20% of the seeds in the treated soil were viable, whereas in the nontreated soil 89% were viable. Apparently, the nondormant seeds were lost from the seed pool through decay and germination (Samimy and Khan, 1983b).

REFERENCES

Arnold, S.M. (1973) Interactions of light and temperature on the germination of Plantago maritima L. New Phytologist 72, 583-593.

Ballard, L.A.T. (1958) Studies of dormancy in the seeds of subterranean clover (Trifolium subterraneum L.). I. Breaking of dormancy by carbon dioxide and by activated carbon. Australian Journal of Biological Sciences 11, 246-260.

Ballard, L.A.T.; Grant Lipp, A.E. (1969) Studies of dormancy in the seeds of subterranean clover (Trifolium subterraneum L.). III. Dormancy breaking by low concentrations of oxygen. Australian Journal of Biological Sciences 22, 279-288.

Baskin, J.M.; Baskin, C.C. (1980) Ecophysiology of secondary dormancy in seeds of Ambrosia artemisiifolia. Ecology 61, 475-480.

Baskin, J.M.; Baskin, C.C. (1981) Seasonal changes in germination responses of buried seeds of Verbascum thapsus and V. blattaria and ecological implications. Canadian Journal of Botany 59, 1769-1775.

Baskin, J.M.; Baskin, C.C. (1983) Seasonal changes in the germination responses of Fall panicum to temperature and light. Canadian Journal of Plant Science 63, 973-979.

Baskin, J.M.; Baskin, C.C. (1984a) Role of temperature in regulating timing of germination in soil seed reserves of Lamium purpureum L. Weed Research 24, 341-349.

Baskin, J.M.; Baskin, C.C. (1984b) Effect of temperature during burial on dormant and non-dormant seeds of Lamium amplexicaule L. and ecological implications. Weed Research 24, 333-339.

Baskin, J.M.; Baskin, C.C. (1985a) The annual dormancy cycle in buried weed seeds: A continuum. BioScience 35, 492-498.

Baskin, J.M.; Baskin, C.C. (1985b) Does seed dormancy play a role in the germination ecology of Rumex crispus? Weed Science 33, 340-343.

Baskin, J.M.; Baskin, C.C. (1986) Temperature requirements for after-ripening in seeds of nine winter annuals. Weed Research 26, 375-380.

Baskin, J.M.; Baskin, C.C. Temperature requirements for after ripening in buried seeds of four summer annual weeds. Weed Research, in press.

Bazzaz, F.A. (1970) Secondary dormancy in the seeds of the common ragweed Ambrosia artemisiifolia. Bulletin of the Torrey Botanical Club 97, 302-305.

Bewley, J.D. (1980) Secondary dormancy (skotodormancy) in seeds of lettuce (Lactuca sativa cv. Grand Rapids) and its release by light, gibberellic acid and benzyladenine. Physiologia Plantarum 49, 277-280.

Brennan, T.; Willemsen, R.; Rudd, T; Frenkel, C. (1978) Interaction of oxygen and ethylene in the release of ragweed seeds from dormancy. Botanical Gazette 139, 46-49.

Chancellor, R.J. (1981) The manipulation of weed behavior for control purposes. Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences 295, 103-110.

Cohn, M.A.; Butera, D.L.; Hughes, J.A. (1983) Seed dormancy in red rice. III. Response to nitrate, nitrite and ammonium ions. Plant Physiology 73, 381-384.

Cook, C.E.; Whichard, L.P.; Turner, B.; Wall, M.E.; Egley, G.H. (1966) Germination of witchweed (Striga lutea Lour.): Isolation and properties of a potent stimulant. Science 154, 1189-1190.

Courtney, A.D. (1968) Seed dormancy and field emergence in Polygonum aviculare. Journal of Applied Ecology 5, 675-684.

Davis, W.E. (1930) Primary dormancy, after-ripening, and the development of secondary dormancy in embryos of Ambrosia trifida. American Journal of Botany 17, 58-76.

Downs, R.J. (1964) Photocontrol of germination of the seeds of Bromeliaceae. Phyton (Argentina) 21, 1-6.

Fenner, M. (1980a) Germination tests on thirty-two east African weed species. Weed Research 20, 135-138.

Fenner, M. (1980b) The induction of a light requirement in Bidens pilosa seeds by leaf canopy shade. New Phytologist 84, 103-106.

Gorski, T. (1975) Germination of seeds in the shadow of plants. Physiologia Plantarum 34, 342-346.

Gorski, T.; Gorska K.; Nowicki, J. (1977) Germination of seeds of various herbaceous species under leaf canopy. Flora 166, 249-259.

Harper, J.L. (1957) The ecological significance of dormancy and its importance in weed control. Proceedings of the International Congress on Crop Protection 4, 415-420.

Hendricks, S.B.; Taylorson, R.B. (1974) Promotion of seed germination by nitrate, nitrite, hydroxylamine, and ammonium salts. Plant Physiology 54, 304-309.

Hilton, J.R. (1984) The influence of temperature and moisture status on the photoinhibition of seed germination in *Bromus sterilis* L. by the far-red absorbing form of phytochrome. *New Phytologist* *97*, 369-374.

Holm, R.E. (1972) Volatile metabolites controlling germination in buried weed seeds. *Plant Physiology* *50*, 293-297.

Hurtt, W.; Taylorson, R.B. (1986) Chemical manipulation of weed emergence. *Weed Research* *26*, 259-267.

Jackson, J.R.; Willemsen, R.W. (1976) Allelopathy in the first stages of secondary succession on the piedmont of New Jersey. *American Journal of Botany* *63*, 1015-1023.

Jones, J.F.; Hall, M.A. (1979) Studies on the requirement for carbon dioxide and ethylene for germination of *Spergula arvensis* seeds. *Plant Science Letters* *16*, 87-93.

Justice, O.L. (1941) A study on dormancy in seeds of *Polygonum*. *Cornell University Agricultural Experiment Station Memoir 235*.

Karssen, C.M. (1980/81a) Environmental conditions and endogenous mechanisms involved in secondary dormancy of seeds. *Israel Journal of Botany* *29*, 45-64.

Karssen, C.M. (1980/81b) Patterns of change in dormancy during burial of seeds in soil. *Israel Journal of Botany* *29*, 65-73.

Katoh, H.; Esashi, Y. (1975) Dormancy and impotency of cocklebur seeds I. CO_2, C_2H_4, O_2 and high temperatures. *Plant and Cell Physiology* *16*, 687-696.

Khan, A.A.; Karssen, C.M. (1980) Induction of secondary dormancy in *Chenopodium* *bonus*-*henricus* L. seeds by osmotic and high temperature treatments and its prevention by light and growth regulators. *Plant Physiology* *66*, 175-181.

Le Deunff, M.Y. (1973) Interactions entre l'oxygene et la lumiere dans la germination et l'induction d'une dormance secondaire chez les semences de *Rumex* *crispus* L. *Comptes Rendus hebdomadaires des Seances de l'Academie des Sciences*. *Paris*. (*Series D*) *276*, 2381-2384.

McDonough, W.T. (1968) Secondary dormancy in seeds: Effects of substrate hydration. *Botanical Gazette* *129*, 361-364.

Negm, F.B.; Smith, O.E.; Kumamoto, J. (1973) The role of phytochrome in an interaction with ethylene and carbon dioxide in overcoming lettuce seed thermodormancy. *Plant Physiology* *51*, 1089-1094.

Nikolaeva, M.G. (1977) Factors controlling the seed dormancy pattern. pp. 51-74. In: A.A. Khan (ed.). The physiology and biochemistry of seed dormancy and germination. North-Holland Publishing Co, Amsterdam, New York and Oxford.

Oomes, M.J.M.; Elberse, W. Th. (1976) Germination of six grassland herbs in microsites with different water contents. *Journal of Ecology* *64*, 745-755.

Pons, T.L. (1982) Factors affecting weed seed germination and seedling growth in lowland rice in Indonesia. *Weed* *Research* *22*, 155-161.

Pons, T.L. (1983) Significance of inhibition of seed germination under the leaf canopy in ash coppice. *Plant, Cell and Environment* *6*, 385-392.

Pons, T.L. (1986) Response of *Plantago* *major* seeds to the red/far-red ratio as influenced by other environmental factors. *Physiologia* *Plantarum*. *68*: 252-258.

Pons, T.L.; Schroder, H.F.J.M. (1986) Significance of temperature fluctuation and oxygen concentration for germination of the rice field weeds *Fimbristylis littoralis* and *Scirpus juncoides*. *Oecologia 68*, 315-319.

Popay, A.I.; Roberts, E.H. (1970a) Factors involved in the dormancy and germination of *Capsella bursa-pastoris* (L.) Medik. and *Senecio vulgaris* L. *Journal of Ecology 58*, 103-122.

Popay, A.I.; Roberts, E.H. (1970b) Ecology of *Capsella bursa-pastoris* (L.) Medik. and *Senecio vulgaris* L. in relation to germination behaviour. *Journal of Ecology 58*, 123-139.

Powell, A.D.; Leung, D.W.M.; Bewley, J.D. (1983) Long-term storage of dormant Grand Rapids lettuce seeds in the imbibed state: Physiological and metabolic changes. *Planta 159*, 182-188.

Quinlivan, B.J. (1971) Seed coat impermeability in legumes. *Journal of the Australian Institute of Agricultural Science 37*, 283-295.

Rethy, R.; Dedonder, A.; Fredericq, H.; De Greef, J. (1983) Factors affecting the induction and release of secondary dormancy in *Kalanchoe* seeds. *Plant, Cell and Environment 6*, 731-738.

Roberts, E.H. (1972) Dormancy: A factor affecting seed survival in soil. pp. 321-359. In: E.H. Roberts (ed.). Viability of seeds. Syracuse University Press, Syracuse, New York.

Roberts, H.A. (1979) Periodicity of seedling emergence and seed survival in some Umbelliferae. *Journal of Applied Ecology 16*, 195-201.

Roberts, H.A. (1981) Seed banks in soils. *Advances in Applied Biology 6*, 1-55.

Roberts, H.A.; Chancellor, R.J. (1979) Periodicity of seedling emergence and achene survival in some species of *Carduus*, *Cirsium* and *Onopordum*. *Journal of Applied Ecology 16*, 641-647.

Saini, H.S.; Bassi, P.K.; Spencer, M.S. (1985a) Interactions among ethephon, nitrate, and after-ripening in the release of dormancy of wild oat (*Avena fatua*) seed. *Weed Science 34*, 43-47.

Saini, H.S.; Bassi, P.K.; Spencer, M.S. (1985b) Seed germination in *Chenopodium album* L.: Further evidence for the dependence of the effects of growth regulators on nitrate availability. *Plant, Cell and Environment 8*, 707-711.

Saini, H.S.; Bassi, P.K.; Spencer, M.S. (1986) Use of ethylene and nitrate to break seed dormancy of common lambsquarters (*Chenopodium album*). *Weed Science 34*, 502-506.

Samimy, C.; Khan, A.A. (1983a.) Secondary dormancy, growth-regulator effects, and embryo growth potential in curly dock (*Rumex crispus*) seeds. *Weed Science 31*, 153-158.

Samimy, C.; Khan, A.A. (1983b) Effect of field application of growth regulators on secondary dormancy of common ragweed (*Ambrosia artemisiifolia*) seeds. *Weed Science 31*, 299-303.

Schafer, D.E.; Chilcote, D.O. (1969) Factors influencing persistence and depletion in buried seed populations. I. A model for analysis of parameters of buried seed persistence and depletion. *Crop Science 9*, 417-419.

Schafer, D.E.; Chilcote, D.O. (1970) Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. Crop Science 10, 342-345.

Schonbeck, M.W.; Egley, G.H. (1980) Redroot pigweed (*Amaranthus retroflexus*) seed germination responses to afterripening, temperature, ethylene, and some other environmental factors, Weed Science 28, 543-548.

Sexsmith, J.J.; Pittman, U.J. (1963) Effect of nitrogen fertilizers on germination and stand of wild oats. Weeds 11, 99-101.

Shannon, P.R.M.; Jeavons, R.A.; Jarvis, B.C. (1983) Light-sensitivity of hazel seeds with respect to the breaking of dormancy. Plant and Cell Physiology 24, 933-936.

Simpson, G.M. (1966) A study of germination in the seed of wild rice (*Zizania aquatica*). Canadian Journal of Botany 44, 1-9.

Smith, A.M. (1976) Ethylene in soil biology. Annual Review of Phytopathology 14, 53-73.

Smith, H. (1982) Light quality, photoperception, and plant strategy. Annual Review of Plant Physiology 33, 481-518.

Taylorson, R.B. (1970) Changes in dormancy and viability of weed seeds in soils. Weed Science 18, 265-269.

Taylorson, R.B.; Hendricks, S.B. (1976) Interactions of phytochrome and exogenous gibberellic acid on germination of *Lamium amplexicaule* L. seeds. Planta 132, 65-70.

Tester, M.; Morris, C. (1987) The penetration of light through soil. Plant, Cell and Environment 10, 281-286.

Thompson, K.; Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67, 893-921.

Thompson, K.; Grime, J.P. (1983) A comparative study of germination responses to diurnally-flunctuating temperatures. Journal of Applied Ecology 20, 141-156.

Vanlerberghe, K.A.; Van Assche, J.A. (1986) Dormancy phases in seeds of *Verbascum thapsus* L. Oecologia 68, 479-480.

Vasquez-Yanes, C., Orozco-Segovia, A. (1982) Seed germination of a tropical rain forest pioneer tree (*Heliocarpus donnell-smithii*) in response to diurnal fluctuation of temperature. Physiologia Plantarum 56, 295-298.

Vidaver, W.; Hsaio, A.I. (1975) Secondary dormancy in light-sensitive lettuce seeds incubated anaerobically or at elevated temperature. Canadian Journal of Botany 53, 2557-2560.

Vincent, E.M.; Cavers, P.B. (1978) The effects of wetting and drying on the subsequent germination of *Rumex crispus*. Canadian Journal of Botany 56, 2207-2217.

Wesson, G.; Wareing, P.F. (1969) The role of light in the germination of naturally occurring populations of buried weed seeds. Journal of Experimental Botany 63, 402-413.

Westwood, M.N.; Bjornstad, H.O. (1968) Chilling requirements of dormant seeds of 14 pear species as related to their climatic adaptation. Proceedings of the American Society of Horticultural Science 92, 141-149.

SURVIVAL AND FATE OF WEED SEED POPULATIONS : INTERACTION WITH CULTURAL PRACTICE

R.J. FROUD-WILLIAMS

Department of Agricultural Botany, Plant Science Laboratories, University of Reading, Whiteknights, Reading, Berks, U.K.

ABSTRACT

Factors affecting the fate and survival of weed seeds following dissemination and the influence of cultural practice on weed seed persistence are discussed. Particular emphasis is given to the fate of seeds post-harvest, as influenced by soil disturbance and depth of burial. Consideration is also given to the effect of other agronomic factors on seed decline, including crop rotation and use of herbicides. The seed population dynamics of three major annual grass-weeds Avena fatua, Alopecurus myosuroides and Bromus sterilis are compared in relation to cultivation and straw-disposal regimes. It is concluded that, although of great importance to the success of annual broad-leaved weeds, the production of seeds of potentially long-lifespan is of lesser importance to the success of annual grass-weeds.

INTRODUCTION

The ecological roles of seeds are i) to carry species to new habitats, ii) to provide resources for initial growth and iii) to enable the offspring to survive unfavorable conditions for growth. Successful regeneration depends on the dispersal of seeds to situations suitable for germination and establishment. Situations where such conditions may be met are referred to as 'safe-sites' (Harper 1977). A 'safe-site' may be envisaged as providing the necessary stimuli required for the breakage of dormancy, the conditions required for the germination process to proceed and the resources which are consumed during the course of germination and establishment. In addition a 'safe-site' should be free from specific hazards such as predators, pathogens, competitors and allelochemicals. Although the size of a single species population is ultimately dependent on the seed supply, it is initially determined by the availability of 'safe-sites'.

The size of a seed population on a soil surface for a given area in time depends on i) the rate of recruitment from seed rain, ii) rate of emigration and immigration of seeds from the soil profile and surface surrounding area iii) rate of germination and iv) rate of loss through seed mortality and predation. Clearly any discussion of the dynamics of seed populations must concern itself with the parameters of such a flux. In a recent essay on seed demography it is suggested that the fate of a given plant population may be decided by the pattern of mortality exhibited by its seeds and that losses through seed mortality greatly exceed losses at any other stage of plant development (Cavers 1983).

LOSSES FROM THE SOIL SURFACE

Following dissemination, retention of seeds on the soil surface may be of remarkably short duration, even in the absence of cultivation. Seeds do not necessarily remain where they land after dispersal. The hygroscopic awns of grasses many serve to facilitate lateral seed movement into suitable microsites for germination, although, the presence of soil cracks may prove essential to effect self burial (Stamp 1984, Somody et al 1985). By means of mark and recapture technique, Mortimer was able to show that seed losses from the soil surface during the space of one year may be considerable, many of which become buried (Mortimer, 1976). Opportunities for seed burial were high for Poa annua (50%) and Plantago lanceolata (30%) but less likely for Holcus lanatus (13%) and Dactylis glomerata (8%). Thus, whereas 37% of H. lanatus gave rise to seedlings in the year of sowing, only 7% of P. annua produced seedlings. In general the probability of burial increased with habitat disturbance and invertebrate activity. The rate of seed loss was substantially reduced in a closed sward. Similarly, Williams, (1984) monitoring changes in the size and composition of the seed bank beneath permanent pasture over a period of three years, concluded, that in the absence of grazing the chances of seeds becoming permanently incorporated were slight. However, when plots were mown infrequently, allowing considerable seed shed, numbers of Cerastium fontanum ssp glabrescens showed a marked transient increase while approximately 20% of Agrostis capillaris became more permanently incorporated.

McRill (1974) has implicated earthworms in the incorporation of weed seeds. Seed ingested by earthworms may pass through the gut in a viable state and become deposited within the cast. In particular large numbers of seeds have been associated with worm casts in grassland, the position of the cast within the soil profile being dependent on the species of earthworm. Considerable selectivity in weed species preference may occur, for 66% of Veronica persica seeds offered to Lumbricus terrestris were ingested whereas only 1% of Ranunculus repens were taken. The number of viable seeds egested may vary also. Thus, whereas over 80% viable seeds of Sonchus spp were recovered, only 50% of Poa spp and 0% of Agrostis capillaris were retrieved.

Losses from predation by vertebrates may also be considerable. The fate of seed of three species of buttercup, Ranunculus acris, R. bulbosus and R. repens sown onto the soil surface of a grazed pasture were monitored over a period of 15 months (Sarukhan 1974). Predation was mainly by rodents which accounted for between 38-54% loss of R. repens, 32-35% of R. bulbosus and 20-25% of R. acris seeds. Despite the greater predation of R. repens, the rate of seed decline was slower than for the other two species. Seed mortality during dispersal can also be influenced by seed size. For example, whereas seeds of Polygonum lapathifolium and P. persicaria pass through the alimentary tract of cottontail rabbits in a viable condition, the larger seeds of P. pensylvanicum were totally destroyed (Staniforth & Cavers 1977).

LOSSES AT HARVEST

Agrestal weeds have poorly developed abiotic methods of dispersal and rely exclusively on man the agriculturalist for their dissemination. The role of harvesting equipment in seed dispersal has been investigated by Petzold (1979) and Fogelfors (1982). In Argentina, Ballaré et al (1987) have demonstrated that only a small proportion of Datura ferox seeds were shed prior to harvesting soybeans. Greater than 90% of capsules were collected by the combine harvester and in two experiments between 7 and 40% of seeds were returned to the field, the viability unaffected by passage through the combine.

Of particular importance is the spread of agrestals as contaminants of crop seed. Despite improvements in seed cleaning, crop contamination remains an important means of weed dissemination. Improvements in seed cleaning were responsible for the demise of Agrostemma githago which lacks seed dormancy and is of short lifespan, necessitating repeated introduction. Thus, the success of arable weeds is primarily attributed to the persistence of seeds in the soil, itself a function of dormancy and potentially long lifespan. Consequently, two questions are particularly pertinent to the study of weed seed biology; when do they germinate? and for how long can they persist?

SEED LONGEVITY

When flowering plants are compared with respect to the fate of their seeds two contrasting groups may be recognised. In one, most if not all of the seeds germinate soon after release, whilst in the other group many become incorporated into a bank of dormant seeds which is detectable in the habitat at all times during the year and may represent an accumulation of many years. (These two groups represent two extremes of seed bank behaviour, and between them, there are species and populations in which the seedbank, although present throughout the year, shows pronounced seasonal variation in size. It has been found convenient to refer to these two groups as transient and persistent (Thompson, 1987). There exists between species great variation in the lifespan of their seeds.

Essentially two approaches to the study of seed longevity have been adopted. The first involves long-term burial of species in containers, subsequently exhumed at various intervals to determine percentage viability (Egley & Chandler 1983). The former include the classic studies of Dr Beal initiated in 1879 and continued for 100 years (Kivilaan & Bandurski, 1981). Of the 23 spp included, three species Rumex crispus, Oenothera biennis and Verbascum blattaria showed viability even after burial for 80 years. However, caution should be exercised in interpretation of results for species which exhibit cyclic changes of dormancy or restricted germination periodicities may escape detection from sampling at a single time of year. The seeds of Ambrosia artemisiifolia germinated once only during the period of study, forty years after burial. A possible explanation of this relates to the restricted germination pattern of this species, such that only at the 40 year period were assessments carried out early enough in spring to detect seeds in a non-dormant state (Baskin & Baskin 1977). The second approach involves exhumation of seeds from soils that have remained undisturbed for long periods (Chancellor 1986). Confirmation of considerable longevity of weed seed populations has been obtained from examination of seedbanks beneath pastures of known age. For example viable weed seeds have been detected beneath soils not disturbed for 58 years (Brenchley 1918).

A major limitation of both approaches is that they involve determination of seed lifespan under comparatively atypical conditions, for such seeds are not subject to cultivation which may result in exposure to light, greater diurnal amplitude of temperature fluctuation and modification of gaseous environment, factors known to influence dormancy loss and seed germination. To some extent these problems have been mitigated by the comprehensive studies of H.A. Roberts and co-workers. Typically, they have mixed seed to various depths in soil contained in open ended cylinders and monitored subsequent seedling emergence. Periodically, the soil has been disturbed to simulate cultivation and at the end of a specified period, survival of remaining viable ungerminated seed determined (Roberts & Neilson 1980, 1981a, Roberts & Boddrell 1983a, 1983b). Seed decline was found to be exponential. In addition, not only does the seed population decline in this manner but, so too, individual species decline at specific rates. For example in one experiment the annual decline of Fumaria officinalis was 26% whereas that of Veronica arvensis was 60%. The rate at which a population of viable seeds decline depends on several factors including dormancy characteristics, depth of seed incorporation, frequency, timing and depth of cultivation.

LOSSES OF BURIED SEEDS

Depth of burial

Typically seed decline is more rapid following shallow rather than deep burial (Dawson & Bruns 1975). For example Thomas et al, (1986) have shown that less than 1% of Setaria viridis seed sown on the soil surface was viable after six years, whereas buried seeds remained viable up to 17 years (Thomas et al, 1986). Likewise, seed of Sorghum halepense survived six years at a depth of 22.5 cm in undisturbed soil but less than 2 years when buried less deep. Seed survival in disturbed soil was less than 2.5 years (Leguizamon 1986). Conversely seeds of Bromus diandrus enforced into dormancy on the soil surface persisted for six months whereas seeds buried at 5 or 15 cm germinated or lost viability within one month (Harradine 1986). Likewise, seeds of Raphanus raphanistrum on the soil surface developed induced dormancy whereas shallow burial enhanced dormancy loss (Cheam 1986).

Depth of burial had little influence on the survival of populations of Avena fatua in Colorado (Zorner et al., 1984). However the mode of disappearance was closely related to depth. Loss through germination in situ increased with depth of burial whereas depletion as a consequence of non-viability increased with decreasing depth.

Effect of cultivation

Roberts & Feast (1973a) incorporated seed of 20 species to a depth of 15 cm. In the absence of disturbance seed decline of the entire population was 12% per annum, with a range of 6-21% for individual species. In contrast where soil was disturbed, mean seed decline was 32% per annum with a range of 20-26% for Chamomilla suaveolens, Matricaria perforata, Fumaria officinalis and Papaver rhoeas to 44-48% for Senecio vulgaris, Veronica hederifolia and Veronica persica. The mean numbers of seeds remaining viable after six years amounted to 5.9% of those initially sown in cultivated soil and 27.5% for undisturbed soil. In a similar experiment in which seeds were incorporated to depths of 2.5, 7.5 or 15 cm seedling emergence was 75, 65 and 54% respectively for cultivated soil and

58, 36 and 21% for uncultivated soil. The corresponding number of viable seeds remaining were 2.3, 4.0 and 7.7 for cultivated and 6.8, 16.5 and 31.6% for uncultivated soil (Roberts & Feast 1972).

Frequency of cultivation

Over a period of six years the rate of decline recorded for viable seed within a natural population was 22% per annum in the absence of cultivation, 38% when dug twice and 36% when dug four times (Roberts & Dawkins 1967). In a subsequent study numbers of naturally occurring seeds in the top 23 cm of soil declined at rates of 34% on plots which were undisturbed but left bare, 31% and 32% respectively for mulched or grassed down plots, 42% where dug twice and 56% where dug seven times (Roberts & Feast 1973b). Elsewhere, even after seven years 50% of Brassica Kaber seeds remained viable under undisturbed soil (grass or chemical fallow) compared with 3% following intensive cultivations which involved ploughing three times per annum plus additional cultivation (Warnes & Andersen 1984).

VERTICAL DISTRIBUTION OF SEEDS

The distribution of seeds with depth depends very much on when the soil is examined in relation to cultivation and time of seed production. Mouldboard ploughing may result in a particularly uneven distribution of seed (Rottele & Koch 1981). However, Fay & Olson (1978) report a more even distribution of wild oat seeds with mouldboard than chisel ploughing. Thus, with mouldboard ploughing 43% of seeds were in the top 0-5 cm, 37% in the 5-10 cm layer and 20% in the 10-18 cm layer whereas with chisel ploughing no seeds were buried below 10 cm and 60% of all seeds were located in the top 0 - 25 cm. Vertical distribution of seed within the soil profile has important implications for subsequent infestation, particularly where minimal tillage is practiced and freshly shed seeds are located at or near the soil surface. Using a mark and recapture technique, Naylor (1972) was able to demonstrate that the majority (90%) of blackgrass seedlings were derived from freshly shed seed in the top 2.5 cm of soil.

RELATIONSHIP BETWEEN SEED NUMBER AND SEEDLING EMERGENCE

Although the size of the seedbank may be considerable, comparatively few seeds contribute to the annual seedling recruitment. For example Roberts & Feast (1973b) reported that only 6% of viable seeds per annum emerged as seedlings. Similarly, Roberts & Ricketts (1979) estimated that between 3 and 6% seeds per annum emerged as seedlings when moisture was adequate and the percentage was even lower when moisture availability was inadequate. However, rates of seed decline greatly exceed losses from successful seedling emergence. For example, the proportion of seed not accounted for either as seedlings or as viable seed remaining after six years ranged from 20-60% in cultivated soil to 33 - 70% in undisturbed soil (Roberts & Feast, 1973a). This apparent discrepancy has been attributed to post-germination mortality of seed in the soil, not resulting in successful seedling emergence. Confirmation of such a fate is provided by Schafer & Chilcote (1970) who reported 85% seed mortality of Lolium perenne spp perenne from germination at depth, whereas a comparative figure of 49% mortality was obtained for Lolium multiflorum. This supports the observations of Rampton & Ching (1970) that buried seeds of L. multiflorum could persist for seven years whereas only a trace of L. perenne remained after three years, and partly explains the greater prevalence of L. multiflorum as a weed.

ONE YEARS SEEDING SEVEN YEARS WEEDING

Despite some forty years of intensive chemical control, the size of seedbanks remains vast with as many as 67000 seeds m^{-2} (Roberts & Chancellor 1986). Although seed replenishment has obviously occurred, the composition of the seedbank is also indicative of seed persistence. Nonetheless, Schweizer & Zimdahl (1984) report seed decline over a period of 6 years of 99 and 94% for Amaranthus retroflexus and Chenopodium album, but when weed control was discontinued at the beginning of the fourth year the weed seed burden reached 50% of its original value after only three years. Similarly, Burnside et al (1986) reported that a weed seed population declined by 95% over five years in the absence of seed return but recovered to 90% of its original value following a single year of non-weed control. Consequently, there is considerable evidence for the adage one years seeding, seven years weeding. Nonetheless, despite a 98% reduction of Amaranthus palmeri over a six year period, some 18 m seeds ha^{-1} remained (Menges, 1987).

EDAPHIC FACTORS

The influence of soil type on seed persistence has received little attention. However, Lewis (1973) observed that seed deterioration occurred more rapidly in acid peat than in loam soil. In Nebraska, buried seeds of Sorghum bicolor lost viability more rapidly in fine sandy loam as compared with silt loam or clay loam (Burnside et al., 1977). In Finland, Pessala (1978) observed that during the first two years of burial, decline of Avena fatua was more rapid in sandy than clay soil. Such results may be related to soil moisture retention, for Lewis demonstrated the importance of waterlogging in enhancing seed survival. Consequently, it is likely that soil drainage would reduce seed persistence and hence facilitate seed decline. Information concerning the effect of soil fertility on seed decline is similarly scant. Banks et al (1976) recorded least number of weed seeds on nutrient deficient plots. In contrast Pulcher & Hurle (1984) observed reduction in seed density of plots receiving high intensities of nitrogen fertilizer.

AGRONOMIC FACTORS

Crop rotation

The season in which a crop is planted is probably the main factor determining weed flora composition, but although species composition is likely to be somewhat similar for autumn and spring-sown crops, their relative contribution will differ greatly. Hence, in the absence of seed return, seed decline will be influenced by the crop sown. Beuret (1980) reported that five times as many Apera spica-venti seedlings emerged in an autumn-sown wheat crop as compared with spring-sown barley. Total seed numbers declined more rapidly following continuous maize then either continuous small-grain cereals or rotational cropping, indicative of more efficient chemical control in maize. In contrast, following eight years of continuous rape, the seedbank was considerably greater. Similarly, Zawislak (1980) reported an increase of weed seed density of 46% in continuous rape and of 101% in continuous field beans, whereas seed density increased less markedly for rotational sequences. Elsewhere, decline of Brassica kaber was more rapid in a corn-soybean rotation than for continuous wheat; and has been attributed to greater use of tillage in the former situation (Warnes & Andersen, 1984).

Herbicides

Hurle (1974) estimated seed numbers after various weed control measures. Greatest number of seeds were present on plots subject to mechanical weed control measures and least following herbicide treatments. Similarly, seed number after seven years monoculture of winter wheat were highest for hand-weeded plots and lowest for plots receiving a combination of herbicide treatments (Pulcher & Hurle 1984). A greater than ten-fold increase of weed seed number was recorded over eight years of regular cultivation in a raspberry plantation, whereas plots receiving simazine treatment showed no such increase (Clay & Davison 1976). Although there may be little change in the overall size of the seedbank, repeated application of the same herbicide may substantially affect species composition (Hurle, 1974). Nonetheless, Roberts & Neilson (1981b) found little qualitative effect of repeated herbicide application on species composition despite quantitative differences between treated and untreated plots.

FATE OF ARABLE GRASS-WEEDS

Detailed investigations of seedbank dynamics of major annual arable grass-weeds have been conducted by staff of the former Weed Research Organization and include *Avena fatua*, *Alopecurus myosuroides* and *Bromus sterilis*. The fate of seeds of these species may be considered in relation to the regulatory factors already discussed.

Avena fatua

Losses of *A. fatua* seeds as contaminants of grain and straw will be related to the degree of shedding at harvest (Wilson 1970). Although most seeds will shed prior to harvesting winter wheat, contamination of winter barley may be severe. For example in one trial 77% passed though the combine but only 21% of these were recovered from the grain tank.

Substantial seed losses have been observed post-harvest when seed remain on the soil surface throughout the autumn. Losses of between 76 and 85% have been reported between harvest and December (Wilson 1972). Such losses can not be attributed to predation or microbial decay, but more likely, seeds suffer post-germination mortality. In contrast, shallow incorporation of seed by cultivation in early-autumn largely preserves seed (Wilson & Cussans 1972).

Freshly-shed seeds exposed on the soil surface are prone to destruction by stubble burning. Where straw was burnt in swathes, an overall reduction of 32% was obtained (Wilson & Cussans 1975) although losses through straw burning were considerably lower than for natural mortality. Thus seed decline was 32% where straw was burnt, 67% where cultivation was delayed and 73% where straw was burnt and cultivation delayed. In comparison with delayed cultivation there were twice as many seedlings in the following spring.

Greatest losses of seed through germination occurred in the second spring giving typical rates of decline of 50% in the first year and 90% in the second. Losses from a seedbank of mixed aged are most likely to result from seeds greater than one year old (Wilson 1985). However, a relatively small proportion (11-14%) of seeds may give rise to seedlings and even less (0.4%) if deeply buried (Wilson 1981). Depth of burial may affect persistence, for seeds buried deeply were found to show greater survival.

Studies of seed longevity indicate a total eradication of the seedbank over three years of spring barley cut for arable silage, whereas some seeds persisted for six years under grass (Wilson & Phipps 1985). In a further study, viable seeds were still present after four years of winter barley cropping (Wilson 1985) while Peters (1986) observed that on average less than 1% viable seeds remained after five years in uncropped and undisturbed soil.

Type of cultivation influenced seed distribution in the soil profile and hence emergence pattern. It is suggested that with no herbicidal control, tine cultivation will lead to a more rapid build up of seeds than ploughing, but where seed production is prevented, seed decline will be more rapid (Wilson 1978, 1981). He concludes that persistence of A. fatua as a weed appears to be related to seed production by survivors rather than persistence of seed in the soil.

Alopecurus myosuroides

The early shedding habit of A. myosuroides reduces the likelihood of contamination during harvesting although perhaps only 50% of seed will have been shed prior to harvest of winter barley. However, seed viability tends to be lower at the beginning and the end of shedding than at its peak during late July/early August (Moss 1983).

As with Avena fatua considerable seed mortality may occur on the soil surface, such that as little as 32% viable seed remained ten weeks after shedding (Moss 1980a). Straw burning can cause substantial losses of seeds on the soil surface (Moss 1980b), the magnitude of loss (61-94%) being dependent on the amount of straw burnt and hence temperature attained. Moss reports a 16 fold reduction compared with baled plots. In previous studies considerable variation in seed mortality following straw burning has occurred (Moss 1978, 1979, 1980c). Also the level of control will be influenced by subsequent cultivation regime such that the reduction in seed number following straw burning may be nullified by ploughing up old seed reserves.

In contrast to A. fatua, seed decline is most rapid in the first year after shedding (Moss 1985). At two sites sown to winter wheat, the mean annual decline of an artificially established population was 73-88% over a 2 or 3 year period. At five sites with natural populations, seed numbers declined to an average of 3% of the original amount present after three years and to 1% after four years. However, despite the low proportion surviving after four years, appreciable numbers of seed remain (Moss 1985). Rates of seed decline under grass were similar to arable cropping. Rate of decline is similar irrespective of cultivation system, although where seeds are ploughed down and crops subsequently direct-drilled, rate of decline may be impaired.

Bromus sterilis

Despite the early maturation of B. sterilis, contamination of winter barley may be considerable. As with the other two species germination losses from the soil surface may be substantial (Froud-Williams 1983). For example a decline of 85% occurred between July and August, 41% which suffered post-germination mortality, and by December only 6% viable seed remained.

Straw burning too, may destroy a large proportion of seeds, as many as 96% where straw was spread. Cultivations and seed burial serve to deplete the seedbank to a greater extent and more rapidly than retention on the soil surface. Thus shallow cultivations reduced seed numbers by a further 34%, while ploughing (to a depth in excess of 12 cm) resulted in total depletion of the seed bank.

CONCLUSION

Whereas the success of annual broad-leaved weeds has been partly attributed to an intrinsically high seed output, discontinuous germination and formation of persistent seedbanks; it is apparent that the success of annual grass-weeds; of relatively lower seed output, lack of inherent dormancy and of short seed lifespan, is largely a function of current agronomic systems. Seed survival is markedly influenced by cultural practice, albeit opportunities to effect seed decline will be greater for grass-weeds than broad-leaved species. Nonetheless, seed persistence may still be compounded by seed number.

REFERENCES

Ballaré, C.L.; Scopel, Ana L.; Ghersa, C.M.; Sánchez, R.A. (1987) The demography of Datura ferox L. in soybean crops. Weed Research 27, 91-102

Banks, P.A.; Santelmann, P.W.; Tucker, B.B. (1976) Influence of long-term soil fertility treatments on weed species in winter wheat. Agronomy Journal 68, 825-827.

Baskin, J.M.; Baskin, C.C. (1977) Dormancy and germination in seeds of common ragweed with reference to Beals buried seed experiment. American Journal of Botany 64, 1174-1176.

Beuret, E. (1980) Influence de la monoculture dt des methodes de travail du sol sur la flore adventice et le stock granier du sol. Comptes Rendus du 6eme Colloque International sur l'Ecologie, la Biologie et la Systematique des Mauvaises Herbes, Montpelier 389-399.

Brenchley, W.E. (1918) Buried weed seeds. Journal of Agricultural Science 9, 1-31.

Burnside, O.C.; Wicks, G.A.; Fenster, C.R. (1977) Longevity of shattercane seed in soils across Nebraska Weed Research 17, 139-144.

Burnside, O.S.; Moomaw, R.S.; Roeth, F.W.; Wicks, G.A.; Wilson, R.G. (1986) Weed seed demise in soil in weed-free corn (Zea mays) production across Nebraska. Weed Science, 34, 248-251.

Cavers P.B. (1983) Seed demography. Canadian Journal of Botany 61, 3578-3590.

Chancellor, R.J. (1986) Decline of arable weed seeds during 20 years in soil under grass and the periodicity of seedling emergence after cultivation. Journal of Applied Ecology 23, 631-637.

Cheam, A.H. (1986) Seed production and seed dormancy in wild radish (Raphanus raphanistrum L.) and some possibilities for improving control. Weed Research 26, 405-413.

Clay, D.V.; Davison, J.G. (1976) The effect of 8 years of different soil-management treatments in raspberries on weed seed and worm populations, soil microflora and on chemical and physical properties of the soil. Proceedings 1976 British Crop Protection Conference-Weeds 1, 249-258.

Dawson, J.H.; Bruns, V.F. (1975) Longevity of barnyard grass, green foxtail, and yellow foxtail seeds in soil. Weed Science 23, 437-440.

Egley, G.H.; Chandler, J.M. (1983) Longevity of weed seeds after 5.5 years in the Stoneville 50-year buried seed study. Weed Science 31, 264-270.

Fay, P.K.; Olson, W.A. (1978) Technique for separating weed seed from soil. Weed Science 26, 530-533.

Fogelfors, H. (1982) Collection of chaff, awns and straw when combining and its influence on the seed bank and weed flora. Proceedings 23rd Swedish Weed Conference 2, 339-345.

Froud-Williams, R.J. (1983) The influence of straw disposal and cultivation regime on the population dynamics of Bromus sterilis. Annals of Applied Biology 103, 139-148.

Harper, J.L. (1977) Population biology of plants. Academic Press.

Harradine, A.R. (1986) Seed longevity and seedling establishment of Bromus diandrus Roth. Weed Research 26, 173-180.

Hurle, K. (1974) Effect of long-term weed control measures on viable weed seeds in the soil. Proceedings 12th British Weed Control Conference 3, 1145-1152.

Kivilaan, A.; Bandurski, R.S. (1981) The one hundred-year period for Dr Beals seed viability experiment. American Journal of Botany, 68, 1290-1292.

Leguizamón, E.S. (1986) Seed survival and patterns of seedling emergence in Sorghum halepense (L.) Pers. Weed Research 26, 397-403.

Lewis, J. (1983) Longevity of crop and weed seeds : Survival after 20 years in soil. Weed Research 13, 179-191.

McRill, M. (1974) The ingestion of weed seed by earthworms Proceedings 12th British Weed Control Conference 2, 519-524.

Menges, R.M. (1987) Weed seed population dynamics during six years of weed management systems in crop rotations on irrigated soil. Weed Science 35, 328-332.

Mortimer, A.M. (1976) Aspects of the seed population dynamics of Dactylis glomerata L., Holcus lanatus L., Plantago lanceolata L. and Poa annua L. Proceedings 1976 British Crop Protection Conference - Weeds 3, 687-694.

Moss, S.R. (1979) The influence of tillage and method of straw disposal on the survival and growth of black-grass, Alopecurus myosuroides, and its control by chlortoluron and isoproturon. Annals of Applied Biology 91, 91-100.

Moss, S.R. (1980a) The agro-ecology and control of blackgrass, Alopecurus myosuroides Huds., in modern cereal growing systems. ADAS Quarterly Review 38, 170-191.

Moss, S.R. (1980b) Some effects of burning cereal straw on seed viability, seedling establishment and control of Alopecurus myosuroides Huds Weed Research 20, 271-276.

Moss, S.R. (1980c) A study of populations of blackgrass (Alopecurus myosuroides) in winter wheat, as influenced by seed shed in the previous crop, cultivation system and straw disposal method. Annals of Applied Biology 94, 121-126.

Moss, S.R. (1983) The production and shedding of *Alopecurus myosuroides* Huds seeds in winter cereal crops. Weed Research 23, 45-51.

Moss, S.R. (1985) The survival of *Alopecurus myosuroides* Huds. seeds in soil. Weed Research 25, 201-211.

Naylor, R.E.L. (1972) Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds in winter cereal crops. Journal of Applied Ecology 9, 127-139.

Pessala, B. (1978) Longevity of *Avena fatua* seeds in the field. Proceedings Swedish Weed Control Conference, C14-C24.

Peters, N.C.B. (1986) Factors affecting seedling emergence of different strains of *Avena fatua* L. Weed Research 26, 29-38.

Petzold, K. (1979) Mähdrusch und unkraut, Proceedings European Weed Research Society 'Symposium on the influence of different factors on the development and control of weeds,' Mainz 309-315.

Pulcher, M.; Hurle, K. (1984) Unkrautflora und Unkrautsam -envorrat in Weizen monokulture bei unterschiedlicher Pflanzenschutz intensität. Zeitschrift für Pflanzen Krankheiten X, 51-61.

Rampton, H.H.; Ching, T.M. (1970) Persistence of crop seeds in soil.Agronomy Journal 62, 272-277.

Roberts, H.A.; Boddrell, J.E. (1983a) Seed survival and periodicity of seedling emergence in ten species of annual weeds. Annals of Applied Biology 102, 523-532.

Roberts, H.A.; Boddrell, J.E. (1983b) Seed survival and periodicity of seedling emergence in eight species of Cruciferae. Annals of Applied Biology 103, 301-309.

Roberts, H.A.; Chancellor, R.J. (1986) Seed banks of some arable soils in the English midlands. Weed Research 26, 251-257.

Roberts, H.A.; Dawkins, P.A. (1967) Effect of cultivation on the numbers of viable weed seeds. Weed Research 7, 290-301.

Roberts, H.A.; Feast, P.M. (1972) Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. Weed Research 12, 316-324.

Roberts, H.A.; Feast, P.M. (1973a) Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. Journal of applied Ecology, 10, 133-143.

Roberts, H.A.; Feast, P.M. (1973b) Changes in the numbers of viable seeds in soil under different regimes. Weed Research 13, 298-303.

Roberts, H.A.; Neilson, J.E. (1980) Seed survival and periodicity of seedling emergence in some species of *Atriplex*, *Chenopodium*, *Polygonum* and *Rumex*. Annals of Applied Biology 94, 111-120.

Roberts, H.A.; Neilson, J.E. (1981a) Seed survival and periodicity of seedling emergence in twelve weedy species of Compositae. Annals of Applied Biology 97, 325-334.

Roberts, H.A.; Neilson, J.E. (1981b) Changes in the soil seedbank of four long-term crop/herbicide experiments. Journal of Applied Ecology 18, 661-668.

Roberts, H.A.; Ricketts, M.E. (1979) Quantitative relationships between the weed flora after cultivation and the seed population in the soil. Weed Research 19, 269-275.

Rottele M.; Koch, W. (1981) Verteilung von Unkrautsamen im sclen und konsequenzen für die bestimmung der samendichte. Zeitschrift fur Pflanzen-Krankheiten und Pflanzen-schutz IX, 383-391.

Sarukhan, J. (1974) Studies on plant demography : *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. : II Reproductive strategies and seed population dynamics. Journal of Ecology 62, 151-177.

Schafer, D.E.; Chilcote, D.O. (1970) Factors influencing persistence and depletion of buried seed populations. II. The effects of soil temperature and moisture. Crop Science 10, 342-345.

Schweizer, E.E.; Zimdahl, R.L. (1984) Weed seed decline in irrigated soil after six years of continuous corn (Zea mays) and herbicides. Weed Science 32, 76-83.

Somody, C.N.; Nalewaja, J.D.; Miller, S.D. (1985) Self burial of wild oat florets. Agronomy Journal 77, 359-362.

Stamp, N.E. (1984) Self burial behaviour of Erodium cicutarium seeds. Journal of Ecology 72, 611-620.

Staniforth, R.J.; Cavers, P.B. (1977) The importance of cottontail rabbits in the dispersal of Polygonum spp. Journal of Applied Ecology 14, 261-267.

Thomas, A.G.; Banting, J.D.; Bowes, G. (1986) Longevity of green foxtail seeds in a Canadian prairie soil. Canadian Journal of Plant Science 66, 189-192.

Thompson, K. (1987) Seeds and seedbanks New Phytologist 106 (Supplement) 23-34.

Warnes, D.D.; Andersen, R.N. (1984) Decline of wild mustard (Brassica Kaber) seeds in soil under various cultural and chemical practices. Weed Science 32, 214-217.

Williams, E.D. (1984) Changes during 3 years in the size and composition of the seed bank beneath a long term pasture as influenced by defoliation and fertilizer regime. Journal of Applied Ecology, 21, 603-615.

Wilson, B.J. (1970) Studies of the shedding of seed of Avena fatua in various cereal crops and the presence of this seed in the harvested material. Proceedings of the 10th British Weed Control Conference 2, 831-836.

Wilson, B.J. (1972) Studies of the fate of Avena fatua seeds on cereal stubble as influenced by autumn treatment. Proceedings 11th British Weed Control Conference 1, 242-247.

Wilson, B.J. (1978) The long term decline of a population of Avena fatua L. with different cultivations associated with spring barley cropping. Weed Research 18, 25-31.

Wilson, B.J. (1981) The influence of reduced cultivations and direct drilling on the long-term decline of a population of Avena fatua L. in spring barley. Weed Research 21, 23-28.

Wilson, B.J. (1985) Effect of seed age and cultivation on seedling emergence and seed decline of Avena fatua L. in winter barley. Weed Research 25, 213-219.

Wilson, B.J.; Cussans, G.W. (9172) The effect of autumn cultivations on the emergence of Avena fatua seedlings. Proceedings 11th British Weed Control Conference 1, 234-241.

Wilson, B.J.; Cussans, G.W. (1975) A study of the population dynamics of Avena fatua L. as influenced by straw burning, seed shedding and cultivations. Weed Research 15, 249-258.

Wilson, B.J.; Phipps, P.A. (1985) A long term experiment on tillage, rotation and herbicide use for the control of A. fatua in cereals. Proceedings 1985 British Crop Protection Conference - Weeds 693-700.

Zawíslak, K. (1980) Stopién specjalizacji zmianowán a aktualnei potencjalne záchwaszczenie stanowisk. Zeszyty Nankowe Akademii Rolniczo-Technicznej w Olsztynie 29, 283-293.

Zorner, P.S.; Zimdahl, R.L.; Schweizer, E.E. (1984) Sources of viable seed loss in buried dormant and non-dormant populations of wild oat (Avena fatua L.) seed in Colorado. Weed Research 24, 143-150.

THE MANIPULATION OF WEED SEED DORMANCY

M.A. HALL, M.A. ACASTER, I.C. CANTRELL, A.R. SMITH & O.A.F. YOUSIF

Department of Botany & Microbiology, University College of Wales,
Aberystwyth, Dyfed SY23 3DA, U.K.

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 thiourea, 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.

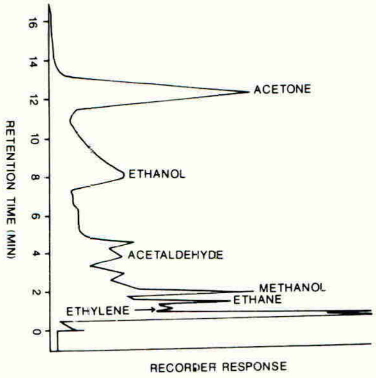


Fig. 1. Total ion current scan of a gas sample collected from seeds of *Spergula arvensis* L. buried in sand at 60% moisture content. Sample taken after four weeks incubation at 20°C.

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.

REFERENCES

Hendricks, S.B.; Taylorson, R.B. (1975) Breaking of seed dormancy by catalase inhibition. Proceedings of the National Academy of Sciences, USA 72, 306-309.

Hobson, G.E.; Harman, J.E.; Nichols, R. (1984) Ethylene and the control of tomato fruit ripening. In: Ethylene: Biochemical, Physiological and Applied Aspects Y. Fuchs and E. Chalutz (Eds), The Hague: Martinus Nijhoff/Dr W Junk Publishers, pp. 281-290.

Jacobsen, J.V.; Chandler, P.M.; Higgins, T.J.V.; Zwar, J.A. (1982) Control of protein synthesis in barley aleurone layers by gibberellin. In: Plant Growth Substances 1982 P.F. Wareing (Ed.), London, New York: Academic Press, pp. 111-120.

Jones, J.F.; Hall, M.A. (1979) Studies on the requirement for CO_2 and ethylene for germination of *Spergula arvensis* seeds. Plant Science Letters 16, 87-93.

Jones, J.F.; Hall, M.A. (1981) The effect of ethylene on quantitative and qualitative aspects of respiration during the breaking of dormancy of *Spergula arvensis* L. seeds. Annals of Botany 48, 291-300.

Karssen, C.M. (1981) The pattern of change in dormancy during burial of seeds in soil. Israel Journal of Botany 29, 65-73.

Koorneef, M.; Reuling, G.; Karssen, C.M. (1984) The isolation and characterisation of abscisic acid insensitive mutants of *Arabidopsis thaliana*. Physiologia Plantarum 61, 377-383.

Roberts, E.H. (1972) Oxidative processes and the control of seed germination. In: Seed Ecology, W. Heydecker (Ed.), London:Butterworths, pp. 189-218.

Taylorson, R.B.; Hendricks, S.B. (1973) Promotion of seed germination by cyanide. Plant Physiology 52, 23-27.

Trewavas, A. (1981) How do plant growth substances work? Plant, Cell and Environment 4, 203-228.

Venis, M.A. (1985) Hormone binding sites in plants. Research Notes in the Biosciences. New York, London: Longman.

Wesson, G.; Wareing, P.F. (1969) The induction of light sensitivity in weed seeds by burial. Journal of experimental Botany 63, 414-425.

Williams, R.A.N.; Smith, A.R.; Hall, M.A. (1987) In preparation.

Zeroni, M.; Hall, M.A. (1980) Molecular effects of hormone treatment on tissue. In: Encyclopedia of Plant Physiology, New Series, Vol. 9. Hormonal Regulation of Development I. Molecular Aspects of Plant Hormones J. Macmillan (Ed.), Berlin-Heidelberg: Springer-Verlag, pp. 511-586.

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

D.S.H. DRENNAN and A.B. BAIN

Department of Agricultural Botany, The University, Whiteknights, Reading RG6 2AS.

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.

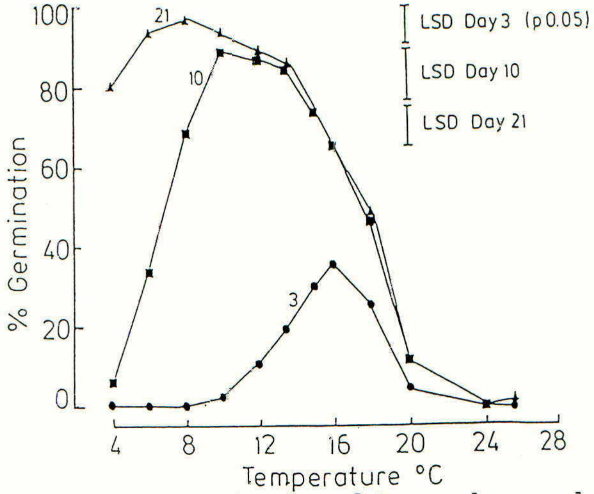


Fig. 1. The germination of P. paradoxa seed at constant temperatures counted at 3, 10 and 21 days

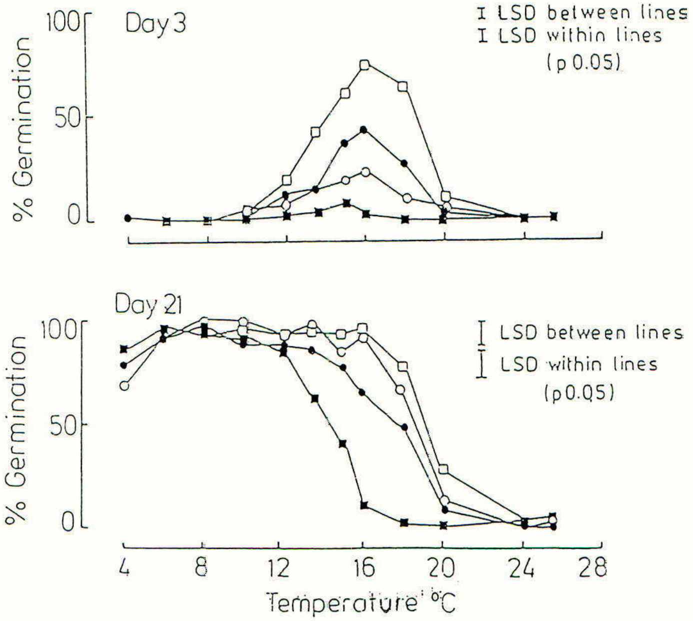


Fig. 2. The germination of P. paradoxa seed at constant temperatures counted at 3 and 21 days for P(25) (North Essex ●, P(34) Kent ■ , P(55) (South Essex) O, and P(68) (Worcestershire) □.

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

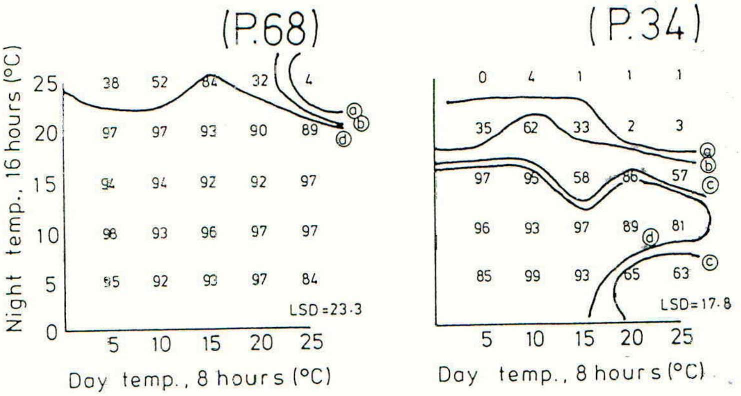
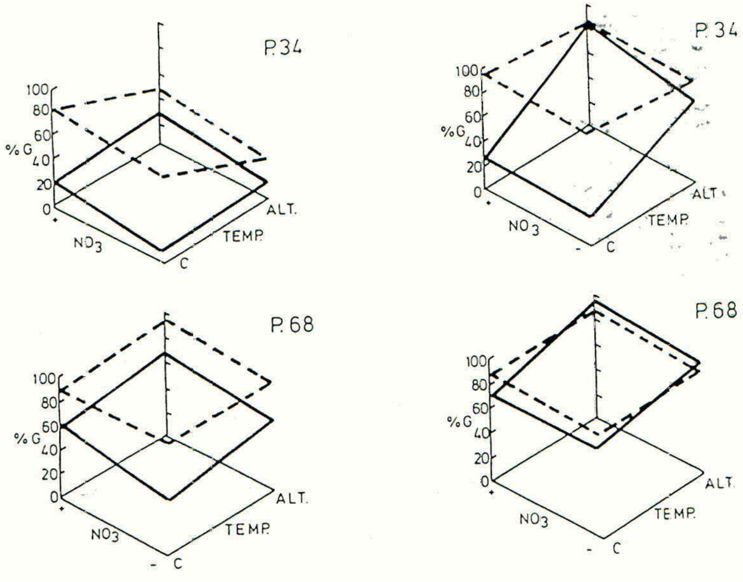


Fig. 3. Germination of seed of P(68) (Worcestershire) and P(34) (Kent) populations of P. paradoxa after 30 days at alternating temperatures in the light



Seed + glume

Caryopses

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.

REFERENCES

Catizone, P.; Viggiani P. (1980) Forty years of research into Phalaris spp infestation of wheat. Ali Giôrnate Fitopathogiche, Suppl 3, 257-311.

Fox, D.J.C.; Thompson, P.A. (1971) A thermo-gradient apparatus designed for biological investigations over controlled temperature ranges. Journal Experimental Botany, 22, 741-748.

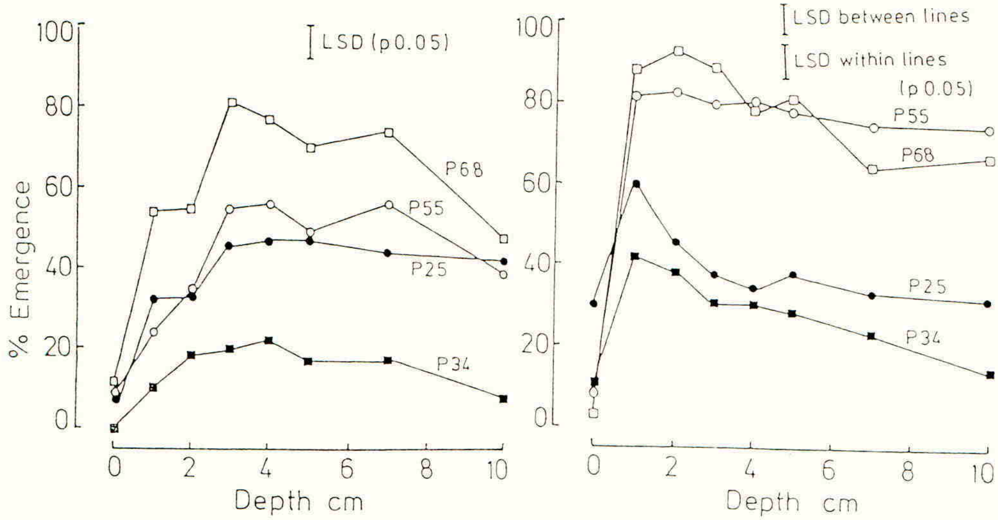


Fig. 5. Final emergence percentage of seed with glumes of *P. paradoxa* sown in soil at depths to 10cm outdoors (left) or at 15^{o}C in a controlled environment room. The populations are those of figure 2.

Horowitz, M. (1964) Observations sur la gemination et le developpment de *Phalaris paradoxa* L. et quelques donnes biologique sur *Avena sterilis* L. *Report of the Volcani Institute of Agronomic Research*, No 484, 1-29.

Palti, J. (1964) Research Weeds and their control in Israel, Journal d'Agriculture tropicale et de Botanique appliqué *11*, 468-72.

Thurley, B.; Chancellor, R.J. (1985). Observations on the occurrence of *Phalaris paradoxa* L. in England and Wales. *Annals of Applied Biology*, *107*, 79-86.

Wilson, B.J. (1981) Effects of time of seedling emergence on seed production and time of flowering of eight weeds, *Proceedings of 6th Australian Weeds Conference* *1*, 35-38.

Yadaraju, N.T.; Casely, J.C.; Drennan D.S.H. (1984) Some studies on germination, emergence and growth of *Phalaris minor* Retz and *Phalaris paradoxa* L. *Proceedings EWRS 3rd Symposum on Weed Problems in the Mediterranean Area*, 447-454.