DX

83992

THE POPULATION DYNAMICS OF FIELD PANSY (*VIOLA ARVENSIS*) AND RED DEADNETTLE (*LAMIUM PURPUREUM*) IN WINTER CEREAL AND OILSEED RAPE FIELDS.

by

Jane Gilbert

A thesis submitted to the University of Keele for the Degree of Doctor of Philosophy. August 1987

For Mum and Dad

"Those who honour me I will honour"

1 Samuel 2:30

Acknowledgements

I would like to express my thanks to Professor C. Arme in whose Department this work was carried out; to Dr. S. J. Bostock for his guidance and encouragement; to the staff and technicians of the Department of Biological Science; to Mr. D. Thompson of the University Botanical Gardens; to Mrs. K. Bromage for her time and effort in typing this thesis; to the University of Keele for financing the research.

ABSTRACT

The population dynamics of Viola arvensis Murr. and Lamium purpureum L. were studied in winter cereal and oilseed rape fields in North Staffordshire and Cheshire. The seedling emergence, seedbank density, population survival and potential seed input were recorded. Transition probabilities for each stage were calculated.

For both species, annual emergence was positively related to the seedbank. For Lamium purpureum, the adult population was also positively related to the seedbank. The seedbank of V.arvensis was positively related to the sandiness of the soil and to the number of years sown to winter barley. In a garden experiment, emergence was greater in more sandy soil (though containing less inorganic nitrate).

Emergence patterns in garden experiments reflected those in the fields despite monthly cultivation and are explicable by seasonal changes in germination requirements for temperature and light, which were studied on a thermogradient bar. Peak emergence coincided with minimum dormancy and would occur in the second autumn of burial for V.arvensis and in each autumn for L.purpureum.

Collection date and burial time did not affect dormancy of L.purpureum. However, for V.arvensis, earlier dispersed and earlier buried seeds were less dormant.

Dormancy changes of seeds in a Stevenson Screen resembled those of buried seeds for V.arvensis, though changes were more abrupt. There was no dormancy cycle in seeds stored in a refrigerator for either species.

A greenhouse experiment revealed phenotypic and genotypic variation in dormancy in both species. Genetic variation was apparent both between plants and fields for V.arvensis but only between plants for L.purpureum.

Life cycle data from the fields were incorporated into a Leslie Matrix population model and the effects on the population of varying the seed input were simulated. The implications for control measures are discussed.

Contents

CHAPTER 1

Introduction and Literature Review

1.1 The species

Viola arvensis Murr. (the field pansy) is an annual or overwintering member of the Violaceae (Plate 1). It is widespread throughout Europe and is primarily a weed of winter cereal crops. It can be found in all arable areas and on most soil types, though it is less prevalent on poorly aerated and waterlogged ground. Flowering is largely from April to October but can be all year round. It is not tolerant of shading.

Lamium purpureum.L. (the red deadnettle) is an annual or biennial member of the Labiatae (Plate 2). It occurs throughout Europe and Asia in lawns, meadows, waste grounds and fields, and especially in hedgerows. It prefers loose, nutrient-rich mildly humus or sandy loam soils. The main flowering period is from April to late autumn but it may continue throughout the winter.

Both species can behave both as winter and summer annuals. Chancellor (1965) found equal peaks of seedling emergence in spring and autumn for V.arvensis. Froud-Williams et al (1984) found spring and autumn emergence to be similar in quantity, especially in the second year of burial. Here, emergence continued into winter. However, Brenchley and Warington (1930,1933) reported autumnal periodicity of V.arvensis in winter wheat, whilst Jensen (1969) in Denmark found spring emergence to exceed autumn emergence. This would explain its predominance in spring cereals in Denmark. Beuret (1984) found the same behaviour in France.

Ervio (1981) reported a mid-summer peak for both species in Sweden, being determined by the temperature 12 days before emergence.

Plate 1

Viola arvensis

Plate 2

Lamium purpureum

Low temperatures in early summer were correlated with maximum emergence and the rate of emergence increased with the rise in the temperature sum but by mid-summer, rainfall became important. However, H A Roberts (pers. comm.) found minimal germination of V.arvensis at higher temperatures, though summer temperatures in Sweden are more representative of spring and autumn temperatures in Britain (Ervio 1981). Roberts (pers.comm.) and Baskin and Baskin (1984) found field emergence of L.purpureum began in June with an autumn peak, declining abruptly to zero in December. Leguizamon and Roberts (1982) found it among the most abundant species in August and Beuret (1984) found a summer peak.

V.arvensis and L.purpureum are increasing in frequency in early winter-sown crops such as winter cereals and oilseed rape, V.arvensis being a particular problem due to numbers of large plants appearing recently. Both species emerge with the crop after cultivation and are becoming an increasing problem, firstly due to the increasing acreage of early winter-sown crops which allows less time to clear the land of weeds between crops. For example, in Ireland from 1976 to 1981 the acreage of winter wheat increased from 2% to 85% of the wheat area, and the acreage of winter barley increased from 0% to 4% (Frost 1982). Earlier drilling also encourages late summer germinators like L.purpureum. Secondly, herbicides give inadequate control: Only 50% of the pre-emergence herbicides used by Frost (1982) gave complete control and control was low with all the post-emergence herbicides. Thirdly, competition from weeds which are effectively controlled is decreasing. Finally, the increased use of potash and phosphate may encourage L.purpureum and the increased leaf-area of well-fertilized crops will favour shade-tolerant species like L.purpureum (Chancellor

and Froud-Williams 1986).

Chancellor and Froud-Williams (1986) list several attributes that are likely to favour success in a weed species over the next few years in view of changing patterns of husbandry: Autumn-germination, short lived innate dormancy, a light-requirement for germination, the ability to establish at or near the soil surface, a high relative growth rate under conditions of high nitrogen and shade, the production of many seeds which are difficult to separate from the grain, and a tolerance of herbicides. They suggest that L.purpureum and V.arvensis have the necessary attributes. Successful control of any persistent species may only be achieved through an understanding of the population dynamics of the species.

1.2 Population dynamics

The long term success of any weed control program depends, to a large extent, on an understanding of the mechanisms that regulate the size of the weed population in the crop environment. The acquisition of life historical data is increasingly being realised to be of importance in the understanding of the biology and control of weeds. Many workers have collected such data and have produced models to predict population size (Mortimer 1976). In such models, the life history is structured into different phases through which there is a flux of individuals and this flux is described by a series of transition probabilities which express the chance of an individual moving from one phase to the next. Mortimer (1976) discusses such a model for four species in a range of artificially managed habitats. This approach illustrates parts of the life cycle where regulation is naturally occurring and thus focuses

attention on the transition probabilities that may be potentially reduced even further to allow effective control of population size.

A considerable insurance element is present in the use of herbicides due to lack of precision on threshold and prediction of infestations (Hubbard 1985). Prediction of weed infestations requires a knowledge of the seedbank dynamics of annual weeds. For annual weeds, seed behaviour is the most important factor enabling them to be problem weeds (Chancellor and Froud-Williams 1986). Weedy annuals like V.arvensis can produce a lot of seed (up to 2000 per plant, Hanf, 1984) with the potential for a prolonged life span and can therefore build up large seedbanks.

Roberts (1981) defined the seedbank as 'the reserve of viable seeds present in the soil and on its surface'. Reviewing the literature on arable seedbanks, Kropač (1966) and Roberts (1970) conclude that annual weeds account for at least 95% of all seeds. The size and composition of the seedbank reflect past crop history and weed control success as much as physical characteristics of the soil and dormancy of the species in the soil. Roberts (1970) reviewed studies on the longevity of weed seeds but such studies are of limited use in predicting the fate of naturally occurring populations since the seeds used were of uniform age, buried under artificial conditions and using relatively small sample sizes. Studies of natural seedbanks under arable conditions are much more relevant.

Schafer and Chilcote (1969) proposed a model for the dynamics of the seed population (Figure 1.1):

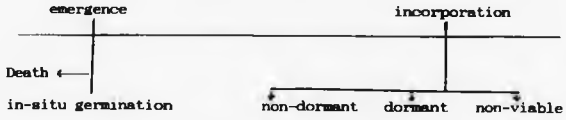


Figure 1.1 A model for the dynamics of the seed population (Schafer and Chilcote 1969)

Roberts (1972) developed this into an equation to describe the seed population (S) in terms of those germinating to die (Dgd), those emerging (Dge), those initially non-viable (Dni), those dying due to age (Dna), those predated or diseased (Dnp), and those under induced, innate and enforced dormancy (Pind, Pinn, Penf):

$$S = Pinn+Pind+Penf+Dgd+Dge+Dni+Dna+Dnp$$

Few studies have analysed the dynamics of seed populations of arable weeds due to practical difficulties but several non-arable species have been studied. Schafer and Chilcote (1970) found in Lolium perenne that 85% of the loss was Dgd, as opposed to 49% for L.multiflorum. 30% of the latter being in enforced dormancy (Penf) and 7% complete dormancy (Pind and Pinn) L.multiflorum, having a persistent seedbank, was the most problematic of the two. Sarukhan (1974) performed a similar experiment on three Ranunculus species using a mark and recapture technique (Table 1.1). (See Appendix 15 for a list of species names and authorities).

Table 1.1 Proportion of seeds germinating, dying or dormant in three Ranunculus spp (after Sarukhan 1973)

	Germination	Enforced dormancy	Induced dormancy	Predation	Death
R.repens	6-9%	39-22-44% Aug Dec Apr	3-14-2-0% June	38-54%	3-6-10 June
R.bulbosus	20-41% Aug Oct	27-5-0 Aug Dec Feb	10-3 Aug Oct	32-35%	7-15 Aug Oct
R.acris	50% May	13-2 Aug Apr	2-9	20-25%	10-17-21 Aug Apr Jun

He found the rates of decay of the seedbank varied between species as expected but all showed exponential decay. The reduction of R.acris and R.bulbosus was mainly due to germination, both having little dormancy, but R.repens is highly dormant and only 6-9% of the decline was due to germination in this species. Predation and decay also differed between species (though Sarukhan, 1974 suggested that no difference was apparent). There were also seasonal changes in the proportion of seeds in each category. Mortimer (1976) performed a similar experiment on four species of agricultural importance in order to produce a model of the life cycle under different management regimes and Doyle et al (1986) illustrated the seedbank dynamics of Alopecurus myosuroides. Pavone and Reader (1982) noted spatial variations in the proportion of seeds in each category for Medicago lupulina.

The most important loss from the seedbank is thought to be due to emergence at depth and thus involves deterioration of dormancy

mechanisms (Taylorson 1970, Schafer and Chilcote 1970, Roberts and Feast 1972, Roberts 1972, Mortimer 1979). Roberts and Boddrell (1985) showed that species with low dormancy did not build up seedbanks.

Without a significant input to the arable seedbank, it declines exponentially (Roberts 1962, Roberts and Dawkins 1967) the rate of decline depending on the species composition, the frequency of cultivation and possibly soil type (discussed later). The curve of this decline has been described by the equation:

$$N = No \exp(-gt)$$

where N is the number of survivors at time t of the initial population No and g is the decay rate (Cook 1980), which depends on the deterioration of dormancy mechanisms in the component species leading to germination, (Roberts 1970, Roberts and Feast 1972, 1973) and also the longevity of the seeds. However, Roberts and Neilson (1980) found a curvilinear decline for three out of eight species and suggested this was due to seedcoat-imposed dormancy which was only gradually overcome. Roberts and Dawkins (1967) postulated that a change in species composition of the seedbank should lead to a change in the rate of decline for the whole population but this was not observed. Such changes would probably be masked if the new dominant species had similar dormancy mechanisms to the previous one. Compiling data from various authors under different climates and cropping systems they constructed a graph of the number of seeds remaining after one years cultivation against the initial number and found a decrease of between 30% and 60% irrespective of the initial seed population size.

The frequency of cultivation is important to the rate of decline. Roberts and Dawkins (1967) found a 36% decrease p.a. with four

cultivations a year, 22% with none; Froud-Williams et al. (1983) found a 72.4% decrease on ploughed plots, against 52.4% on unploughed plots; and Roberts and Feast (1972) found only 0.6 to 8.8% were viable after five years, depending on the depth of incorporation and the frequency of cultivation. The rate of decrease may also vary spatially due to microenvironmental effects, as Pavone and Reader (1982) found in a pasture. However, this is probably less important in arable situations since microtopography is modified each time cultivation occurs.

The cropping system is also important in determining the decrease or increase in the seedbank and its composition. Autumn cultivation will increase the frequency of autumn-germinating species and spring cultivation will increase the frequency of spring-germinating species. Furthermore, the use of herbicides in conjunction with a particular crop rotation can be extremely effective in eliminating particular species. Brenchley and Warington (1930, 1933, 1936) were among the first to study arable seedbanks and found that two years fallow followed by three years winter wheat led to an increase in the seedbank. Thurston (1969) obtained similar results. Roberts (1963) observed a fourfold increase when cleaning was prevented in a pea crop. One year fallow can reduce the seedbank by 30 to 60% but cumulative reductions are difficult to obtain and rotations do not always succeed in reducing the seedbank. Wilson and Cussans (1975) found that leaving stubble uncultivated in autumn reduced the population of Avena fatua more than burning. Dvorak and Krejcir (1980) found the seedbank varied according to the percentage cereals in the rotation and the use of herbicides. Bridges and Walker (1985) found that a significant decline in seedbank size for Cassia obtusifolia only occurred when summer fallow each year prevented replenishment of the seedbank and repeated disking favoured germination

and emergence. Chemical fallow, relying on post-emergence control did not disturb the soil and was less effective. Permitting subcompetitive densities to set seed increased the seedbank size. Early emerging plants (favoured by tilled culture) produced more seed. (This may be one effect of earlier drilling in winter cereal fields on the field pansy population). In general, an intensive weed management system offered more stability in seedbank size, leading to a slight decrease. Similarly, non-till systems were more stable and reduced and/or delayed emergence as did delayed planting, leading to fewer mature plants, which were smaller and produced less seed. Roberts (1981) indicated that traditional cropping methods only achieve moderate reductions in the seedbank over extended periods but selective herbicides allow more complete control of particular species, leading to cumulative losses in a few years. However, the use of selective herbicides also allows tolerant species to proliferate and thus may simply change the composition of the seedbank and weed flora.

Cultivation causes reductions in the seedbank by releasing seeds from dormancy as they are exposed to light (Wesson and Wareing 1969), releasing them from volatile inhibitors (Holm 1972), increasing the amplitude of temperature to which they are exposed (Stoller and Wax 1973, Thompson et al. 1977), or removing soil capping to allow emergence (Chepil 1946). However, if seeds are completely dormant, cultivation and a changed seed environment will not cause germination. So, the timing of cultivation in relation to the seeds dormancy status is important. For example, Roberts and Feast (1973) observed a 60% reduction if cultivation took place during the growing season but Courtney (1968) found no decline of Polygonum aviculare if cultivation

occurred when seeds were dormant. The depth of cultivation will also determine its effects on the seedbank by influencing the numbers of seeds disturbed (Froud-Williams et al. 1983).

A knowledge of seedbank dynamics for the component species enables prediction of weed infestations in any particular season under a particular cultivation regime. Once the relationship between the potential and the actual weed population has been established, control can be made much more efficient. Barralis (1965) and Kropač (1966) showed that only 2.5% p.a of viable seeds in the top 10 cm appeared after cultivation. Roberts (1963) reported 10% p.a in the top 15 cm appeared with frequent disturbance and between 2.8% and 15.5% p.a has been reported by others (Roberts and Dawkins 1967, Carratero 1977, Cox 1977). Roberts and Ricketts (1979) found generally less than 5% p.a., provided there was adequate soil moisture. The timing of cultivation between March and November had little effect on this relationship (supported by Chancellor 1965), though species composition obviously differed. However, the proportion emerging does vary markedly between species due to dormancy differences. Lambelet - Haueter (1985) found a mean of 10% germination but varying between 33 and 84% between four plots according to the percentage of each species. Roberts and Boddrell (1985) found similar differences between Ranunculus, Rumex and Geranium species. For example, Beuret (1984) found an overall decline of 3.3% over two years, whilst Viola arvensis showed a 6% decline from April to May, being low for the rest of the year. Paterson et al. (1976) found 6 to 8% of A.fatua seeds in the soil produced seedlings each year. Froud-Williams (1983) found 60% of Bromus sterilis seeds could be accounted for by successful emergence.

In general, less than 16% of the seedbank produces seedlings each year, differences between studies reflecting sampling depths, number of cultivations, seed numbers and sampling techniques which tend to be very crude (Seely 1976, in Roberts 1981). A consistent frequency of cultivation generally leads to a constant between numbers emerging per year and the number of viable seeds present at the beginning of the year (Roberts and Dawkins 1967, Roberts and Feast 1973), the change in species composition reflecting different rates of decrease. However, cultivation once a year leads to a poorer correlation (Barralis and Chadoeuf 1976). Silvertown's (1982) survey indicates that a positive relationship exists between the seedbank and seedling populations of any particular species in arable situations. Wilson and Cussans (1975) found a linear relationship between numbers of A.fatua incorporated the previous autumn and seedlings emerging in spring. In contrast, Thompson and Grime (1979) and Jensen (1969) found no relationship between the non-dormant seed population and the seedling population. Kropač (1966) noted wide variation in the relationship between fields and Barralis and Chadoeuf (1976) between years. Williams (1984), using intensive sampling of a small area in a pasture, found a poor correlation for all species together but individual species did show a correlation between seedbank size and seedlings emerging.

Numbers appearing at any time depend firstly on the weather: Roberts and Potter (1980) found soil temperature and rainfall were important. Secondly, soil type may be important. Thirdly, the age of the seeds will influence emergence and this is related to cropping history. Most A.fatua seedlings are derived from seeds less than two years old (Wilson 1985) and Naylor (1972) indicated that fresh seeds of Alopecurus myosuroides contribute little to the next years seedling population.

Ploughing tine cultivation favours the persistence of A.fatua seeds more than ploughing (Wilson 1985). Such information for individual species could be used to predict necessary control measures. Roberts and Ricketts (1979) examined data for three species and produced curves enclosing about 80% of the data to avoid extreme values. But Fosseti and Beuret (1984) proposed that predictions must be based on data for particular fields due to complexities of microclimate, past histories, soil type etc. They found that two fields with the same climate, soil type and altitude, and the same cultivation for the previous two years had different principle species. In practical terms, the species composing the seedbank are more important than numbers of seeds since control measures need to be applied for particular species.

The second major consideration is the seasonality of the seedbank, so the timing of sampling in relation to the vegetation cycle is important and can reveal seasonal changes. Thompson and Grime (1979) found most viable seeds in autumn and least in spring and summer during one year, though by relying on emergence of seeds to estimate density they ignored seasonality of dormancy. Williams (1984) studied seasonal changes in a pasture. Several authors have studied particular species: Wilson and Cussans (1975) found the reserve of Avena fatua seeds to be lowest in June just before dispersal. Pavone and Reader (1982) found the seedbank of Medicago lupulina in a pasture to be smallest after spring and summer germination and largest after seed dispersal in late winter. Baalen (1982) found similar changes for Digitalis purpurea. Thill et al. (1985) found seasonal changes in achene survival of common crupina which were not due to germination and suggested predation and pathogens varied seasonally.

Many weed seeds do not enter the seedbank in arable situations but are removed with the crop or are destroyed before burial. Wilson and Cussans (1975) found large losses of fresh Avena fatua seeds occurred due to death and predation on the soil surface when not ploughed in. The timing of harvest can be crucial in this respect and up to 95% of A.fatua seeds are removed with the crop (Thurston 1964). Cook (1980) and Mortimer (1976) also found that most seeds do not enter the persistent seedbank.

It is not only the likely emergence of a particular species that is important to the farmer, but also the probable size of the adult population and thus the subsequent seed input. It is therefore necessary to study the fate of the seedling population and produce transition probabilities for this stage. Density-dependent regulation of the population may occur, and deaths due to frost, drought, wind, predation and herbicides. All these factors must be taken into account in any population dynamics model. Mortimer (1976) produced such a model for four agricultural weeds with transition probabilities for each stage. The chance of establishment of adults from seedlings was only 1 - 8% mainly due to predation. Doyle et al. (1986) produced a similar model for Alopecurus myosuroides studying the long-term economic implications of control in winter wheat based on a model of the life-history together with the economics of benefits and costs of control (discussed in Chapter 7).

The aim of this thesis is the study of the dynamics of V.arvensis and L.purpureum populations in winter cereal fields in order to produce a model which could be used practically for control of the two species.

1.3 Seasonal changes in dormancy

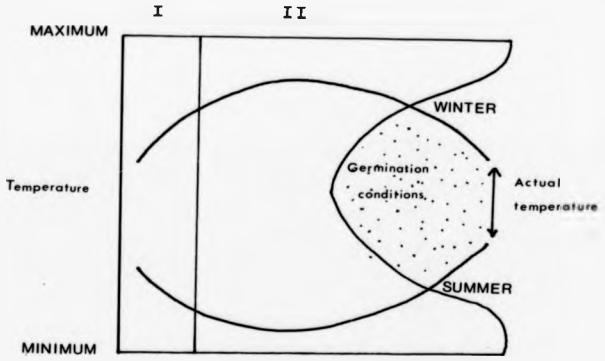
Many species undergo seasonal changes in dormancy level during burial from non-dormant to partially dormant to completely dormant and vice versa (Roberts 1964, Courtney 1968, Thompson 1970, Taylorson 1970, 1972, Vincent 1974, Watanabe and Hirokawa 1975, Roberts and Lockett 1978, Baskin and Baskin 1972, 1978, 1979b-e, 1980, Chancellor 1979, Karssen 1980/1, Roberts and Neilson 1981). Seeds which are under enforced dormancy may eventually be induced into dormancy. Such cyclic changes enable prolonged persistence in the soil since seeds then only germinate when the probability for seedling survival is high. For example, low temperature in darkness induced Lolium multiflorum into dormancy but not L.perenne, the former thus persisting in the soil longer (Schafer and Chilcote 1969).

Karssen (1982) reviews studies on cyclic changes in dormancy and suggests that induction of dormancy occurs in two stages: Firstly, conditional or partial dormancy is induced in non-dormant seeds before a state of complete dormancy is reached. For example, in Ambrosia artemisiifolia (Bazzas 1970, Baskin and Baskin 1980) non-dormant seeds were induced into conditional dormancy by 15/6°C in darkness in spring, and became light-requiring. During late spring at 20/10°C or 25/15°C in darkness, the seeds became completely dormant. Thus, complete induction of dormancy in this summer annual required sequential exposure to progressively higher temperatures in darkness. In winter annuals, the reverse occurs (Baskin and Baskin 1972, Roberts and Lockett 1978). Karssen (1982) suggested that these two stages involved hormones, ABA inhibiting germination and facilitating the development of an

ABA-independent dormancy. Factors restricting germination for a prolonged period operated via hormones to induce dormancy. However, hormonal control of dormancy is controversial (Baskin and Baskin 1985). Come and Thevenot (1982) suggested that although induced and innate dormancy levels were often identical they were different physiologically. Induced dormancy allows greater flexibility in response to environmental conditions than innate dormancy, since it is controlled by the environment itself. These cyclic changes in dormancy generally appear to be related to seasonal changes in soil temperatures. When the temperature requirements for germination coincide with the prevailing soil temperatures, germination occurs (Figure 1.2). Seasonal emergence patterns for Chenopodium album and Echinochloa crus-galli were controlled mainly by soil surface temperature, expected germination coinciding with that observed. Chancellor (1979) and Hakansson (1979) also found temperature to be the most significant factor determining peak emergence, with winter annuals emerging during rapidly falling temperatures and summer annuals during rapidly increasing temperatures. Vincent (1974) found emergence of C.album and Rumex crispus was correlated with mean soil temperature rather than temperature range, the accumulated temperature above freezing giving the best correlation. Baskin and Baskin (1983) suggested that for winter annuals, habitat temperatures were more important than moisture levels.

However, in several cases, soil moisture levels appear to be equally or more important than temperature (Newman 1963). Arabidopsis thaliana is conditionally dormant until September when soil moisture stress becomes the controlling factor (Baskin and Baskin 1972). Avena fatua germination in autumn was related to rainfall rather than to temperature (Paterson et al. 1976). Phacelia dubia (Baskin and Baskin 1971) and

Figure 1.2. Temperature control of dormancy (after Vegis 1964). Germination occurs when temperature requirements coincide with ambient soil temperatures.



I Dormant

II Partially/Conditionally Dormant

Teesdalia nudicaulis (Newman 1963) show a similar response. Roberts and Potter (1980) found flushes of germination in summer annuals were related to rainfall, though the overall pattern of emergence was unaffected and was related to temperature. Pemadasa and Lovell (1975) found soil moisture controlled the emergence and germination rate of many summer annuals, though Rozijn and Van Andel (1985) found the reverse for germination of seven dune annuals. The controlling factor probably depends on the time of emergence for each species. Early emerging species would rely more on temperature during spring, those with mid-summer peaks would depend more on rainfall, and those with late summer peaks would depend on temperature again (Roberts and Potter 1980, Ervio 1981).

Adequate moisture is necessary for imbibition to occur, but it is often alternate wetting and drying that proves stimulatory. Berrie and Drennan (1971) suggest alteration of cuticular structure and hysteretic seed proteins may cause faster germination. Vincent and Cavers (1978) and Baskin and Baskin (1982) found in Rumex crispus seeds, the longer the duration of imbibition at alternating temperatures, the faster was germination on reimbibition after drying and they lost dormancy at constant temperatures. Thus, biochemical changes that occurred during imbibition were retained. They also suggested changes in permeability, hysteretic proteins or hydration of phytochrome occurred at moisture contents insufficient for germination. Rozijn and Van Andel (1985) suggested intermittent wetting and drying was an important factor stimulating germination in seven dune annuals.

Finally, seasonality in nitrate availability may also instigate flushes of germination, either alone or acting synergistically with other

factors (Taylorson 1969, Popay and Roberts 1970). However, Vincent (1974) found no correlation with nitrate levels for Rumex crispus and Chenopodium album, although it may be important for many other species which can be stimulated to germinate by nitrate.

Three common seasonal responses have been reported, that of the winter annual, that of the summer annual, and that of species acting as both. Winter annuals are generally dormant when dispersed and require high temperature after-ripening to relieve dormancy, seeds germinating at progressively higher temperatures, low temperature inducing dormancy (Baskin and Baskin 1972, 1976). For example, 10°C to 30°C promoted after-ripening of fresh Veronica hederifolia and overcame dormancy of buried seeds, whilst 4°C induced dormancy (Baskin and Baskin 1976, Roberts and Neilson 1982). However, induction of dormancy was insufficient to account for observed dormancy so other factors must be involved. Fresh seeds were dormant but after one month's burial seeds became conditionally dormant. By early autumn the temperature range for germination had widened, declining again during winter, spring and early summer to be repeated the following year. Phacelia dubia var. dubia showed a similar pattern, with germination spread over several seasons since only some after-ripened sufficiently for autumn germination. This was possibly due to unfavourable microenvironments for germination and/or after-ripening, or due to innate differences within the seed population (Baskin and Baskin 1973). Similar patterns have been reported for other winter annuals (Håkansson 1982) such as Silene secundifolia (Thompson 1970), Sedum pulchellum (Baskin and Baskin 1977), Thlaspi perfoliatum (Baskin and Baskin (1979) and Torilis japonica (Baskin and Baskin 1973, 1975). However, Roberts (1979) found spring emergence in T. japonica which may reflect the different origins

of the seeds (see later). Cyperus inflexus had an autumn peak but after one or two year's burial, the peak was deferred to late winter and probably reflected the loss of the least dormant seeds in a heterogeneous population (Baskin and Baskin 1978). In most cases, peak emergence occurs in the second autumn after burial and probably reflects a requirement for prolonged after-ripening (more than is achieved during the summer of dispersal), or seqential temperature changes before dormancy is relieved.

Summer annuals show the opposite behaviour to winter annuals, being released from dormancy by low winter temperatures and induced into dormancy by high summer temperatures (Pemadasa and Lovell 1975). As they come out of dormancy they can germinate at progressively lower temperatures (Baskin and Baskin 1985a). Several species require chilling to overcome dormancy (Roberts 1979, Baskin and Baskin 1981, Roberts and Boddrell 1984), allowing germination in early spring. Baskin and Baskin (1977) found all the summer annuals they studied were dormant when dispersed in autumn, dormancy decreasing during spring. Non-dormant seeds of Ambrosia artemisiifolia that did not germinate were induced into dormancy in late spring, dormancy again being alleviated by winter temperatures. However, Amaranthus retroflexus and Chenopodium album were only conditionally dormant in autumn. Cyperus inflexus (Baskin and Baskin 1978), Euphorbia supina (Baskin and Baskin 1979b), and Plantago major (Roberts 1979) behaved similarly. Sawhney et al. (1984) found Avena fatua was induced into dormancy by prolonged high temperatures followed by sub-optimal temperatures, implying sequential temperature changes were important. Prolonged stratification was required before spring germination of Rumex obtusifolius and R.crispus (Totterdell and Roberts 1981). In A.artemisiifolia, Willemsen (1975)

found an interaction between stratification temperature, stratification time and germination temperature. Increasing the severity of stratification decreased dormancy but dormancy was induced by 15 weeks stratification in darkness, high temperatures in darkness, high stratification temperatures or long stratification. Thus, summer germination was favoured above spring germination, seeds being conditionally dormant. Aster pilosus (Baskin and Baskin 1979c) also showed an interaction between stratification temperature and light. Stratification in the light at relatively high temperatures (over 15°C/6°C) allowed germination in late summer as well as early spring.

Several species behave as both summer and winter annuals, with two flushes of germination. Spring-produced Lamium amplexicaule seeds were dormant when dispersed but by autumn 85% germinated in the light at warm temperatures, and at cooler temperatures in the dark, germination was increased (Baskin and Baskin 1981). During winter, dormancy increased but by the second autumn seeds were less dormant than in the first autumn. Autumn-produced seeds were also dormant when dispersed but lost dormancy by spring at spring temperatures and continued to after-ripen during summer. Thus, seeds could germinate in late summer, autumn and spring, and during both seasons the previous years crop could germinate. Similarly, Veronica arvensis seeds lost the ability to germinate at high temperatures during winter but some retained the ability to germinate at spring temperatures in the light (Baskin and Baskin 1983). Roberts (1979) found spring and autumn emergence for Torilis japonica in the UK, though this was not the case in the USA (Baskin and Baskin 1973). However, seed was collected in November in the UK, which is impossible in the USA due to climatic differences and so the seeds had ripened under different conditions and germination was

adapted to different climates. Similarly, Baskin and Baskin (1984) found Lamium purpureum behaved as a winter annual in the USA, after-ripening over the range of 5°C to 35°C/20°C. So exposure to high summer temperatures was not an absolute requirement but determined when emergence occurred (later at cooler temperatures). In the UK and Europe, germination peaks occur in spring and summer. Thlaspi arvense also behaves as a winter and summer annual (Baskin and Baskin 1979). Marks and Prince (1982) found Lactuca serriola had two peaks for emergence and demonstrated that they were not a passive response to changing temperatures but that physiological changes occurred in overwintering seeds. Fresh seeds sown in spring would not germinate in spring.

Changes in dormancy level do occur in dry storage, generally leading to a gradual release of dormancy (Karssen 1982), though less than occurs in soil (Hakansson 1979, Froud-Williams 1985), but cyclic changes depend on environmental conditions (Karssen 1980/1). Differences in the response to temperature of summer and winter annuals may arise from differences in the maturation environment of the seeds. Summer annuals mature faster than winter annuals and under different conditions and so may be physiologically different. Differences between early-dispersed and late-dispersed seeds from the same species demonstrate this. Aphanes arvensis seeds collected in September were less dormant at winter temperatures than those collected later (Roberts and Neilson 1982).

Hakansson (1979) found germination of summer annuals to be more restricted and to more specific temperatures in summer and autumn, whereas winter annuals had less marked seasonal variation and no preference for early spring germination, restricted summer germination

being less marked. Thus, species behaving as both are more likely to be winter annuals that are not induced into complete dormancy by low temperatures, than summer annuals which have gained the ability to after-ripen during summer. Within these categories, patterns of response vary between species since each is adapted to a particular niche. Rozijn and Van Andel (1985) studied seven species of dune annuals and all differed in terms of the length of after-ripening required, the optimum temperature for germination and percentage dormancy. They suggested that species specific temperature ranges to break dormancy were related to species specific temperature dependent physiological processes of after-ripening.

Cyclic changes in dormancy status thus ensure that the species is adapted to respond to environmental conditions only when there is a high probability that a particular seed population will be able to complete its life-cycle.

1.4 Factors affecting dormancy and germination of buried seeds

Studies on the principles of environmental control of germination may ultimately result in the interpretation and, if possible, prediction of the field behaviour of troublesome weeds (Karssen 1982). Harper (1957) classified dormancy into three types: innate, induced and enforced. Innate dormancy is present when the seed is dispersed, whilst induced dormancy results from conditions inclement for germination but remains even when favourable conditions return. Enforced dormancy is that which occurs when environmental conditions are unfavourable for germination, but does not remain once the conditions have changed.

Enforced dormancy is often the major determinant of seed survival during burial when innate dormancy breaks down, and prevents *in situ* germination which may lead to the death of the individual if the seedling is unable to reach the surface, or if conditions are unfavourable for growth. For example, Roberts and Feast (1972) found burial enforced dormancy of 20 arable weeds and depressed germination.

There is often a positive relationship between burial depth and degree of enforced dormancy (Holm 1972, Frankland 1977), whilst induced dormancy shows the reverse trend in several species (Thompson 1970, Taylorson 1972, Karssen 1982), suggesting that enforced dormancy replaces innate dormancy with increasing depth of burial. For example, *Setaria faberi* (Taylorson 1972) and *Crupina vulgaris* (Thill et al. 1985) seeds lost viability most at intermediate depths, possibly reflecting a critical depth where both innate and enforced dormancy were relatively low. However, Sawhney et al. (1984) found *Avena fatua* seeds were induced into dormancy as depth of burial increased, so a general rule may not be applicable in all situations.

Several factors have been implicated in enforcement of dormancy during burial: Lack of light (Wesson and Wareing 1969), high carbon dioxide levels and low oxygen levels (Bibbey 1947), anaerobically produced volatiles (Holm 1972), low alternation of temperature (Stoller and Wax 1973, Thompson et al. 1977), osmotic inhibition, supra-optimal temperatures (Khan and Karssen 1981) and low nitrate levels.

1.4.1 Gaseous environment

The oxygen requirements for dormancy-breaking and initiation of germination have not been established. Oxygen/carbon dioxide ratios

are lower in soil than in air (Russell 1961) and Bibbey (1947) and Barton (1962) suggested that this maintained dormancy during burial. For example, Harper (1957) found that many light-insensitive species germinated when exposed to the air which implied that the soil atmosphere and temperature were important in preventing germination. However, many species are only initially insensitive to light and - as will be shown later - lack of light is also an important factor enforcing dormancy during burial.

Sensitivity to a low oxygen/carbon dioxide ratio varies between species (Barton 1962, Roberts 1972). Popay and Roberts (1970) found Senecio vulgaris and Capsella bursa-pastoris were inhibited from germinating by such ratios, and induction into complete dormancy has been reported (Cumming 1959). Similarly, Longchamp and Gora (1979) found germination of three annual weeds was reduced at below 8% oxygen and seeds became completely dormant after lower levels for longer periods unless aerated with nitrogen or 2% oxygen.

However, low oxygen/carbon dioxide ratios are unlikely to be a major factor enforcing dormancy in soil. For example, laboratory results were not confirmed in the field for several species investigated by Longchamp and Gora (1979). Furthermore, increased oxygen had no effect on two species tested by Kolk (1962) and some species germinated without oxygen (Kolk 1962, Benjamin 1974) or with increased carbon dioxide (Roberts 1972). In fact, Rumex crispus seeds were induced into dormancy by oxygen.

In waterlogged soils, the oxygen/carbon dioxide ratio is reduced even further and under such anaerobic conditions, anaerobic respiration

produces volatiles which can inhibit germination (Wesson and Wareing 1969, Karssen 1982). However, induction of dormancy is generally aerobic (Karssen 1981) though different mechanisms may exist since water-stress-induced dormancy is terminated by light whereas thermodormancy is not, though this may reflect quantitative differences. High levels of ethylene are produced in waterlogged conditions or in compacted soil and these are generally inhibitory (Smith and Russell 1969) though low levels can break dormancy (Olatoye and Hall 1973). Karssen (1982) suggested that the degree of anaerobic respiration, and therefore the degree of enforced dormancy, depends on depth, soil moisture and soil type. However, the sensitivity of the seed population to such conditions must also be considered and may partly explain species and even population differences in in situ germination. Sensitivity may vary seasonally with the dormancy status of the seed population.

Except in waterlogged conditions, the soil atmosphere generally contains less than 1% carbon dioxide and over 19% oxygen (Russell 1961). However, in the microenvironment of the seed, the ratio presented to the embryo is affected by respiration of the seed and microorganisms, humidity and temperature, and also mucilage (as occurs in the seedcoat of Viola arvensis), or covering structures which may render gas exchange difficult.

1.4.2 Light

Light stimulates germination in the majority of species studied and Froud-Williams (1985) found it to be the predominant factor affecting germination in five grass species. Lack of light is considered to be a

major factor enforcing dormancy in soil. Deeply buried seeds (deeper than a few centimetres) can show physiological changes attributable to an absence of light (Bliss and Smith 1985). However, Woolley and Stoller (1978) have shown that light does penetrate significantly into certain soils. They found that the quantity and quality of light which penetrates soil depends on soil type and its physical state. A dry sandy loam transmits less light than a moist one, whilst a dry silty clay-loam transmits more than a moist one. Less than 1% of incident light penetrates more than 2.2 mm in clay loam or sand, though more in sandy than in less sandy soil (Karssen 1980/1).

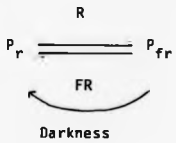
Several workers have shown lack of light to be important in enforced dormancy. Sauer and Struik (1964) showed that disturbing soils in trays in the light caused 90% of the trays to have more seedlings than those disturbed in the dark. Wesson and Wareing (1967) and Feltner and Vesecky (1968) found most germination occurred on exposure to light. Wesson and Wareing (1969) showed complete dependence on light at all depths, though the effects of alternating temperatures were not considered. Sinapsis arvensis and Plantago major responded negatively to light as depth of soil cover increased and light quality and fluence rate decreased (Frankland and Taylorson 1985).

Attempts have been made to determine, directly, the response of seeds to below-soil light. Using lettuce seeds, Woolley and Stoller (1978) noted a significant increase in germination over dark controls when seeds were buried beneath 2mm of 0.84-1 mm diameter silty clay-loam peds. However, they assume that the covering soil is well-aerated and supplies moisture to the seeds equally at all depths. Van der Meijden and van der Waals-Keoi (1979) attempted to control such factors by using

filter paper beneath a window covered by sand of different depths so air and moisture supply was constant. Germination of Senecio jacobaea was promoted by light filtered through up to 4mm of sand.

Sensitivity depends on the pigment phytochrome. Phytochrome exists in two states,: inactive (Pr) and active (Pfr) which are interconvertible. Red light (R) transforms Pr to Pfr and far red light (FR) or darkness transforms Pfr to Pr. (Figure 1.3). The rate of these reactions is temperature-dependent (Hsaio and Vidaver 1984)

Figure 1.3 Phototransformation of phytochrome (after Borthwick et al. 1954)



The two states exist in equilibrium, the ratio depending on the proportion of R/FR present. Irradiation with R shifts the equilibrium to 81% Pfr and 19% Pr (Black 1970). Visible light maintains a relatively high proportion as Pfr. Bonnewell et al. (1983) recently found that, at least in Typha latifolia, FR did not revert active to inactive phytochrome but simply 'turned off' the germination process which could be resumed again by a second R irradiation. It is unknown how widespread this effect is likely to be. Sensitivity to light

varies between species (Gross 1985). Germination can be stimulated by a green "safe" lamp (Pressman et al. 1977, Baskin and Baskin 1979) and even FR is promotive when sensitivity is high.

Wesson and Wareing (1969) found burial induced a light requirement for germination in many light-insensitive or light-inhibited seeds. This has been discussed in terms of gaseous inhibitors, temperature and anaerobiosis in soil, but any factor inhibiting germination of non-dormant seeds can induce dormancy and render seeds light-requiring. In some species, a light requirement is induced by contact with soil. Gross (1985) and Froud-Williams (1985) found that four weeks dry storage induced a light requirement in Avena fatua seeds. The degree of induction varied between populations and may have reflected differences in initial dormancy or microenvironmental differences experienced by the seeds during burial. The proportion of light-requiring seeds increased with the duration of burial and may reflect induction of dormancy or loss from the population of the least dormant seeds. Taylorson (1970, 1972) supported the findings of Wesson and Wareing (1969). He buried seeds of several weed species in soil in the field, recovered them at three monthly intervals and monitored their response to light and temperature. He found that attainment of light-requiring dormancy mechanisms could occur in at least two ways: Firstly, a relatively nondormant lot of seeds could become light-requiring, presumably by loss of the dark-germinating population; secondly, a relatively dormant lot of seeds could become light-sensitive. However, there were no controls with unburied seeds and it is unclear whether duration of burial or season of burial was important. Taylorson (1972) proposed that burial 'unmasks' a light response rather than leading to the acquisition of a light requirement and suggested that changes in the total phytochrome

concentration were involved rather than changes in the sensitivity of receptors to existing concentrations. In general, Taylorson's studies supported the hypothesis that phytochrome control is a principal dormancy mechanism of weed seeds in soils which might be present initially and retained after burial, or acquired during burial. However, not all species became light-sensitive and other dormancy mechanisms were therefore involved.

Taylorson (1972) proposed soil temperature to be the predominant factor affecting phytochrome during burial. Baskin and Baskin (1972) found retention of a light stimulus in darkness depended on the temperature during burial. Several species during burial lose their light-requirement at low temperatures if they are winter annuals (Baskin and Baskin 1985), or at high temperatures if they are summer annuals (Taylorson and Hendricks 1969), when they are least dormant. This may be due to reduced thermal decay and/or reversion and increased sensitivity to R(Esashi 1985). Reversion of Pfr to Pr in darkness is probably one effect of burial since no light requirement develops if this is prevented in Chenopodium bonus-henricus (Duke et al. 1977). Where germination apparently depends on photoperiod (Taylorson and Hendricks 1971) control probably involves a balance between synthesis and destruction of Pfr. Cone and Spruit (1983) found germination was limited by the availability of a substrate (x) reacting with Pfr and proposed that the onset of secondary dormancy resulted from temperature-dependent loss of x or a decrease in effectivness of Pfr-x.

Prolonged white or red light inhibits germination in fresh seeds of several species (Hsaio and Simpson 1971, Bewley and Black 1982, Froud-Williams et al. 1984, 1985, Bliss and Smith 1985) generally at low

temperatures (Popay and Roberts 1970, Froud-Williams 1985). This effect declines as seeds lose dormancy, so induction of a light-requirement by burial may simply be due to ageing in the soil. Several theories have been proposed to explain light inhibition (see Black and Wareing 1960, Hartmann 1966, Kendricks and Frankland 1969).

Frankland (1980) suggested that two steps are involved in the sequence of events leading to germination, the first being promoted by red light and the second inhibited by high irradiance. The relative importance of the two stages would determine the overall effect on the seed population. In Sinapsis arvensis Bartley and Frankland (1981) found control of germination depended on promoting reaction dependent on the proportion of phytochrome as Pfr and an inhibiting reaction dependant on the rate of cycling. Rapid cycling meant the lifetime of the active complex was too short to achieve physiological action. However, since photoinhibition can operate at a late stage in germination, an effect independent of this depletion of the active complex by rapid cycling was proposed. Since dark germination exceeds that in the light only at lower temperatures in several species (Mithorpe 1950, Popay and Roberts 1970, Froud-Williams et al.. 1984), thermal reversion of Pfr in darkness at higher temperatures may reduce it below a critical level. It is important to note, however, that in Poa pratensis phytochrome is not involved and blue light is responsible for much of the inhibition (Hendricks et al. 1968).

It would be misleading to assume that all changes in phytochrome during burial occur in darkness since many seeds occur within the top 2mm of soil and here light can penetrate, the degree of penetration and the quality depending on soil type. Frankland (1981) showed the R/FR ratio

beneath 1mm layers of dry sandy soil, moist sandy soil and silty clay loam was 0.4, 0.6 and 1.0 respectively. However, Mandoli et al. (1982) found an initial decrease with depth but subsequently, the ratio rose again. Bliss and Smith (1985) found particle size distribution was important due to packing - increasing the amount of fine sand reduced the R/FR ratio. Such variation in the light penetration between soil types would not only affect the state of phytochrome in the seeds and their light-sensitivity but may also lead to genotypic differences in light requirements between populations. In this experiment, seeds responded to very low light levels and even 6mm of sand allowed some species to germinate (though he did use fluorescent lights which have a higher R/FR than natural daylight). Even 9mm of sand only reduced the R/FR to 0.21. However, at this depth thermal reversion probably exceeded phototransformation of phytochrome so little germination would be expected.

Phytochrome may act via hormones since several are implicated in control of dormancy. However, the importance of hormones is unclear. Bewley and Black (1982) reviewed the evidence and found that all hormonal effects require light, implying that Pfr does not simply exert its effect by hormone production.

1.4.3 Temperatures

The reduction of temperature alternations with depth is another factor maintaining dormancy of buried seeds since alternating temperatures between 10°C and 40°C are stimulatory for most species (Steinbauer and Grigsby 1957, Mason 1976, Thompson and Grime 1983, Williams 1983, Thompson and Whatley 1984). Amplitude of diurnal fluctuations may be

more important than light in sensing proximity to the surface since it is not attenuated as effectively by soil as is light. Totterdell and Roberts (1980) listed nine attributes of alternating temperatures which may be stimulatory: The number of cycles, their amplitude, the value of the upper or lower temperature, the time spent at each, the rate of increase or decrease, and the timing of cycles with respect to ontogenetic changes in sensitivity of the seeds. Amplitude within a 15°C to 25°C range was important for Rumex obtusifolius and R. crispus: Vincent, (1974), Grime and Thompson (1976) and Probert et al. (1986) found similar effects. Thompson and Whatley (1984) found a positive relationship between amplitude and stimulus up to 19°C range for several species. In each case, the shorter period was at the higher temperature as it would be in the soil. The number of cycles was also important for the Rumex species and for Dactylis glomerata (Probert et al. 1986). As the upper temperature increased above 25°C, the optimum period spent at it decreased, and vice versa for the lower temperature. Probert et al. (1986) found that seeds of D. glomerata were sensitive to the relative period spent at the warm or cool phase.

Probert et al. (1986) indicated that an alternating temperature requirement does not reflect an adaptation to a diurnal rhythm since shorter changes or shifts are equally effective in many species. Increasing temperature was more stimulatory than decreasing temperature, Vincent (1974) found the value of the maximum temperature was important and Janssen (1973) found the maximum and mean temperatures were most important for Myosotis arvensis. whilst the mimumum and mean values were most important for Veronica arvensis in the light. However, Froud-Williams (1985) found that, for 4 out of 5 grass species, germination at alternating temperatures was not significantly different

from the mean of that range, though these results only applied to one year and to one population.

The relative importance of light or alternating temperatures probably depends on the habitat of the species. Williams (1983) found alternating temperatures to be most important for several grass species whilst Froud-Williams (1985) found light to be most important. The former were from grassland habitats where the canopy is dense such that alternating temperatures would be more important than light and the latter from an arable habitat.

1.4.4. Light and temperature interactions

Light and temperature interact to stimulate germination in many species. Vegis (1964) found the narrow temperature range for germination was often widened by light. Evanari (1957) found the response to light was greatest at unfavourable alternating temperatures, whilst Toole et al. (1957) found the reverse. Alternating temperatures replace light in some species (Toole et al. 1957). Other species require both, at least when fresh and dormant (Thompson and Grime 1983), or there may be a strong positive interaction (Vincent 1974, Vincent and Roberts 1978, Roberts and Totterdell 1981, Probert et al. 1986). Thompson and Grime (1983) found light and alternating temperatures stimulated germination in 46 out of 112 species, the responses varying from an absolute requirement for over 5°C change to polymorphism where some seeds germinated at constant temperatures whilst others responded to small fluctuations. In Ranunculus repens. darkness increased the amplitude required, whilst in small-seeded species with buried seed reserves darkness was completely inhibitory, and species with persistent

seedbanks responded to alternating temperatures in darkness. They found a consistent relationship between seed size and response to light and alternating temperatures, larger seeds requiring smaller fluctuations since they can emerge from greater depths where fluctuations would be smaller.

Hendricks and Taylorson (1978) found the effects of alternating temperatures could be reversed by FR light and Williams (1983) and Washitani (1985) found species requiring large temperature fluctuations were also strongly inhibited by FR. This implies, therefore, that phytochrome is involved in the response and also indicates that 'gap detection is a suite of correlated responses' (Williams 1983). Thompson and Whatley (1984) used a thermogradient bar and soil to test germination requirements of buried seeds. Unlike Thompson and Grime (1983), they found light could not entirely substitute for alternating temperatures and so they suggested that burial induced a requirement for both light and alternating temperatures. The effect of light can also be influenced by constant temperatures though this is not really relevent to field situations. Kolk (1962) reviewed the evidence and found that the higher the temperature and light intensity, the shorter duration was required and Roberts and Totterdell (1981) confirmed this. Wulff and Briceno (1976) suggested that the response to temperature depends on the relative rates of phytochrome destruction and phytochrome controlled reactions. Thus, at 40°C in Ludwigia octovalis little light was needed since the rate of promoting reactions was high so a small amount of Pfr was efficiently used. However, membrane reorganisation may also be involved. Siegel (1950) found crabgrass seeds were light-inhibited if pre-chilled, light-sensitive at room temperature, and light-obligate at higher temperatures. A light requirement was also

induced by high temperatures in Great Lakes lettuce seed (Borthwick et al. 1954) and high dark germination only occurs at low temperatures in several species as discussed earlier.

Chilling temperatures also interact with light (Vincent and Roberts 1978, Roberts and Totterdell 1981). Stratification in the light of Rumex crispus removed the light requirement at high alternating temperatures (Baskin and Baskin 1978). Vincent (1974) found chilling in the dark did not enhance light sensitivity and in some species it induced a light requirement, but one months chilling in the light increased the temperature range for germination in all but Spergula arvensis. Capsella bursa-pastoris and Chenopodium album required stratification before becoming light sensitive (Benjamin 1974). Willemsen (1975) found the temperature of stratification affected optimum germination only in the dark.

Chilling may also have a mechanical effect, creating a more open and porous seed coat in Convolvulus arvensis (Jordan and Jordan 1981) and cracks in the carpel wall in Polygonum pennsylvanicum. Alternating freeze-thaw cycles increased germination of Echinochloa crus-galli, C.album and Amaranthus retroflexus. possibly by affecting the integrity of the seed coat. Roberts and Boddrell (1985) found reduction of dormancy by winter burial probably involved the seed coat since its removal allowed germination in summer and autumn.

The physiological mechanism involved in the stimulation of germination by light and alternating temperatures is unclear. Toole et al. (1957) suggested a new balance of respiratory products were produced at high temperatures which were only favourable for germination at low

temperatures. But this was refuted by Cohen (1958) and it is now accepted that temperature and light interact at the membrane level, temperature affecting membrane organisation and thus phytochrome action by increasing sensitivity to Pfr (Taylorson and Hendricks 1977, VanDerwoode and Toole 1979, Hand et al. 1982, Williams 1983, Chadoeuf-Hannel and Taylorson 1985). However, this does not explain the effect of other stimuli and it is not known whether membrane organisation changes at germination temperatures.

Wulff and Briceno (1976) and others have suggested that temperature affects reaction rates themselves. They suggested that the response to temperature depends on the relationship between the temperature dependent rate of phytochrome destruction and the rate of phytochrome controlled reactions. Whatever the primary effect is, changes in membrane organisation and effects on reaction rates are probably both involved in the interaction of light and temperature in stimulating germination.

1.4.5 Light, temperature and gaseous interactions

Gases may also interact with temperature and light. In lettuce, germination inhibition at 35°C was overcome by high carbon dioxide levels. Thornton (1936) suggested that carbon dioxide prevented thermal inactivation of phytochrome.

1.4.6 Nitrate

Nitrate breaks dormancy of many light-sensitive species, although it generally interacts with other stimuli and in some cases is inhibitory

or ineffective (see Lyne 1985 for review).

Seasonal variations in soil nitrate concentrations occur and may be important in terms of germination flushes. Peak concentrations in spring and autumn coincide with seedling flushes then (Popay and Roberts 1970, Benjamin 1974). Friejsen et al. (1980) found that a loose disturbed soil layer favoured mineralisation and nitrification so this may be one effect of cultivation.

Since there is a seasonal cycle of nitrate availability (Taylorson et al. 1982) there may be a correlation between nitrate availability and nitrate requirement of a species (Walter 1963, Popay and Roberts 1970, Lyne 1985). In particular, Froud-Williams (1985) found that only field populations of Galium aparine were stimulated to germinate by nitrate, not hedgerow populations where nitrate levels were lower.
However, the relevance of such results to field conditions must be demonstrated and this is difficult. The response to nitrate may depend on the environmental history of the seed (Roberts and Lockett 1975). Lyne (1985) found changes in dormancy in Cardamine hirsuta varied with storage conditions such that results from laboratory-stored seeds must be treated with caution. No response to nitrate developed if stored in a Stevenson Screen. Burial resulted in the loss of a response to nitrate in 3 out of 4 species tested but in Artemisia vulgaris a nitrate response developed after three months and was subsequently lost. Cyclic changes were also observed and this must be taken into account when testing seeds. The loss of response to nitrate may reflect the fact that the requirement is satisfied before temperature requirements are met and is only manifested as alternating temperatures increase (Lyne 1985). Naturally buried seedbanks were not stimulated by nitrate

at all and Schimpf (1977) found no response to nitrate after simulated field conditions.

It is also important to ascertain whether the concentrations used reflect field levels; 0.2% KNO_3 has often been used in experiments. It has been suggested that nitrate fertilizer may stimulate germination but there have been few controlled experiments to test this. Less than 0.25% KNO_3 broke dormancy of Avena fatua which is equivalent to 80-100 kg/ha of nitrate nitrogen (Sharma et al. 1976). Taylorson (1969) found Potentilla norvegica was photosensitized by as little as 33 kg/ha equivalent. Watkins (1966) and Roberts (1966) found all applied fertilizers stimulated emergence of Avena ludoviciana, especially in January when nitrogen availability was highest. Pulchar (1984) found plots with higher nitrogen fertilization rates had fewer seeds in the soil but this may have resulted from increased competition reducing reproduction. However, Fawcett and Slife (1978) found field application of ammonium nitrogen had no stimulatory effect and suggested that field levels were already saturating. But in the field, interactions with other stimuli may create discrepancies from expected results (Lyne 1985).

1.4.7 Nitrate and light interactions

Interactions between light and nitrate are well documented (Toole et al. 1957, Wesson and Wareing 1967, 1969, Henson 1970, Vincent and Roberts 1977, 1978, Baalen 1982). Phytochrome enhances nitrate reductase activity in the lichen Evernia prunastri, so light and nitrate may act via the same physiological system (Avalos and Vicente 1985). Baalen (1982) found light and substrate interacted to affect germination of

Digitalis purpurea, so results from filter paper may not reflect field conditions.

1.4.8 Nitrate and temperature interactions

Nitrate also interacts with temperature to stimulate germination (Popay and Roberts 1970, Vincent and Roberts 1978, Karssen 1980/1). Lyne (1985) found the greatest additional germination with nitrate in many of the species tested occurred at the larger alternating temperature ranges. In several cases, promotion by nitrate only occurs at unfavourable temperatures (Toole et al. 1956, Froud-Williams 1985). Chilling can also affect the response to nitrate (Vincent and Roberts 1977, Schimpf and Palmblad 1980). Lyne (1985) found that generally, higher nitrate concentrations occur at the soil surface where the diurnal temperature range is greatest so a synergistic effect may occur.

1.4.9 Interactions between light, temperature and nitrate

Interactions between light, temperature and nitrate also occur (Steinbauer and Grigsby 1957, Roberts 1973, 1975, Vincent and Roberts 1977, 1978, Roberts and Benjamin 1979, Williams 1983 Lyne 1985), absolute requirements for any particular stimulus being rare. Chenopodium album germination was stimulated by an interaction between light, temperature and nitrate, each of which could partially substitute for the other (Henson 1979). Phytolacca americana required all three (Karssen 1980/1, Roberts 1981). Vincent and Roberts (1978) found two major responses. Firstly, some species required alternating temperatures with or without chilling, plus light, the response to light being improved by nitrate after chilling, and nitrate and alternating

temperatures being synergistic. The greatest response was obtained with all three plus chilling. Secondly, Spergula arvensis showed no significant response to any factor alone, except slightly to nitrate and it was inhibited by alternating temperatures and by all factors after chilling, i.e., it was induced into dormancy. Williams (1983) found alternating temperatures had the greatest effect on several grassland species but other factors may have had larger effects had different levels been used. Prechilling increased the germination of most species at constant temperatures but the extent depended on light and nitrate. Persistence in the seedbank was generally related to specificity of germination requirements, though differences in seed morphology and physiology created differences in persistence even when response to stimuli were similar. Froud-Williams et al. (1986) found nitrate had little effect on arable collections of Poa trivialis, unless with light and constant temperatures but it did stimulate germination of grassland populations with alternating temperatures in darkness.

Responses to stimuli reflect dormancy status (Kolk 1962), those requiring more precise stimuli being most dormant. Such information is important in explaining emergence patterns. For example, Capsella bursa-pastoris and Poa annua emergence can be explained in terms of nitrate level, moisture content and temperature in the soil (Benjamin 1974). Interactions not involving light cause in situ germination. For example, the rate of loss of Poa annua from undisturbed soil was greater than that of C. bursa- pastoris or Chenopodium album since after stratification, nitrate, alternating temperatures or light were stimulatory. Differences in rate of loss disappeared in disturbed soil since the other two were stimulated by light.

Adkins (1981) suggested that dormancy is a result of several mechanisms and the balance of their relative importance may change during burial. Metabolic pathways may differ between dormant and non-dormant seeds but this is controversial (Bewley and Black 1982). Changes in sensitivity to hormones may be involved. Since light, temperature, nitrates and gases can act synergistically in removing dormancy, there can be no single mechanism acting upon dormancy during burial and thus laboratory tests must be interpreted with caution. Laboratory results should confirm observed emergence patterns before being accepted.

1.5 Variability in dormancy

Variability in dormancy levels between and within populations, or between years within the same population has been reported for many species. If this is a general phenomenon, interpretation of results from any one source must be treated with caution since they may not be representative of the species as a whole.

Dormancy can be determined genetically or phenotypically, and genetic control of dormancy can be modified by the environment. Thus, innate dormancy of the seeds in the seedbank - that prevailing when the seeds are dispersed - can vary depending on the genetic make-up of the seedbank and on maternal conditions in which the constituent seeds ripened. As Harper puts it: "There is clearly a spectrum of requirements by the seeds in a single sample which may reflect different genotypes, different maternal influences and perhaps different ages and ripening conditions" (in Jain 1982).

Three sources of variation are possible: Variation between populations;

variation between individuals within populations; and variation between seeds on the same individual. Only the first two sources are likely to be attributable to genetic variation.

1.5.1 Interpopulation variation in dormancy - phenotypic and genotypic effects

Phenotypic variation between populations has been demonstrated for several species. Chenopodium album can produce four seed types each with different germination characteristics. Harper and Williams (1965) found individual plants and even whole populations producing only one seed type, whilst others produced the different types in various proportions. Palmblad (1969) tested seeds from 174 populations and 105 species. Of 22 populations from 15 species, 12.5% exhibited germination polymorphism. Miller et al. (1982) found dormancy varied between 230 accessions of Avena fatua and was influenced by location and season of collection. However, they found the most dormant seeds in the coolest areas. Agrostemma githago and Silene secundiflora showed interpopulational differences within Europe in both germination and emergence patterns, southern populations being summer dormant and northern populations being winter dormant (Thompson 1970,1973,). Dactylis glomerata and Lolium perenne showed similar variation between different climatic and altitudinal areas of western Europe. Rai and Agrawal (1985) found seeds of Ipomoea muricata from different localities varied in colour, weight, size, chemical constituents and germination behaviour. They found a positive relationship between seed weight and rainfall, with heavier seeds having a higher percentage emergence. Poa

trivialis seeds from grassland habitats were more responsive to alternating temperatures and seeds from arable habitats to light quality (Froud-Williams et al. 1986). Many other reports of interpopulation variation could be cited (Roberts 1964, Ramakrishnan 1965, Kolk 1978, Roberts and Chancellor 1979, Staniforth and Cavers 1979, Jana et al. 1979, Totterdell and Roberts 1980, Baalen 1982, Naylor and Abdalla 1982, Jain 1982, Naylor 1983, Grubisic et al. 1985, Pegtel 1985, Wilson 1985).

In order to determine whether any genetic differences in dormancy exist between populations, seeds must be taken from plants and grown in a uniform environment in order to eliminate phenotypic effects. Any differences still existing must be genetic. Garbutt and Witcombe (1986) reviewed the literature on genetic control of dormancy. For example, Probert et al. (1985, 1986) grew and stored seed of Dactylis glomerata under uniform conditions and found marked variability only in European populations, not British ones, possibly since the European populations were more isolated from each other. Northern (cooler) populations were dormant and southern populations were not, the mean summer temperature being an important factor.

Harper and McNaughton (1960) and Garbutt and Witcombe (1986) found maternal predominance in determining seed dormancy in Papaver spp. and Sinapsis arvensis and Garbutt and Witcombe (1986) suggested that this would prevent over-reaction to temporarily suitable environments. Hacker et al. (1984) found the control of dormancy in equatorial populations of Digitaria milanjiana operated through a parent-seed interaction, crosses between a dormant maternal genotype and a non-dormant paternal genotype being less dormant than if both were

dormant. They suggested this would be adaptive in situations of rapid environmental change, allowing variation between populations to expand the areas colonised. Dormancy was related to the distribution of wet and dry seasons in the region of origin, high rainfall areas being associated with low dormancy.

Genotypic and phenotypic effects often interact in the control of dormancy, some genotypes being more susceptible to environmental influences than others. Blacklow (1985) found an interaction between the genotype and environment in the control of dormancy of Bromus diandrus in only 1 out of 14 populations. In the other 13 control was genetic. Cheam (1985) found such an interaction only in northern populations of wild radish.

Genetic differences in dormancy have been reported on a smaller scale. Froud-Williams (1985) found hedgerow populations of Galium aparine were less dormant than field populations. Nitrate only stimulated germination of field populations, indicating adaptation to the arable field situation. Naylor and Jana (1976) found the population of Avena fatua from cultivated areas was most dormant and had the highest degree of genetic control of dormancy. Naylor (1983) found such adaptation to particular cultivation regimes in several species. Summer-fallow selected strongly against non-dormant lines during only one three-year rotation. However, 2 out of 8 lines showed no response, so factors other than duration of dormancy contribute to determine fitness. Continuous cropping selected for non-dormant lines and he suggested a relatively greater loss of viability of seeds in soil, a relatively greater seed yield of non-dormant lines, or the genes controlling dormancy may influence other adaptive characteristics. Other workers

suggest that the expression of genes conferring seed dormancy in the Graminae is sensitive to the environment during seed maturation, increasing temperature leading to decreasing dormancy. Water stress during development also reduces dormancy in dormant types. Differences exist between species in the level of response to both.

Few examples of genetic variations can be cited and most reports deal with phenotypic effects since these are easier to determine.

1.5.2 Sources of phenotypic variation

Phenotypic variation is determined by the environment in which the seed develops or may be due to plant size or age. Such effects can create differences in dormancy levels of seeds produced in different seasons, from different plants in a population and even from different positions on the plant. Bewley and Black (1982) and Cutterman (1985) reviewed the literature on variation in dormancy resulting from variation in the pre-burial environment. Roberts (1964) found that in 11 species of annual weeds, maternal conditions affected dormancy, and Roberts and Lockett (1975) suggested that many discrepancies in reports of Stellaria media dormancy were associated with differences in the season of collection, storage conditions and age of seeds. Jain (1982) indicated that storage will influence populations to different extents depending on their initial dormancy level.

A. Seasonal variation

Yearly variation in dormancy level has been reported for several species (Toole et al. 1957, Newman 1963, Baskin and Baskin 1973, 1983, Wilson

1973 Totterdell and Roberts 1980, Roberts and Neilson 1982, Roberts and Boddrell 1984). Roberts (1979) found yearly variation in viability of seed samples of Heracleum sphondylium which could be attributed to dormancy differences since he relied on emergence. However, Thill et al. (1985) found that yearly variation in Crupina vulgaris achenes was inherent yet not related to dormancy since this did not vary. Neither was it due to microclimatic differences since significant germination and decay occurred over a range of precipitation and temperature conditions. They suggested predators and pathogens may have varied. Froud-Williams (1985) found that different collections of Poa annua and Alopecurus myosuroides had different optimum temperatures and dormancy levels: In P.annua later collections were less dormant and in A.myosuroides, vice versa. Staniforth and Cavers (1979) found September achenes of Polygonum species were completely dormant but those collected in October were less so. However, when attributing such variations to the season of collection it must be ascertained whether seeds were from the same population. In spite of this seasonal variation, emergence patterns do not vary greatly so general conclusions obtained from one population are not invalid (Roberts and Neilson 1980).

B. Intra-population variation in dormancy

Between plants within a population, Cavers and Harper (1966) found variation in dormancy. Pitelka et al. (1983) found variations in achene weight and thus probability of germination and survival in Aster acuminatus within flower heads, between heads and between plants, taller plants producing heavier achenes. This variation was mostly phenotypic and they suggested that variation in light intensity within the forest was the major cause. This may also be true within crops, weeds growing

taller in response to crop competition in order to reach the light and this may affect seed weight and possibly dormancy, as it does in Rumex obtusifolius though not in R.crispus (Cideciyan and Malloch 1982)

C. Within plant variation in dormancy

Further variation has also been found between seeds from the same plant. The heaviest and earliest seeds of Scabiosa columbaria (Rorison 1973), Hyptis suaveolens (Wulff 1973) and Lupinus texensis (Schaal 1980) are the least dormant. Chenopodium album has three categories of seeds with different dormancy levels: Brown seeds are non-dormant, black-reticulate seeds are dormant with dormancy broken only by nitrate, and in black-smooth seeds dormancy is broken by nitrate and also partially by chilling. Variability also occurs within categories (Williams and Harper 1965), early seeds having a higher proportion which are brown. The photoperiod can also influence the relative proportions of each type (Cumming 1963). Salsolla volkensii and Aellenia autrani produce two distinct seed types: chlorophyllous seeds are practically non-dormant and achlorophyllous seeds are dormant (Negbi and Tamari 1963, cf. E H Roberts 1972). Commelina benghalensis produces four seed types varying in dormancy and temperature requirements. Walker and Evensen (1985) suggest this is related to different conditions under which aerial and underground seeds ripen. Datta et al. (1972) found seeds from one plant of Aegilops ovata differed in weight and dormancy and this was influenced by the thermoperiods and photoperiods experienced during growth. Thus, a wide range of germination characteristics were produced in seed populations. Such characteristics were heritable so the fate of the third generation was partly determined by factors determining the seed characteristics of the

first generation. Cohen (1966) proposed the ratio of dormant to non-dormant seeds produced by an annual should be directly proportional to the risk of reproductive failure for the progeny.

The position of development of the seed on the plant may affect its dormancy due to variation in the microenvironment, especially light and moisture (Cutterman 1985). Schaal (1980) found that much of the variation within individuals of Lupinus texensis was due to position on the plant. This may influence the weight of the seeds (Cavers and Harper 1968, Datta et al. 1972) and thus its drying rate which will affect the state of phytochrome in the dry seed. However, weight is not always important: Morgan and Berrie (1970) found the larger proximal seed in Atriplex patula to be less dormant than the smaller seed but this reflected the fact that the former acted as a primary sink for promotive substances. Similarly, the smaller basal spikelet of Aegilops kotschyi is more dormant than the others and is probably related to endogenous levels of growth regulators. But imposition of dormancy by the parental environment is not related to the degree of development of the caryopses (Wurzburger and Koller 1976). The order of development of the seed may be important since this will influence the environmental factors experienced. For example, L.purpureum sets seed over an extended period and seeds mature from the base upwards and in first formed flowers first. Thus, first formed seeds in summer experience cooler and wetter conditions during maturation than later formed seeds, and the crop is at a different stage so the light environment will be different. Silvertown (1984) proposed a 'clock model' for seed maturation, whereby fruit, testa and endosperm develop at different rates in different seeds creating different dormancy states.

1.5.3 Factors influencing dormancy status during maturation

Several factors influence the dormancy level of the seed as it matures. These are light, daylength, temperature, moisture availability, gaseous environment, and mineral nutrition.

A. Light

The light environment during maturation has a significant influence on the light requirement of seeds, by affecting the proportion of phytochrome as Pfr when the seed is dry. Phytochrome is preserved in the form corresponding to the irradiation quality as the seed reaches the critical moisture content for phytochrome transformation (Taylorson 1982). This is generally 15% (Bartley and Frankland 1984). However, Bartley and Frankland (1984) found that phytochrome is transformable to some extent in dry seeds so can also be affected whilst on the soil surface, though in lettuce the final state is retained for at least a year (Gorski 1975).

The light environment reaching the seed can vary on the plant (Gray and Thomas 1982) or may be due to investing structures. Cresswell and Grime (1981) found retention of chlorophyll in investing structures to be correlated with a light requirement for germination by affecting the R/FR ratio reaching the seed. Arabidopsis thaliana seeds germinated better in darkness when plants were irradiated with red rather than far red light during seed maturation (McCullough and Shropshire 1970, Smith 1982). Gutterman (1980/1) showed that the light receptors here were the leaves not the seeds by covering the fruits during irradiation.

A light requirement for germination can also be induced by the low R/FR ratio existing beneath a leaf canopy (Taylorson 1982). In daylight this ratio is 1.15 ± 0.02 but beneath a wheat crop it is between 0.5 and 0.6 and in sugar beet between 0.1 and 0.4 (Smith 1982). Silvertown (1980) found 6 out of 7 species showed over 25% leaf-induced dormancy but unlike Taylorson (1982), he found none had acquired a light-requirement for germination. He therefore proposed a different mechanism of inhibition and induction of dormancy to that prevailing in soil. He suggested that induction of dormancy by burial (discussed earlier) is a complementary adaptation to leaf-induced dormancy, ensuring that seeds on the surface do not germinate when buried.

Induction of dormancy in mature seeds often follows inhibition for extended periods and this may be one effect of the investing structures or canopy shade on the maturing plant. Several authors have reported inhibition by a leaf canopy (Cumming 1963, Taylorson and Borthwick 1969, King 1975, Gorski et al. 1978). However, Baskin and Baskin (1983) found that, although leaves and filters inhibited germination of three species, they had high dark germination. Since they used a green lamp to count dark treatments, this may have stimulated germination.

Thus, differences in the degree of canopy shade during seed maturation may create interpopulation and intrapopulation differences in the light requirement and thus the associated crop may be influential in arable weed seed dormancy.

Transparency of the seed coat to light of different fluences will affect the status of phytochrome within the seed. Amaranthus spp. seedcoats transmit FR to a greater extent than R(Taylorson and Hendricks 1971 c.f.

Egley and Duke 1985). Hieracium pilosella and Silene nutans have black testas and do not exhibit leaf-induced dormancy (Silvertown 1980). However, since dormancy was high here, any effects would not have been very marked.

B. Daylength

Daylength during maturation also affects dormancy, especially during the last few days (Bewley and Black 1982 review), probably often acting via phytochrome. Gutterman (1973) found Ononis sicula produced large yellow seeds under long days which were relatively dormant, whilst under short days, for the last eight days, seeds were greenish or brown and were less dormant, differences involving the speed of imbibition. Scanning Electron Microscopy indicated variation in seed coat permeability, scarification causing immediate germination. Chenopodium album and C.amaranticolor produced thicker coats and were more dormant if matured under long days (Toole et al. 1956). Maturation under short days generally reduced dormancy (Cone and Spruit 1983), though in some species the reverse is true (Gutterman 1985). The last few days tend to be the critical period (Wurzburger and Koller 1976, Kigel et al. 1977, Taylorson 1982, Gutterman 1982, 1985) and may involve seed coat permeability, colour or hormone levels, or a combination of factors (Gutterman 1985). Gutterman (1982) found enzymes related to phenolic synthesis were involved and suggested they were involved in permeability changes. Similarly, Morbach and Mayer (1974, 1975) found that oxygen levels during drying influenced seed coat permeability in Pisum species and several legumes, since permeability was related to phenolics content and their level of oxidation. Mature seeds of P. elatius were brown and impermeable while P.sativum had yellowish-green permeable seeds.

However, if seeds of P.elatius were dried without oxygen, seeds remained green and impermeable since a tanning reaction was inhibited. Phytochrome may be the switch to initiate phenolic synthesis and it is phytochrome which perceives the light stimulus thus affecting these processes (Karssen 1970, Frankland and Taylorson 1985). Thus, the light stimulus will affect phytochrome and so phenolic synthesis and will vary on the plant and within and between populations, and the level of oxidation will also vary thus creating great variability in dormancy levels where these are due to seed coat permeability.

The post-flowering environment was also modified by the pre-flowering environment in Amaranthus retroflexus (Kigel et al. 1977). Seeds developing in photoinduced inflorescences responded differently to long days in the post-flowering environment than those developing in non-photoinduced inflorescences. In the former case, parents were smaller when seeds are produced which may be important but differences were not related to size or weight of the seeds or to coat thickness. In Arabidopsis thaliana (Cone and Spruit 1983) daylength influences the rate of after-ripening also.

C.Temperature

The temperature during maturation also affects dormancy. Van Abrams and Hand (1956) found high temperatures thirty days before harvest reduced dormancy in Rosa species as in Chenopodium album (Gutterman 1985) as did extending the development period, though it was not correlated with embryo maturity. Thus, yearly and regional variation was apparent and was related to the degree of development of the seed coat. Thus, there may have been an interaction of temperature with the

light environment as discussed earlier, increasing the temperature causing increased phenolic synthesis or tanning. Aphanes arvensis seeds collected in September were less dormant at winter temperatures than those collected later and may involve the rate of after-ripening which is faster at higher temperatures (Roberts and Neilson 1982). Sawhney and Quick (1985) found low temperatures before anthesis in non-dormant lines of Avena fatua suppressed low temperature germination. Conversely, Pemadasa and Lovell (1975) found dune annual seed to be more dormant if shed early and Dactylis glomerata showed a negative linear relationship between dormancy and seed maturation temperature (Probert et al. 1985). In pearl millet, cardinal temperatures for germination were unaffected by temperature during seed development but seed size, germination rate and viability were affected. Mohammed et al. (1985) suggested that high temperatures caused an increase in nitrogen in the seeds which has been associated with enhanced seed and seedling vigour. Temperature and moisture levels often act together during seed maturation to influence dormancy. Chancellor (1982) indicated that high temperature and dry conditions during maturation reduce dormancy. Premature drying reduces dormancy in wheat and is correlated with lower ABA levels (Sawhney and Naylor 1982). However, Karssen (1980/1) indicated various effects on different Polygonum species. Both moisture stress and temperature may act on the rate of maturation. Dore (1955) found increasing the rate of maturation of rice caryopses reduced dormancy, possibly by decreasing seed size (Thorne 1982). A.fatua under high temperature or drought stress produces smaller seeds which mature earlier and contain more amylase than unstressed seeds (Sawhney and Naylor 1982). However, the reverse occurs in Aegilops kotschyi and Schimpf (1977) found Amaranthus retroflexus seeds were larger in drier conditions, moisture availability being more important

than the length of the growing season in this respect. Blackshaw et al. (1981) also found soil moisture had a greater effect on germination than temperature in Setaria viridis.

D. Drying rate

The rate of drying is important in terms of transformation of phytochrome and thus the proportion of phytochrome as Pfr in the dry seed. If the seed is not dry by harvest, post-harvest conditions can then act on phytochrome. Hilton (1984) suggested that the amount of dark reversion of Pfr is also important and this too depends on the rate of dehydration. Much Pr may accumulate during dehydration as intermediates to be reconverted to Pfr on rehydration. Seed size will affect drying rate and thus may influence dormancy level. Thus, differences in harvesting and drying procedures may account for conflicting reports on light requirements of a species and differential drying rates may be influential in germination polymorphism and intra-and inter-population variation in dormancy. For example, seeds of Alysicarpus monilifer produced in the rainy season were more dormant than those produced in the dry season (Maurya and Ambasht, 1973).

E. Gaseous environment

The gaseous environment of the seed can also affect dormancy. Temperature and oxygen treatment of parents influenced photosynthate uptake by soybean seeds by affecting seed processes (Thorne 1982). Wulff and Alexander (1985) found high carbon dioxide levels caused a decrease in seed weight and an increase in percentage germination rate, and seedling size in Plantago lanceolata. This may act via

respiration, photosynthesis or seed coat permeability. Genetic variability in the response was also apparent. Thus, genetic and environmental effects can lead to wide variation.

F. Mineral nutrition

Finally, mineral nutrition of the parent may influence seed dormancy. Austin (1972) found that fertilizers affected seed composition, though generally differences in seed proteins do not affect dormancy unless hormone levels are affected. Setaria lutescens grown without maize competition produced more dormant seeds than if grown in competition. Jordan and Jordan (1981) suggested mineral nutrition was involved since shading by the canopy would be expected to increase dormancy rather than decrease it.

Dormancy status depends on structural components, food reserves and biochemistry, and pre-imbibition, the rate of water uptake and penetration to the embryo depends on the thickness and permeability of the seed coat. Dormancy is therefore dependent on factors in the environment of the seed which influence these components, mainly light, temperature, the gaseous environment, rate of drying and nutrition. Since these factors can vary on a microclimatic scale or on a macroclimatic scale, results obtained from one population of seeds may not apply at the species level. Holzner (1982) indicated that 'genetic and somatic polymorphism are so common among agrestals that it is difficult and dangerous to generalise results of experiments obtained with limited quantities of seed material', though effects tend to be

quantitative not qualitative. Intrapopulation variability also means that the seedbank population contains seeds with a range of dormancy levels and emergence will therefore be non-synchronous. It could thus be hypothesized that the older the seedbank and the more populations composing it, the less synchronous will be emergence and the more difficult it will be to eradicate. As Templeton and Levin (1979) put it: 'seed pools can greatly reduce the fitness uncertainty generated by cyclical or random environments'.

1.6 The observations and experiments conducted

The study of the population dynamics of V.arvensis and L.purpureum was conducted at three levels. Firstly, quadrats were set up in winter cereal fields and the population dynamics of the two species was monitored monthly. The seedbank, emergence, mortality, survival to reproduce, and seasonal changes in the seedbank were studied. These are discussed in Chapter 2.

Secondly, experiments were conducted in the Botanical Gardens under more controlled conditions in order to explain emergence patterns. Emergence was studied from soil in cylinders sunk to ground level, cultivating at the same time as cultivation occurred in the field. Also in the gardens, an experiment was set up to determine whether the positive relationship between seedbank density and the sandiness of the soil for V.arvensis was related to emergence patterns in different soil types. Emergence from three different soil types for both species was therefore studied, cultivating and counting monthly. Longevity in the three soil types was also studied, burying sachets of seeds mixed with each soil type in these cylinders and testing viability after a year.

In an attempt to determine whether any variation in emergence or longevity from the three soil types was related to the nitrate content, the effects of nitrate on germination were studied in pots in incubators. These experiments are described in Chapter 3. Thirdly, dormancy of the two species was studied in an attempt to explain emergence patterns. Chapter 4 discusses seasonal dormancy changes observed from the thermogradient bar. Seeds were buried in sachets, exhumed monthly and seeds placed on the thermobar at seven temperature regimes representing different times of the year. Germination at each temperature was recorded. Since V.arvensis seeds were inhibited by light until buried, an experiment was set up in the gardens to determine whether burial or contact with soil led to the acquisition of a light requirement after burial. Further experiments were set up to discover the effects of chilling, heating, or scarification on dormancy of V.arvensis.

To determine whether these results were generally applicable to the species as a whole, differences in seasonal changes in dormancy were studied between seeds stored in sachets in a fridge, or a Stevenson Screen, and between seeds dispersed or buried at different times. Germination was studied in seeds exhumed in alternate months for each species and placed in tins in growth cabinets. These experiments are discussed in Chapter 5. Chapter 6 describes genotypic and phenotypic variation in dormancy within and between populations.

From these experiments a model of the population dynamics of the two species in winter cereals and oilseed rape fields will be produced and differences between the two species discussed in terms of seed dormancy. Applicability of the results to other areas will also be discussed.

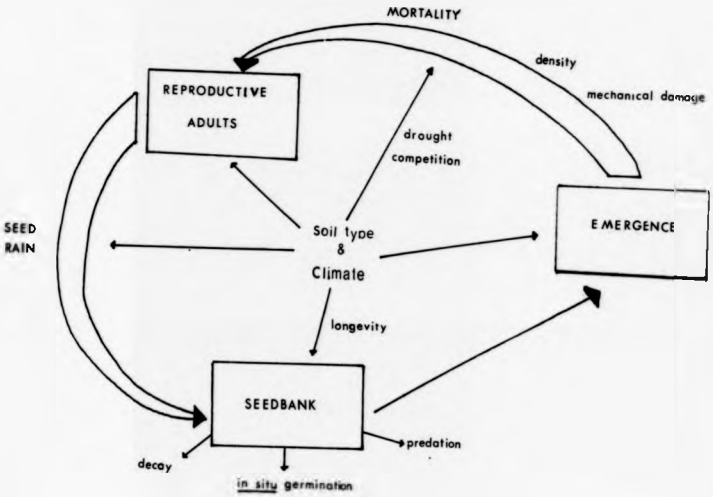
CHAPTER 2

Field observations

Introduction

It would be practically useful to be able to predict the weed density in order to apply herbicide only when and where the density would be deleterious to the crop or to harvest, or to future crops due to the probable seed input. In an attempt to produce data for a model of the life cycle for *V.arvensis* and *L.purpureum*. permanent quadrats were set up in several arable fields to record field populations. From this model it was hoped to provide information on the seedbank in each field and the proportion of seedlings expected to emerge at any one time; the proportion of those emerging which survived to reproduce; the input of seeds to the seedbank; and finally the loss from the seedbank due to *in situ* germination. Factors likely to influence each stage were examined and incorporated into the model to produce as comprehensive a view of the population dynamics as possible. These are illustrated in Figure 2.1 and will be discussed within the appropriate sections.

Figure 2.1: A model of the population dynamics of an annual arable weed.



Materials and Methods

1 Population dynamics

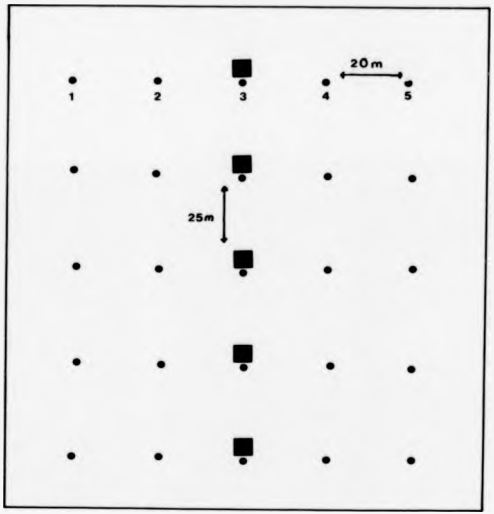
In January 1984 in 65 winter cereal fields, emergence was monitored monthly from 5 metre square quadrats located 25 m apart along a transect. However, it proved impossible to locate the precise position each month. So in April 1984,5 permanent metre square quadrats were set up in 11 of the fields (Figure 2.2). During harvest they were removed and in October 1984 replaced with short canes (0.25 m high) until spraying operations had ceased when 1 m high canes were substituted. This procedure was repeated in the same fields in the 1985-86 season with 2 additional fields and increasing the number of quadrats per field to 10 (Plate 3 and 4).

The numbers of plants at cotyledon stage, young adult stage, and flowering stage were recorded each month, without disturbing them. For V.arvensis in 1984-85 there were 11 winter cereal fields with 5 or 8 quadrats in each. For L.purpureum only three fields contained populations and 5 or 6 quadrats were set up in each. In 1985-86 for V.arvensis there were 6 winter cereal fields with 10 quadrats in each, and 4 oilseed rape fields with 5 quadrats in each. For L.purpureum there was 1 winter cereal field with 10 quadrats and 1 oilseed rape field with 10 quadrats (Plate 5). The location of the farms used is indicated in Map 1 .

2 Estimation of the seedbank density

In January 1984, five soil cores, 7 cm diameter and 15 cm depth, were

Figure 2.2: The arrangement of m^2 quadrats and soil cores in study fields



■ M^2 quadrats.

• Cores.

Plate 3

Layout of quadrats in a winter cereal field

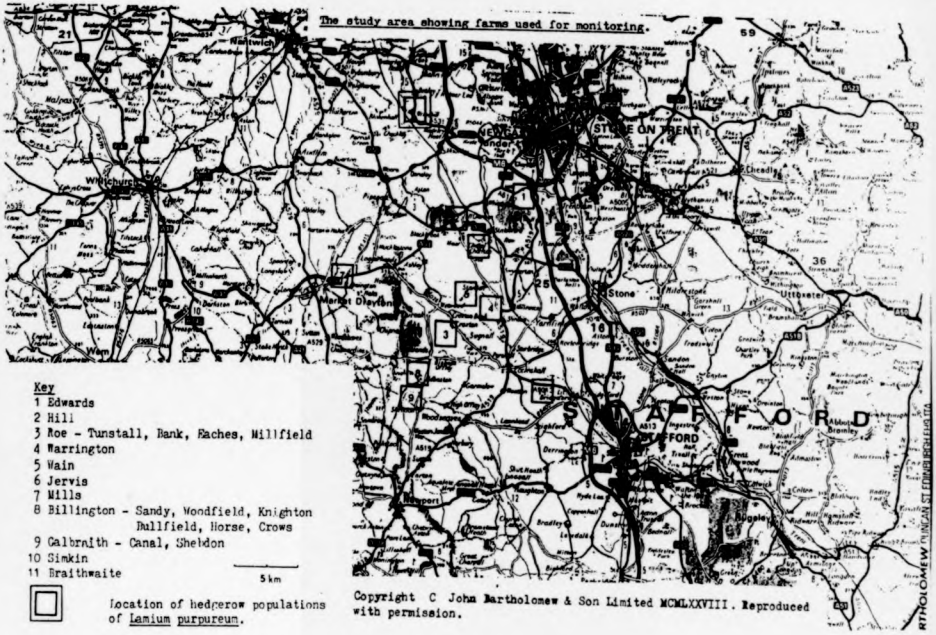
Plate 4

A metre square quadrat in winter wheat

Plate 5

A square metre quadrat in oilseed rape

The study area showing farms used for monitoring.



taken along a transect in the area being monitored for V.arvensis and L.purpureum in the 65 winter cereal fields. To estimate seed density, the cores were initially placed in trays in an unheated greenhouse and then later outside, counting emergence and mixing the soil monthly (Roberts 1981). However, this method was time-consuming and tended to underestimate the seedbank since dormant seeds did not emerge. In October 1984, an extraction method was adopted (Jones and Medd 1984). The sample was dispersed in a solution of sodium hexametaphosphate and sodium bicarbonate (10 g and 5 g respectively in 200 ml of water for 100 g of soil approximately). The soil was then washed through a tier of sieves with pore sizes 2 µm and 900 µm. The residue from the 500 um sieve was washed and then added to a saturated solution of calcium chloride in which seeds and organic debris floated. This treatment did not affect germination. V.arvensis and L.purpureum seeds were removed with forceps and 'apparent viability' checked by applying gentle pressure (Roberts 1981).

In October 1984, 11 out of the 65 fields were chosen for more detailed study and a more accurate estimate of the seedbank was attempted by using 25 smaller cores of 3 cm diameter and 23 cm depth from each field. A row of 5 was taken across the area of each of the permanent quadrats (Figure 2.2). Each row of cores was bulked to represent each quadrat. This procedure was repeated for V.arvensis in July 1985 after most germination had occurred but before seed dispersal, and again in October 1985 and July 1986 in an attempt to monitor any seasonal changes in the seedbank. In several of the study fields, oilseed rape or sugar beet was planted in 1985-86 instead of winter cereals, and 2 new fields were added in October 1985.

In order to determine whether bulked samples within rows were representative of seed densities within quadrats (Figure 2.2), cores were analysed individually in July 1985 to compare variation within and between rows.

L.purpureum populations were scarce in winter cereals in the study area and in 1984-85, few plants were found and no seeds. However, in 1985-86 two hedgerow populations were monitored in a winter cereal field and an oilseed rape field. Again, the seedbank was estimated in October 1985 and July 1986 but cores were taken around the quadrats rather than along a transect.

Soil analysis

Soils from each field were analysed for pH, and percentage sand, silt and clay (after Allen 1974).

Cropping systems

Information about the previous cropping history of each field was obtained for the last four or five years to 1979-80 season, and the number of years since the fields had first been sown to winter cereals.

Statistical analysis

Regression analysis was used to determine possible causal relationships.

3 Input to the seedbank

Seed production per m^2 was estimated for each quadrat according to the following equation:

Seed production per m^2 = mean number of seeds per pod x mean number of pods per plant x mean adult population per m^2 .

The difference between the seedbank before and after seed dispersal indicated the proportion of seeds produced entering the seedbank. This was carried out for each quadrat.

4 Seed dispersal

In the laboratory an experiment was set up to determine the projection distance of seeds of V.arvensis from the parent. Unopened ripe pods were placed on white paper on the floor of the laboratory and left to dry and open (Plate 6). The distance of projection of the seeds from the plant was marked the following day on the paper.

Plate 6

Viola arvensis open seed capsule

Results

Field data is shown in Appendix 1 and weather data in Appendix 2.

1 The seedbank

Insufficient data was available for L.purpureum for a statistical analysis of the relationship between the seedbank and soil factors or crop history since the species was poorly represented in the study area.

For V.arvensis regression analysis for all fields revealed a significant positive relationship between the mean seedbank per m^2 per field and the proportion of sand in the soil (Figure 2.3). In 1985-86 the relationship between the seedbank per m^2 and the proportion of sand in the soil was examined within fields but no significant relationship was apparent on this more detailed basis. This can be explained by the large and significant variation found between cores within a bulked sample found in July 1985 (Appendix 3). This large variation rendered variation between quadrats non-significant.

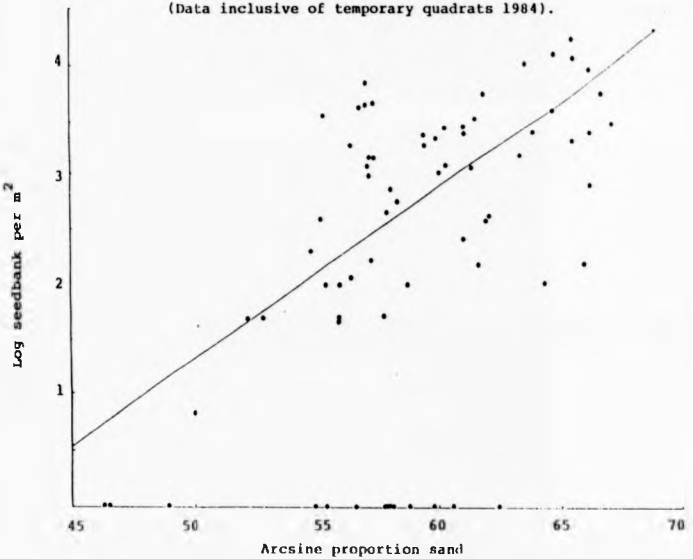
The seedbank was not related to the soil pH of a field.

Analysis of the crop history for each field (Appendix 4) indicated a positive relationship between the mean seedbank per m^2 and the number of years sown to winter barley. However, no other relationship with crop history was apparent. Previous crops of winter wheat, winter cereals, or winter crops in general did not significantly affect the seedbank density of V.arvensis nor did the number of years since the

Figure 2.3 The relationship between the amount of sand in the soil and the mean seedbank per m^2 for *V. arvensis* in winter cereal and oilseed rape fields.

$y = -6.18 + 0.15x \quad p < 0.001$

(Data inclusive of temporary quadrats 1984).



land had been sown with grass. To remove the effects of soil type, the data was analysed in two categories - over 70% sand and below 70% sand - but this did not affect the results.

In 1985-86, the proportion of non-viable seeds in the seedbank was determined for each bulked sample of 5 cores, representing a particular quadrat in the 11 fields. No relationship with the proportion of sand was apparent.

2 Emergence

V.arvenais

Figure 2.4 shows mean emergence per metre^2 for each month. Peak emergence occurred after cultivation in October and November for both seasons, with a slight increase from March to June in 1985 and in April and May 1986. The decline in emergence in December was more rapid in 1985 than in 1986 and spring emergence began earlier. The apparent peak in emergence in May 1984 is due to the fact that counting only began in May.

Figure 2.5 shows the mean proportion of the seedbank emerging per m^2 for each month. This allows for differences in seedbank size between fields and quadrats. The seasonal pattern of emergence was similar to that for mean emergence but as variation about the mean was reduced, the proportion emerging in October 1984 now appeared to be significantly greater than that in November. The extended spring increase in 1985 was also more evident.

Figure 2.4 Mean emergence per m^2 of V.arvensis in winter cereal and oilseed rape fields.
(excluding hedge populations from December 1985)
95 % confidence limits.

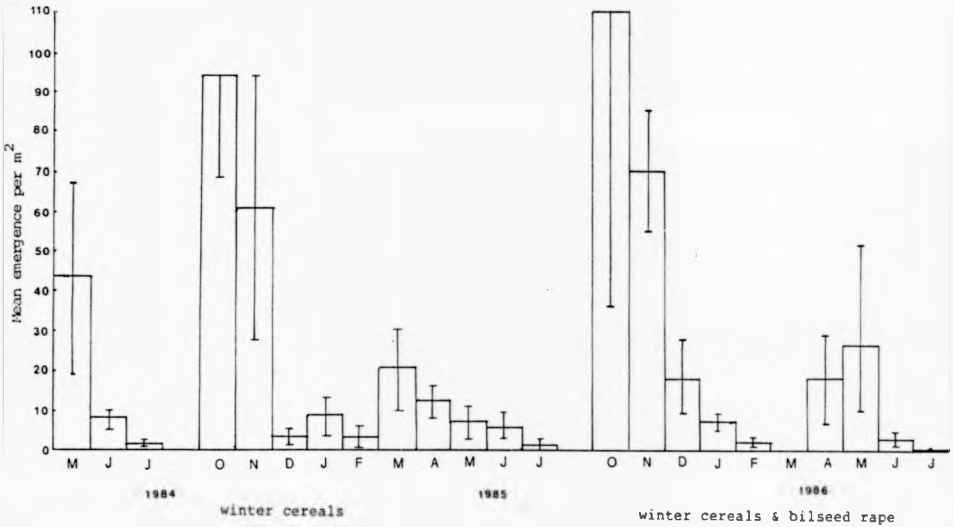


Figure 2.5 Mean proportion emerging per m^2 of V.arvensis in winter cereal and oilseed rape fields.

95% confidence limits

Data includes all preceeding months.

winter cereals only in Oct. '86

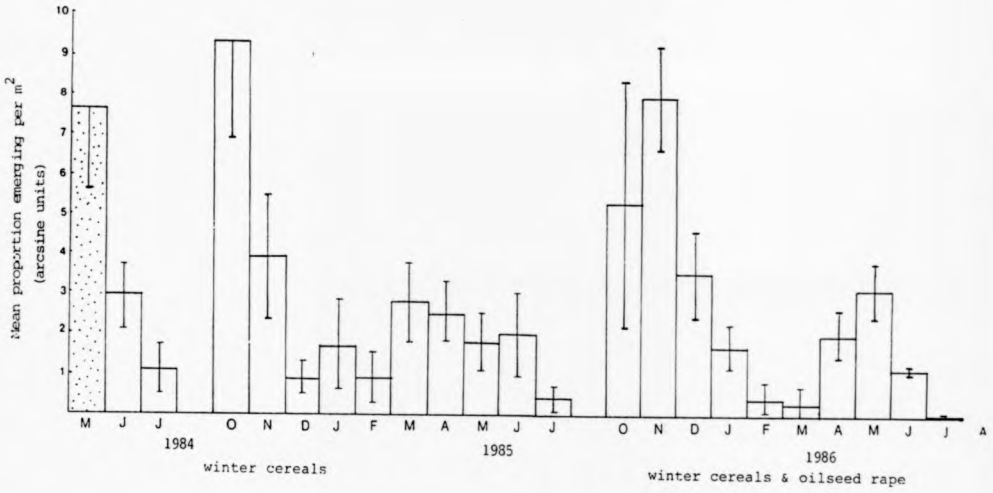
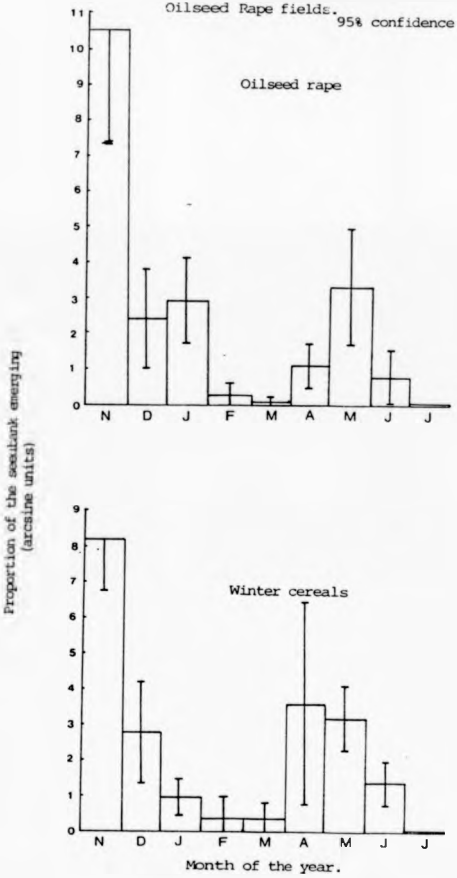


Figure 2.6 Proportion of the seedbank emerging per month of V.arvensis in winter cereal and Oilseed Rape fields. 95% confidence limits



For 1985-86, the mean proportion of the seedbank emerging was plotted separately for oilseed rape and winter cereal fields to determine whether the crop had any effect on the emergence pattern (Figure 2.6). No significant differences were apparent, though earlier cultivation of oilseed rape fields meant that emergence began in October. However, this is not evident from Figure 2.6 since observation did not begin until November. Thus, although the seasonal patterns of emergence were similar under both crops, the average age of V.arvensis plants was older under oilseed rape.

Taking the total annual emergence for each quadrat, the mean annual emergence as a proportion of the seedbank was 0.036 in 1984-85 and 0.033 in 1985-86 but 1984 estimates were underestimated due to lack of observations early in the year. Mean annual emergence per m^2 was 214.3 $\pm$ 35.2 (95% confidence limits) in 1984-85 and 157.5 $\pm$ 28.9 in 1985-86.

Neither emergence, nor the proportion emerging had a significant linear regression with rainfall (Figure 2.7), mean soil temperature at 10 cm depth (Figure 2.8), nor mean air temperature range (Figure 2.9) on a monthly basis.

Quadrats being monitored for L.purpureum along hedgerows in winter cereal and oilseed rape fields were also monitored for V.arvensis. However, they were not set up until December so this data was excluded from Figure 2.4 for the month of December since the seedling population would have included those emerging during October and November.

The mean annual emergence was related to the seedbank (Figure 2.10), increasing as the seedbank increased. Predicted limits are shown on

Figure 2.7 Monthly rainfall totals at Keele

(Data from Keele meteorological station).

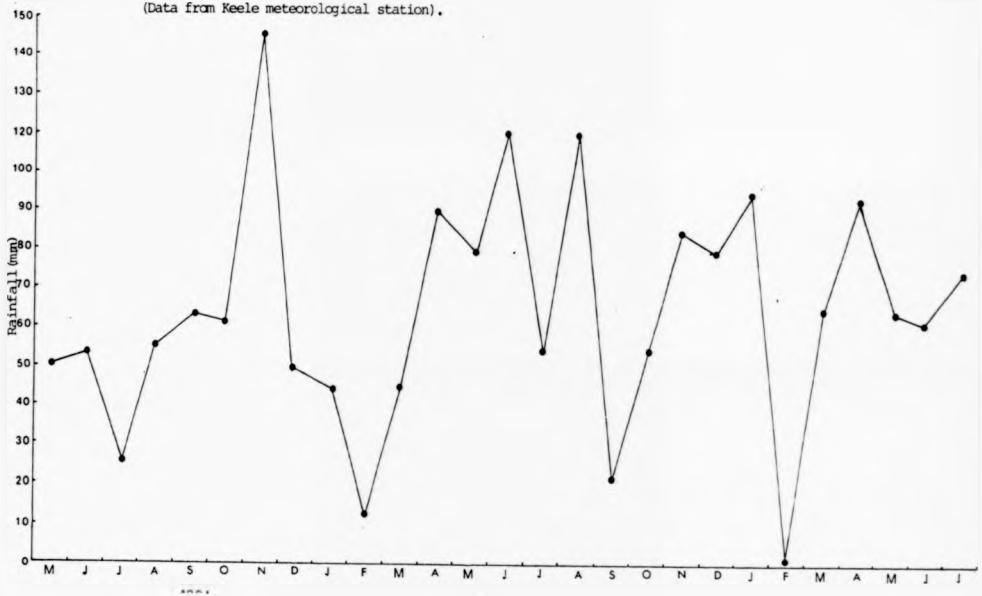


Figure 2.8 Monthly mean soil temperature at 10cm depth at Keele.

(Data from Keele meteorological station).

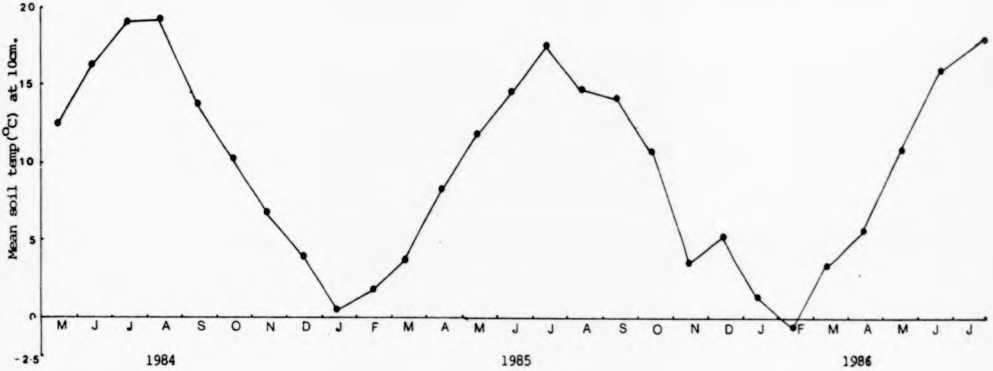


Figure 2.9 Mean daily temperature range at Keele.

(From Keele University Meteorological station)

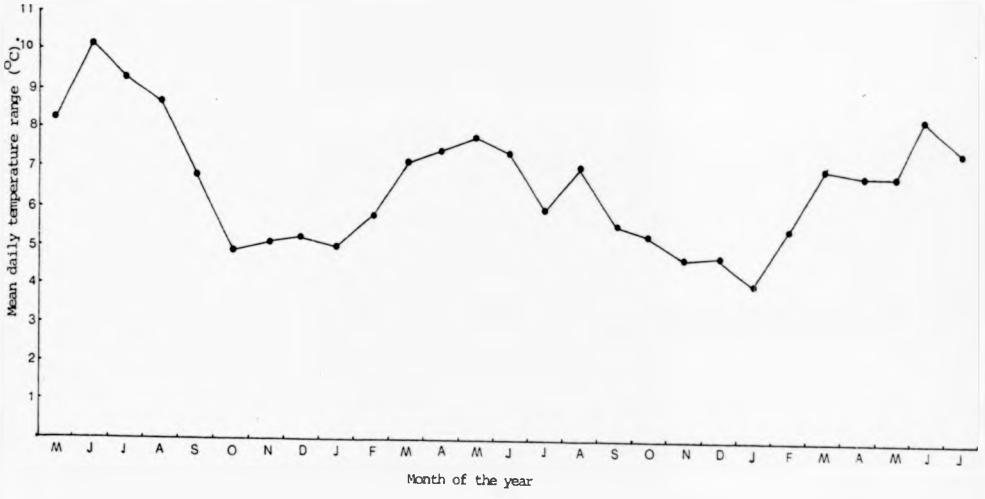
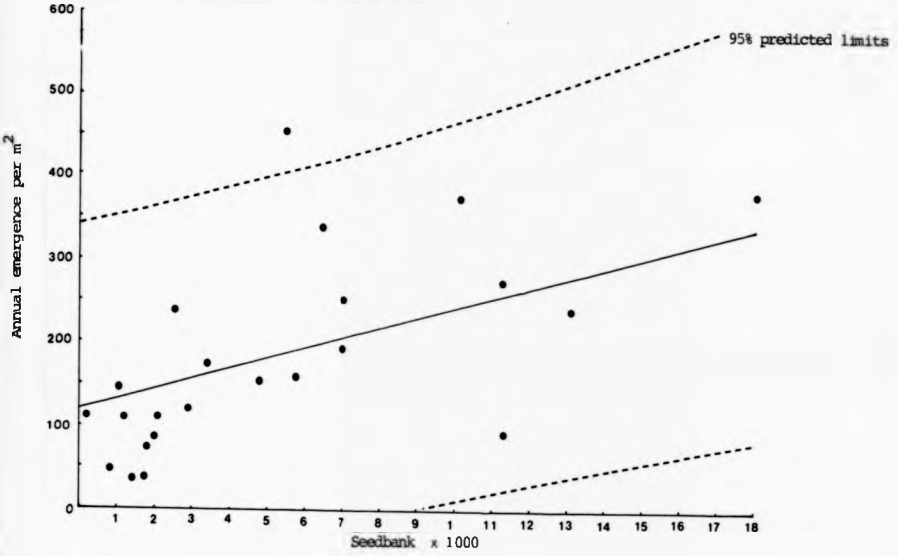


Figure 2.10 The relationship between the seedbank of V.arvensis and the annual emergence per m^2 in winter cereal and oilseed rape fields.

$y = 120.93 + 0.012x \quad p < 0.025$



the graph. In 1984-85, the proportion emerging was not related to the seedbank but in 1985-86 there was a significant negative relationship, and the proportion emerging declined as the seedbank increased (Figure 2.11). Neither the mean proportion emerging nor the mean annual emergence per field was related to the amount of sand in the soil.

Total emergence varied between fields and between quadrats within a field reflecting the heterogeneity of the seedbank (Appendix 5). However, the proportion emerging was relatively consistent with 55.6% and 68.2% of quadrats having less than 5% emergence and 72.2% and 91.8% having less than 10% emergence in 1984-85 and 1985-86 respectively (Figure 2.12).

An attempt was made to study any seasonal changes in the seedbank with a view to determining the loss of seeds due to *in situ* germination (Table 2.3). This would have been determined from the decline of the seedbank between October and July and subtracting emergence. However, no significant decline was apparent and in some fields the seedbank seemed to increase. This was due to sampling error since no seed input had occurred. The seedbank was so heterogeneous that differences found between October and July represented differences in the area sampled, rather than an actual change. More detailed sampling would be required to monitor actual changes.

In October 1985 and July 1986, the proportion of non-viable seeds in the seedbank was counted and revealed 36.1% ± 4.7 and 59.3% ± 5.2 (95% confidence limits).

Figure 2.11 The relationship between the seedbank of V.arvensis and the proportion emerging in 1985-86.

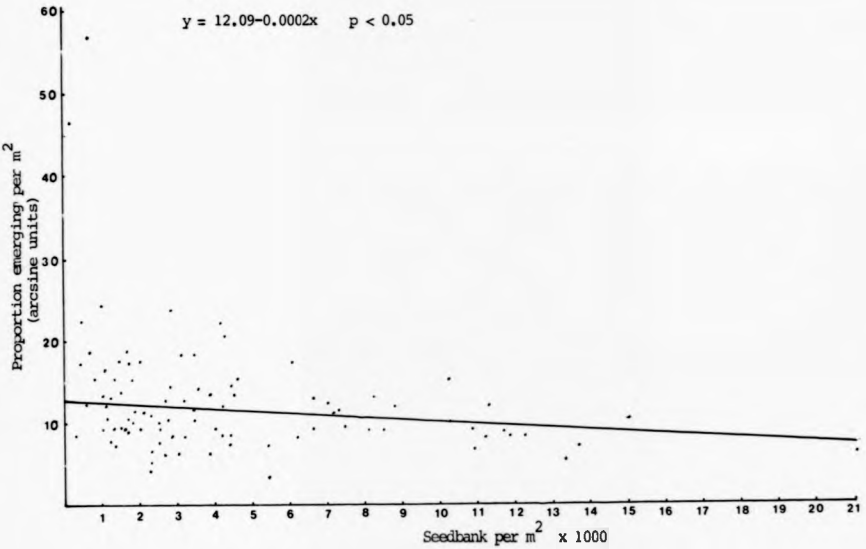


Figure 2.12 The frequency distribution of percentage emergence from the seedbank of V.arvensis.

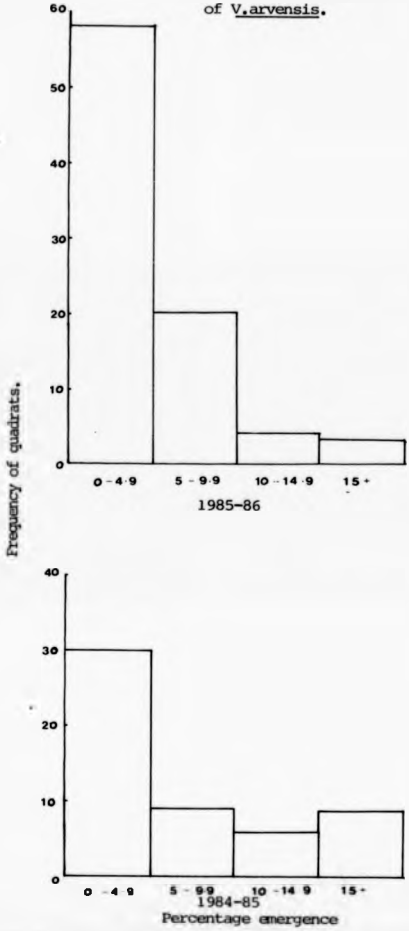


Table 2.3

Seasonal changes in the seedbank of V.arvensis

(means per m² per field)

Field	Oct. '84	July '85	Oct. '85	July '86
Hill	1182	736	4243	3168
Mills 1	15211	15049	8599	9618
Mills 2	11309	6506	5827	5941
Sandy	10054	5827	3621	19405
Bull	5355	3338	3100	6600
Baches	117	1526	2376	1638
Shebdon	1997	1415	2603	2405
Wood	7029	1980	736	2829
Bank	999	905	2320	849
Jervis	752	509	226	188
Canal	18043	8882	9562	16400
Mean	6599	4243	3834	6321
95% C.L	1975	1423	1113	2851
Hill 1			2857	2150
Hill 2			4842	1729
Tunstall			4767	1290
Sandy 2			6349	15864
Wood 2			3423	5155
Jervis 2			1726	2043
Bank 2			1345	1131
Tunstall 2			7044	3969
Mean			3979	5546
95% C.L			1202	2667

L. purpureum

Figure 2.13 shows mean emergence per month for L. purpureum. Peak emergence followed autumn cultivation in October 1984 and December 1985. The apparent delay in 1985 was due to delayed cultivation and also the quadrats were set up later. Emergence declined rapidly after this peak to reach a very low level and no spring peak was apparent. No seeds of L. purpureum were detected in the seedbank in 1984 so the proportion emerging could not be ascertained. However, in 1985-86, the proportion emerging followed the same trend as for total emergence (Figure 2.14). Emergence was not related to rainfall, soil temperature, or air temperature range.

Mean emergence over the year as a proportion of the seedbank in 1985-86 was 0.03. Total emergence was related to the seedbank (Figure 2.15) but the proportion emerging was not. Mean annual emergence per m^2 was 43.7 $\pm$ 40.4 (95% confidence limits) 1984-85 and 30.2 $\pm$ 17.5 in 1985-86. Emergence could not be related to the sandiness of the soil since only 2 fields were used for observations and this was insufficient for statistical analysis.

Again, no significant seasonal change in the seedbank occurred (Table 2.4) as for V. arvensis.

In October 1985 and July 1986, the proportion of non-viable seeds in the seedbank was 45.7% $\pm$ 22.9 (95% confidence limits) and 32.8% $\pm$ 20.5.

Figure 2.13 Mean monthly emergence of L.purpureum in winter cereal and oilseed rape fields.

95% confidence limits.

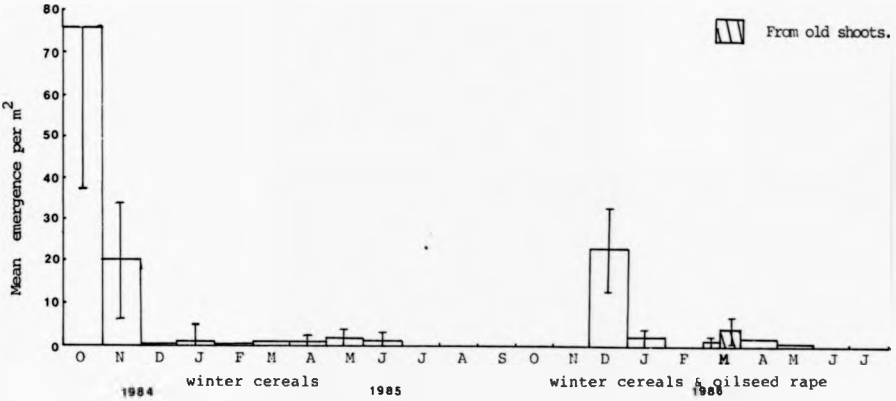


Figure 24 Emergence of *L. purpureum* as a proportion of the seedbank in winter cereal and oilseed rape fields.

95% confidence limits.

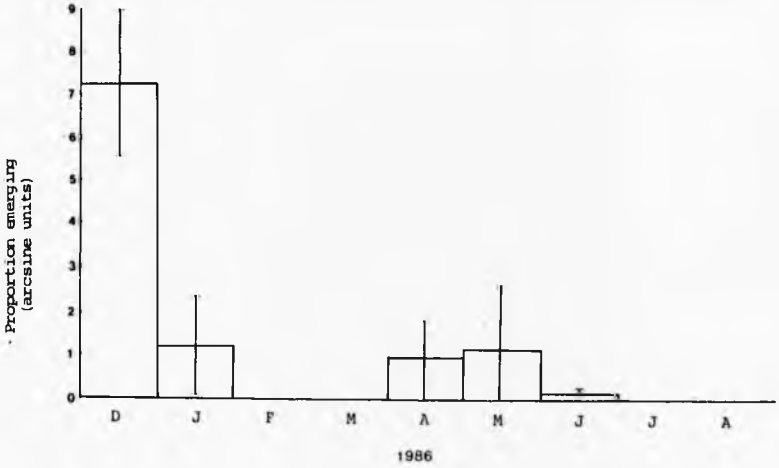


Figure 2.15 The relationship between the seedbank of L.purpureum and the total annual emergence per m^2 in winter cereal and oilseed rape fields.

$y = 17.502 + 0.012x \quad p < 0.001$

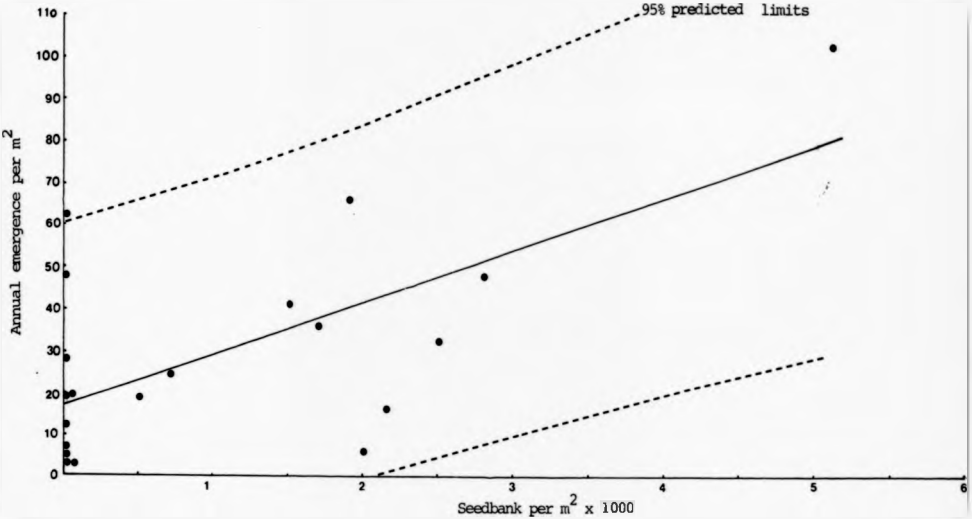


Table 2.4

Seasonal changes in the seedbank per m^2 of L.purpureum

Field		October 1985	July 1986
Bank	1	1697	1213
	2	5131	7072
	3	1937	943
	4	2761	0
	5	2543	2357
	6	509	1414
	7	2159	0
	8	0	943
	9	0	0
	10	0	943
Tunstall	1	1972	0
	2	0	0
	3	698	0
	4	1508	0
	5	0	0
	6	0	0
	7	0	0
	8	0	0
	9	0	0
	10	0	0
Mean		996	896
95% cl		641	844

3 Mortality

V.arvensis

Mortality of V.arvensis as a proportion of the standing population was relatively high throughout the year (Figure 2.16). However, significant peaks occurred in December and February of all 3 years and in July 1984 and 1985. In 1986, this February peak extended into March.

In 1985-86, mortality in oilseed rape and in winter cereal fields was studied separately (Figure 2.17). In both oilseed rape and in winter cereal fields, mortality was high in December, February and March. However, in oilseed rape fields mortality was low in January and July compared to that in winter cereal fields. Conversely, mortality in April was lower in winter cereal fields than in oilseed rape fields.

Regressions of mortality against seedling density revealed a positive relationship in February, April and June 1985, and May and June 1986 (Figures 2.18 to 2.22). A negative relationship was apparent in December and February 1985-86 (Figures 2.23 and 2.24). In all other months no significant relationship existed. Figure 2.25 shows increasing density dependence as the season progresses. In April 1986, the density of other weeds was counted and a negative relationship between V.arvensis mortality and the density of other weeds was apparent (Figure 2.26).

Figure 2.16 Seasonal changes in the mean mortality of V.arvensis seedlings as a proportion of the standing population in winter cereal and oilseed rape fields.

95% confidence limits.

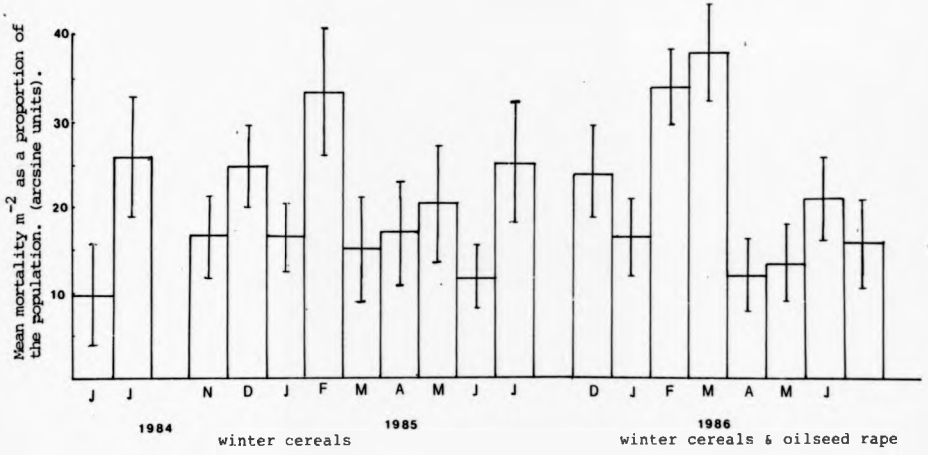


Figure 2.17 The mortality of V.arvensis seedlings as a proportion of the standing population in winter cereal and oilseed rape fields.

95% confidence limits.

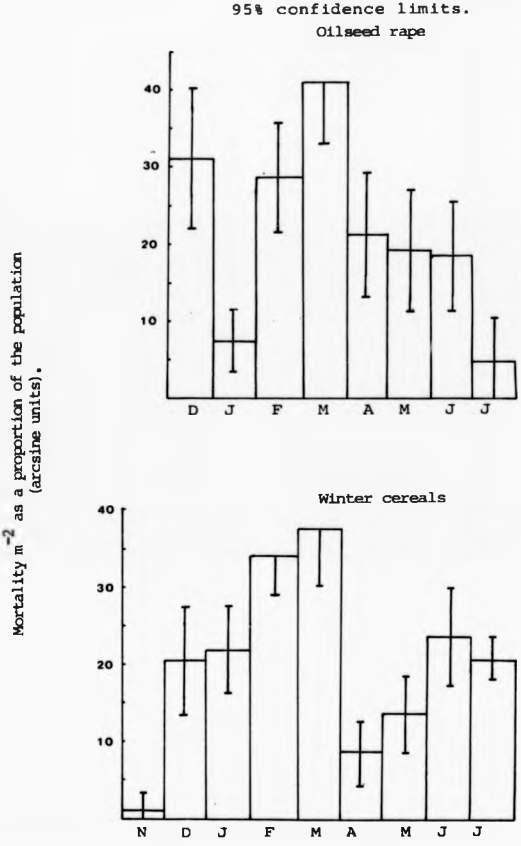


Figure 2.18 The relationship between mortality and seedling density of V.arvensis 27.2.85.

$y = 27.9 + 0.05x \qquad p < 0.05$

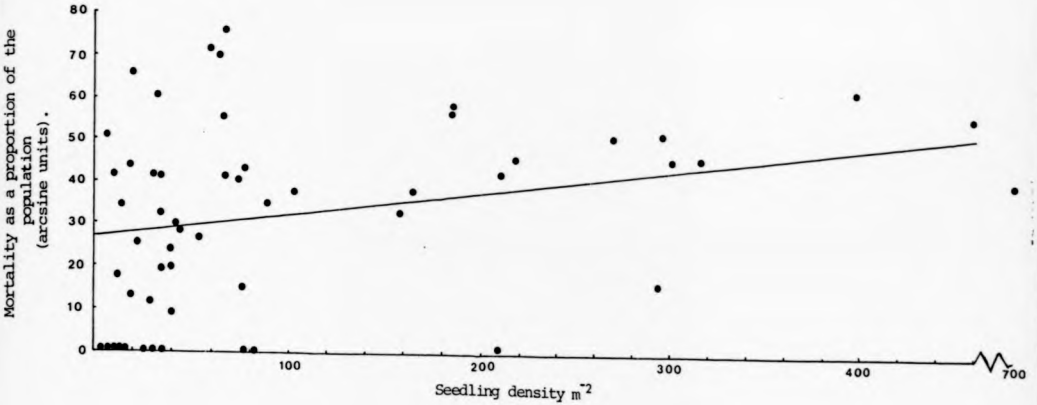


Figure 2.19 The relationship between mortality and seedling density of V. arvensis

19.4.85

y= 12 + 0.07x p< 0.01

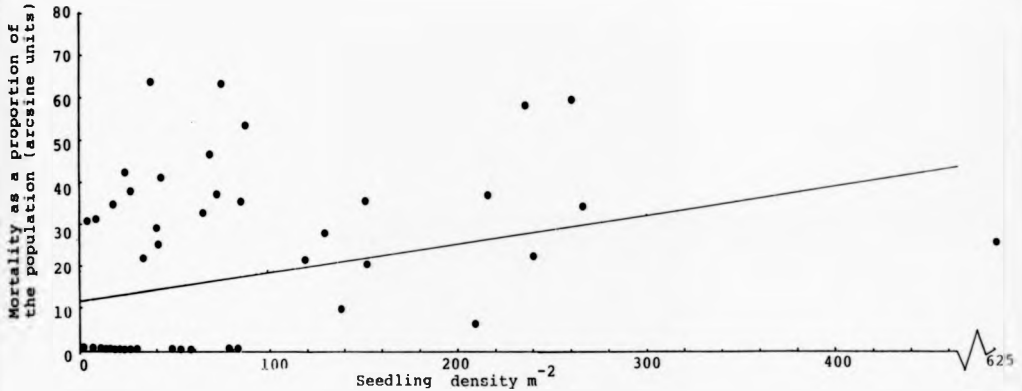


Figure 2.20 The relationship between mortality and seedling density of V.arvensis

10.6.85

$y = 7.3 + 0.08x$ $p < 0.05$

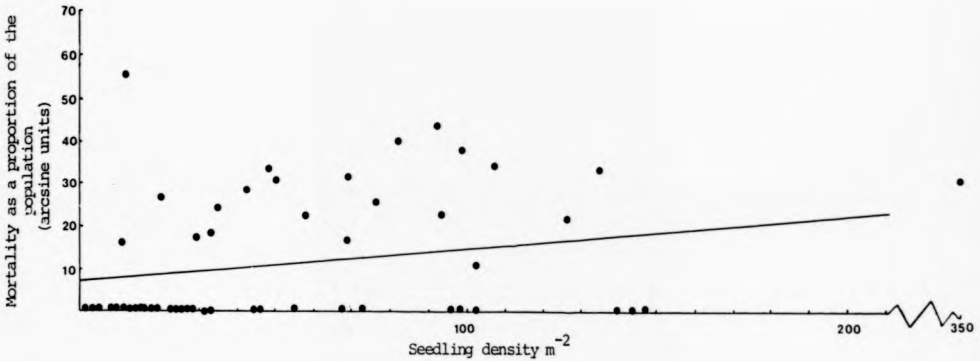


Figure 2.21 The relationship between mortality and seedling density of V. arvensis 13.5.86

$y = 7.4 + 0.1x \quad p < 0.001$.

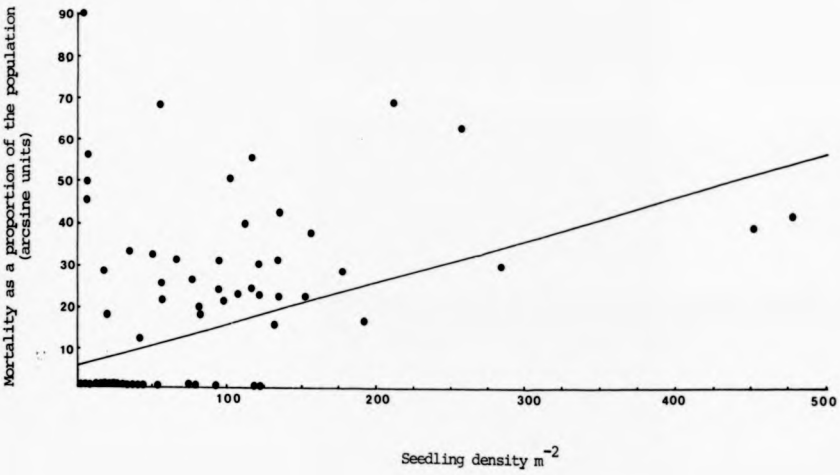


Figure 2.22 The relationship between mortality and seedling density of V.arvensis

16.6.86

$y = 15.6 + 0.1x \quad p<0.01$

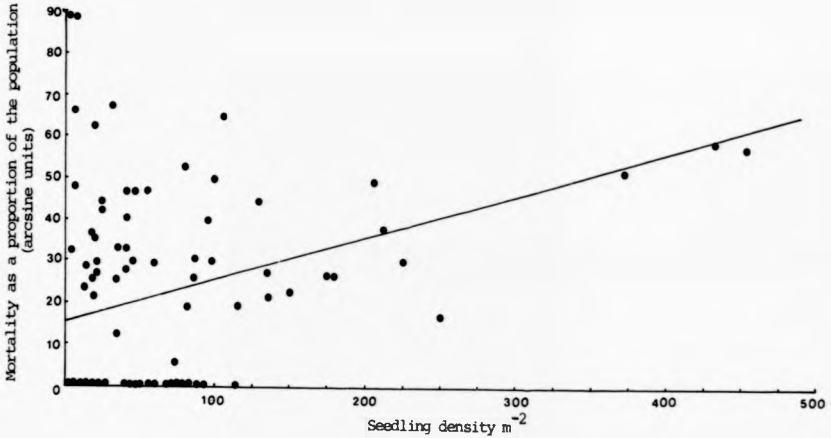


Figure 223

The relationship between mortality rate and seedling density/m^2 of Viola arvensis 10.12.85

$y = 30 - 0.07x$ $p<0.05$

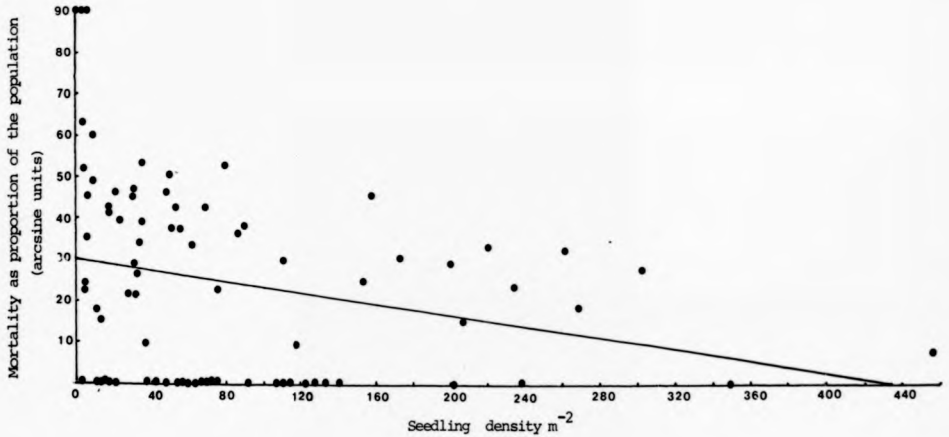


Figure 2.24

The relationship between mortality rate and seedling density/m^2 of Viola arvensis 18.2.86

$y = 38.9 - 0.05x$ $p<0.05$

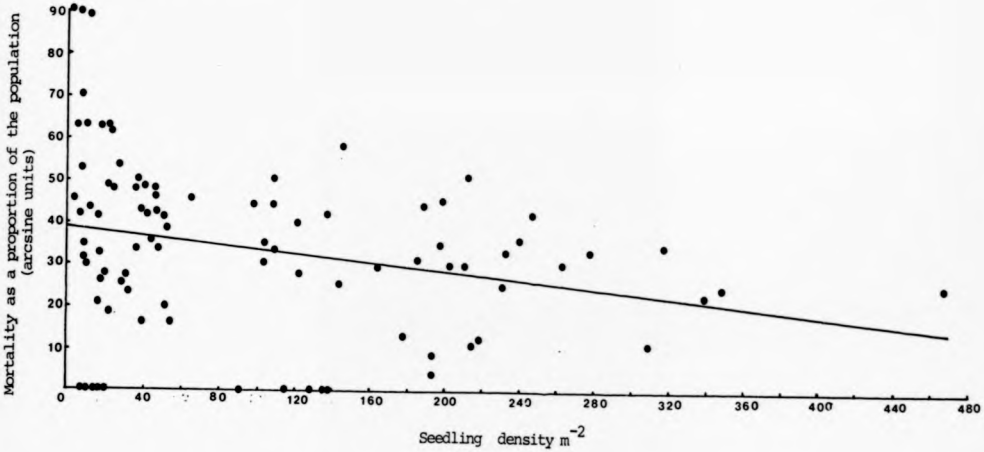


Figure 2.25 The relationship between density and mortality of *V. arvensis* seedlings, showing increasing density dependence as the growing season progresses.
(b values were obtained from regressions of seedling density and mortality each month.)

$y = -0.044 + 0.01x \quad p < 0.05$

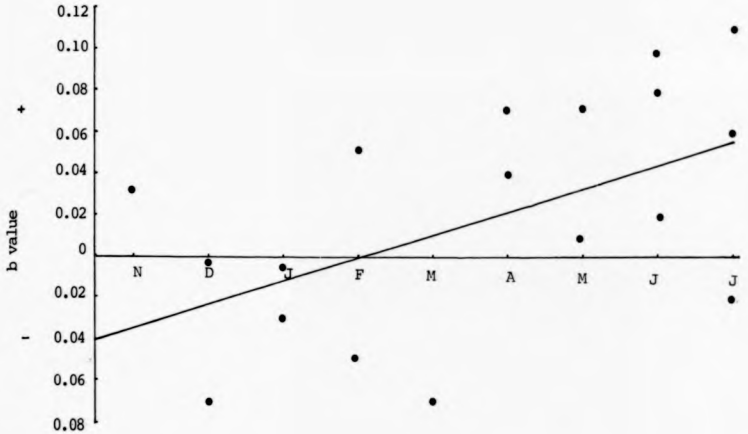
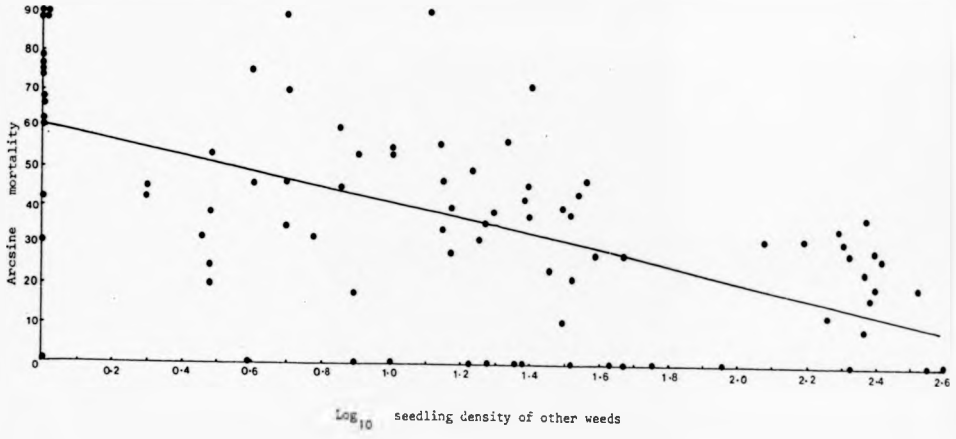


Figure 2.26

The relationship between mortality rate of Viola arvensis and the density of other species 12.4.86.

$y = 60.6 - 19.6x$ $p < 0.01$



Mortality was not significantly related to days of ground frost (figure 2.27) nor to herbicide spraying (Table 2.5).

In 1984-85, the proportion surviving was negatively related to the total emergence (Figure 2.29) such that density dependent mortality occurred. But there was no such relationship in 1985-86. The proportion of the total emergence which survived to reproduce was not related to the sandiness of the soil.

The adult population surviving in July was positively related to the seedbank where $p < 0.005$ both for 1984-85 and 1985-86 separately and combined (Figure 2.30).

Figure 2.27 Seasonal changes in the number of days of ground frost per month at Keele.
(Data from Keele meteorological station).

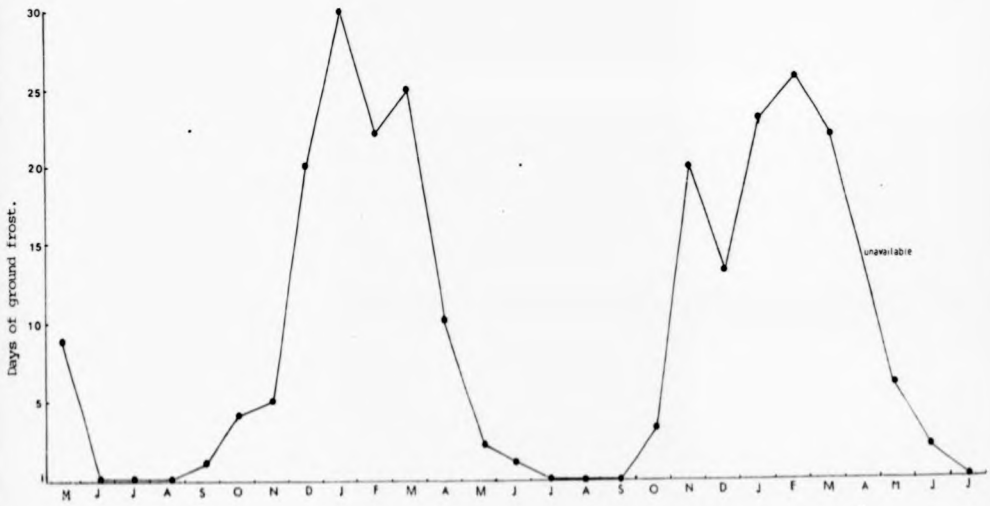


Table 2.5

The effect of herbicide application on mortality of V.arvensis in winter cereals and oilseed rape.

Mean mortality as a proportion of the standing population per m² per field (arcsine transformed)

Field	Sprayed		Unsprayed	
	10/12/85	16/6/86	10/12/86	16/6/86
Eaches	44.3			23.8
Bank	34.4			17.8
Hill A	31.4	15.9		
Hill B	19.0	21.3		
Wood			52.4	47.1
Sandy			0	30.8
Jervis	19.4	9.5		
Tunstall	5.4			11.9
Bank 2				26.3
Tunstall 2		28.8		
	29/11/84	16/5/85	29/11/84	16/5/85
Jervis			7.4	10.7
Hill	9.3	37.1		
Bull	0			25.4
Sandy		0	3.5	
Wood		28.8	14.3	
Eaches	21.3			13.9
Bank	10.2			18.2
Mills 1	31.8			0
Mills 2	39.4			6
Mean	21.4 ± 6.8		19.8 ± 8.1	

Dates refer to counting not to spraying.

Spraying occurred in spring and autumn 1-3 weeks before counting.

Figure 2.29 The relationship between total emergence of *V. arvensis* and survival in 1984-85

$y = 39.7 - 0.03x$ $p < 0.05$

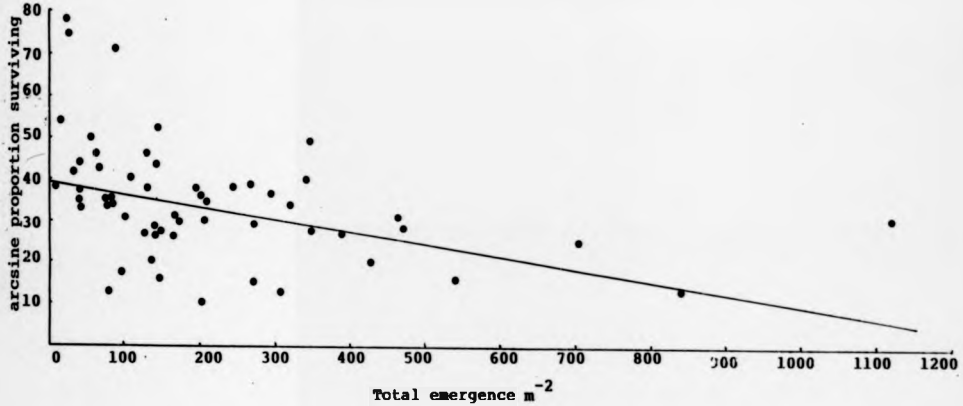
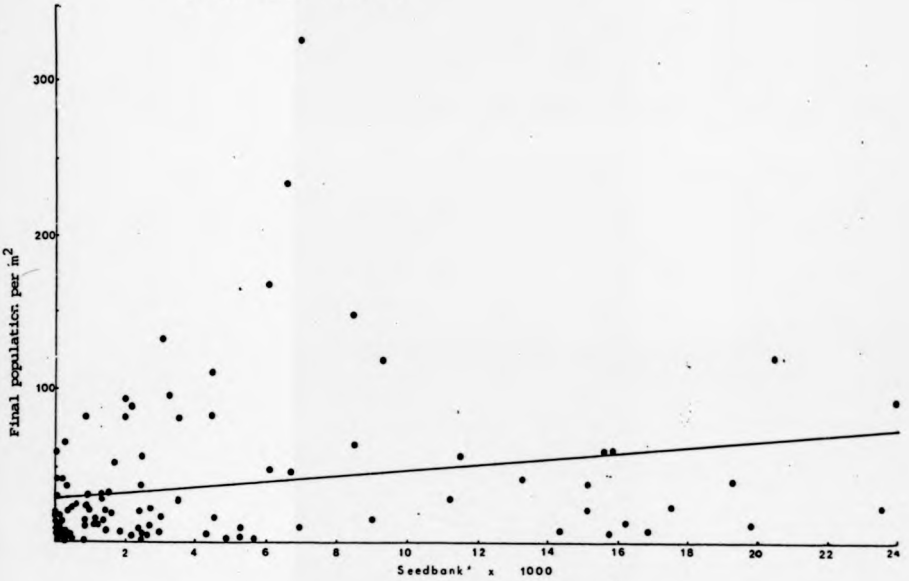


Figure 2.30 The relationship between the seedbank and the final adult population of V.arvensis per m^2 in winter cereal and oilseed rape fields.

$y = 26.8 + 0.002x \quad p < 0.05$



L.purpureum

Mortality of L.purpureum was highest during February and July in both seasons, with a relatively high level in December 1984 (Figure 2.31). Mortality gradually increased rather than there being an abrupt peak and coincided with periods of flowering and seed set (Figure 2.39)

In 1985-86 the two fields were analysed separately (Figure 2.32). The overall pattern was similar but the February peak in the oilseed rape field was much greater than in the winter cereal field. Mortality in April was also higher than in the winter cereal field. However, the June peak was higher in the winter cereal field than in the oilseed rape field.

There was no density dependent mortality and mortality was not related to days of ground frost, although in February 1986, high mortality did coincide with an extended ground frost.

The final adult population was related to the seedbank (Figure 2.33).

4 Survival to reproduce and seed input

V.arvensis

Flowering of V.arvensis began in May (Figure 2.34) and reached a peak in July. Of the total annual emergence, survival to reproduce was 19.2% in 1985 and 25.7% in 1986 with a mean surviving population per m^2 of 41.1 $\pm$ 6.1 (95% confidence limit) in 1985 and 40.5 $\pm$ 9.1 in 1986. The 1984 data was not included since total annual emergence was

Figure 2.31 Mean mortality of L.purpureum as a proportion of the population in winter cereal and oilseed rape fields.

95% confidence limits.

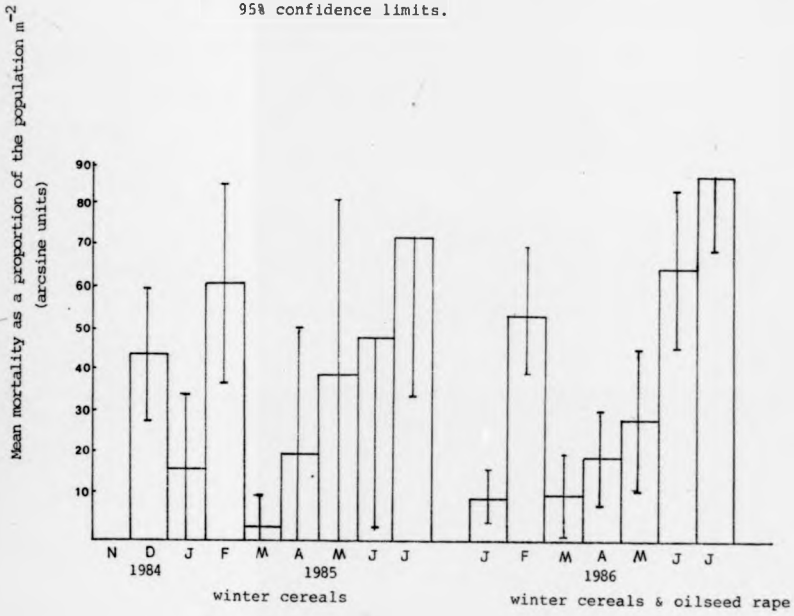
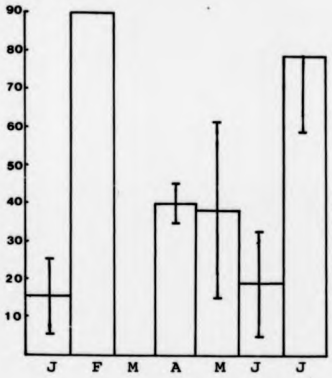
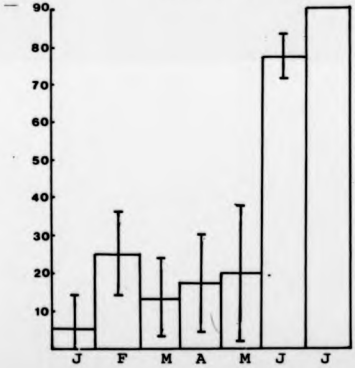


Figure 2.32 Mortality of L.purpureum per m^2
95 % confidence limits.

Oilseed rape



Winter cereals



mortality as a proportion of the population per m^2
(arcsine units)

Figure 2.33 The relationship between the seedbank and the adult flowering population of L. purpureum in winter cereal and oilseed rape fields.

$y = 9.68 + 0.01x$ $p < 0.001$

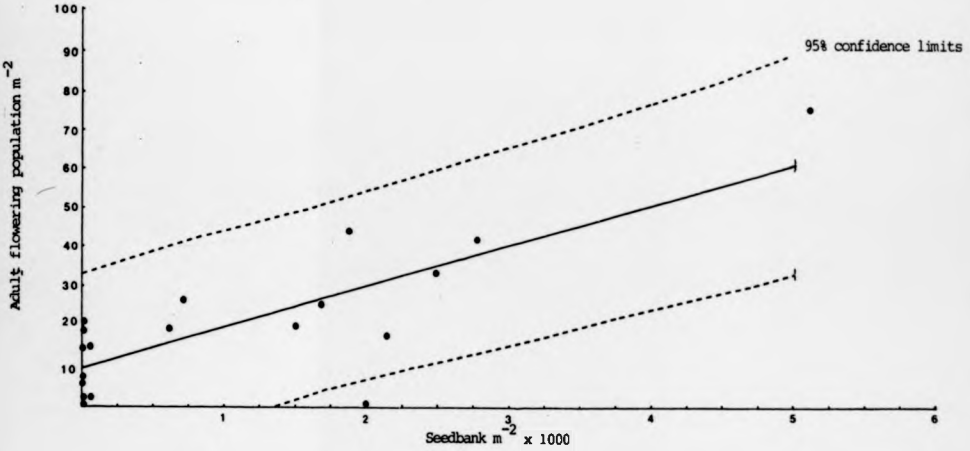
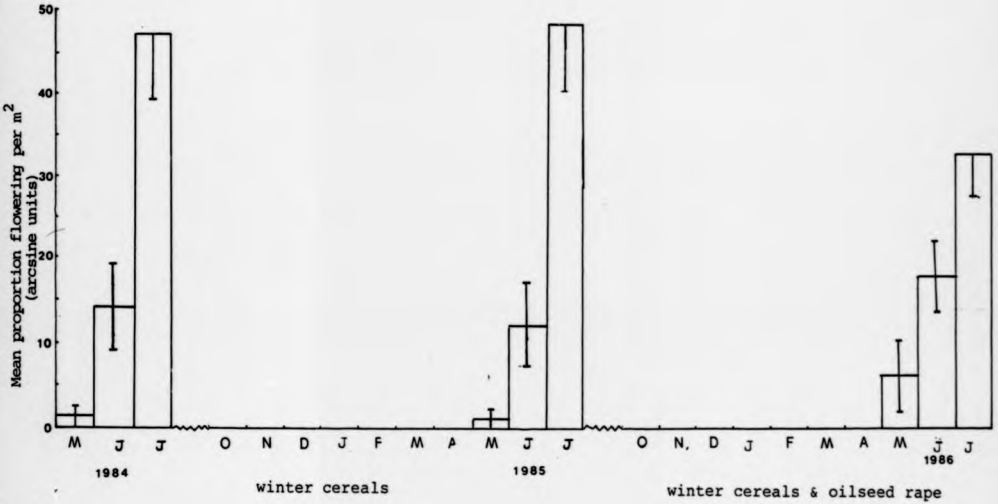


Figure 2.34 The proportion of V.arvensis flowering per m^2 in winter cereal and oilseed rape fields.

95% confidence limits.



not available. Of this surviving population, only 56.2% and 31.1% were flowering by July 1985 and 1986. The mean flowering population per m^2 was 19.7 $\pm$ 7.9 (95% confidence limit) in 1984; 23.1 $\pm$ 9) in 1985 and 14.2 $\pm$ 4.5 in 1986.

In 1986, oilseed rape and winter cereal fields were analysed separately (Figure 2.35). In oilseed rape fields flowering began earlier than in winter cereal fields but by July, the proportion flowering was similar in both crops. A significant difference in the proportion flowering also existed between the two oilseed rape fields. Where the crop was extremely dense, having been sheltered from frost drought during winter, no V.arvensis plants had flowered by July 1986. Buds were present but the shade cast by the crop prevented flowering. The proportion flowering overall was positively related to the number of sunshine hours and to the mean air temperature (Figure 2.36).

The potential seed input per m^2 was calculated from the number of adult plants per m^2, the mean number of fruits and the mean number of seeds per pod (Table 2.6). A mean of 365.4 seeds per plant was expected to be produced in winter cereal crops. In order to determine the actual input, however, removal of seeds with the crop during harvesting must be taken into account. In theory, the actual input could have been calculated from the difference in the seedbank between July 1985 and October 1985. However, due to a large sampling error, no significant difference was observed (Table 2.3).

Figure 2.35 The proportion of V.arvensis flowering in winter cereal and oilseed rape fields.

95% confidence limits.

Bank & Eaches, excluding Shebdon where crop was extremely dense.

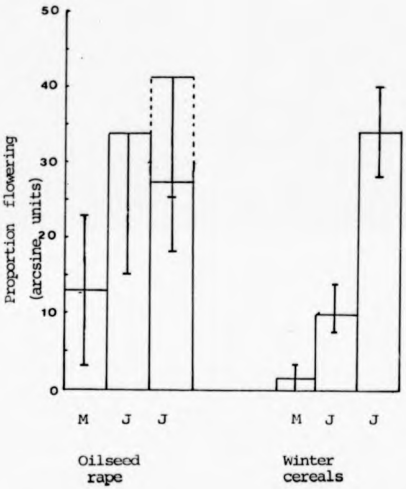


Figure 2.36 The relationship between the proportion of V.arvensis flowering and the number of sunshine hours and air temperature on a monthly basis. (As a threshold is clear, only the highest x value of the zero y values is included in the regressions).

a) Sunshine hours $y = -33.67 + 0.326x_i$ (Not significant)

b) Mean air temperature $y = -60.9 + 6.47X_{ii}$ $p < 0.01$

c) Multiple regression of y on both gives $y = -63.2 + 0.063x_i + 5.87x_{ii}$ $p<0.05$

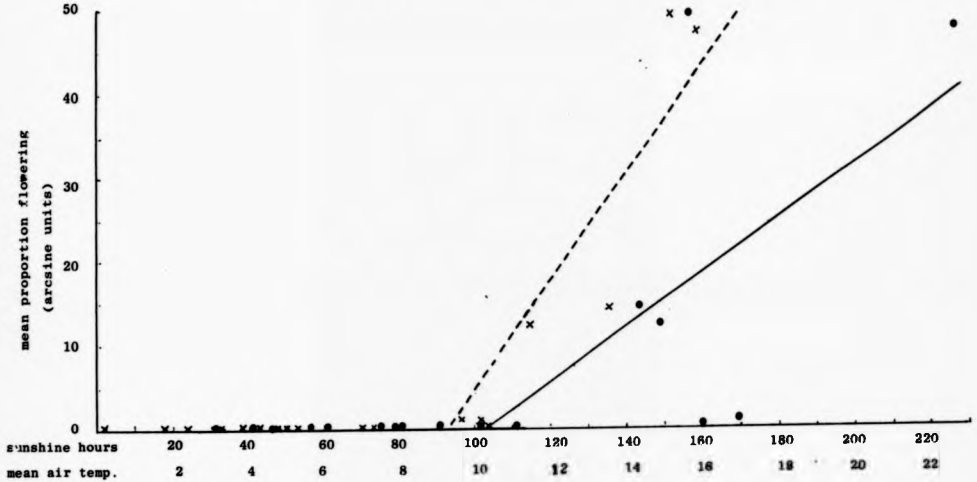


Table 2.6

V.arvensis: Mean expected input per plant

Mean number of seeds per pod	= 42.0
Standard deviation	= 14.0
n	= 27
Mean number of pods per plant	= 8.7
Standard deviation	= 9.1
n	= 20
Mean number of seeds per plant	= 12 x 8.7 = 365.4

Seed dispersal

From the experiment conducted in the laboratory, marking off projection distance of seeds from the parent, 66% of seeds were projected upwards from the plant. The maximum projection distance was 399 cm. 91.8% of the seeds fell within 200 cm of the parent and only 58.6% fell within 100 cm (Table 2.7).

Table 2.7

Dispersal distance of V.arvensis seeds from the parent

Distance from parent (cm)	Percentage of seeds
400	1.5
300	6.8
200	33.2
100	58.6

Ten plants were positioned upright on white paper and the position of the seeds marked after ejection from the pods.

L.purpureum

Two peaks in flowering occurred, one in May, June and July, and another in December and January (Figure 2.37). In 1985-86, oilseed rape and winter cereal fields were analysed separately (Figure 2.38). The winter peak was found only in the oilseed rape field.

Of the annual emergence, mean survival to reproduce in 1985-86 was 67.9 with a mean of 20.5 $\pm$ 8.4 (95% confidence limits) plants per m^2. Flowering was not related to the number of sunshine hours, nor to air temperature. The potential input to the seedbank was calculated from

Figure 2.37 Proportion of L.purpureum flowering per m^2 in winter cereal and oilseed rape fields.

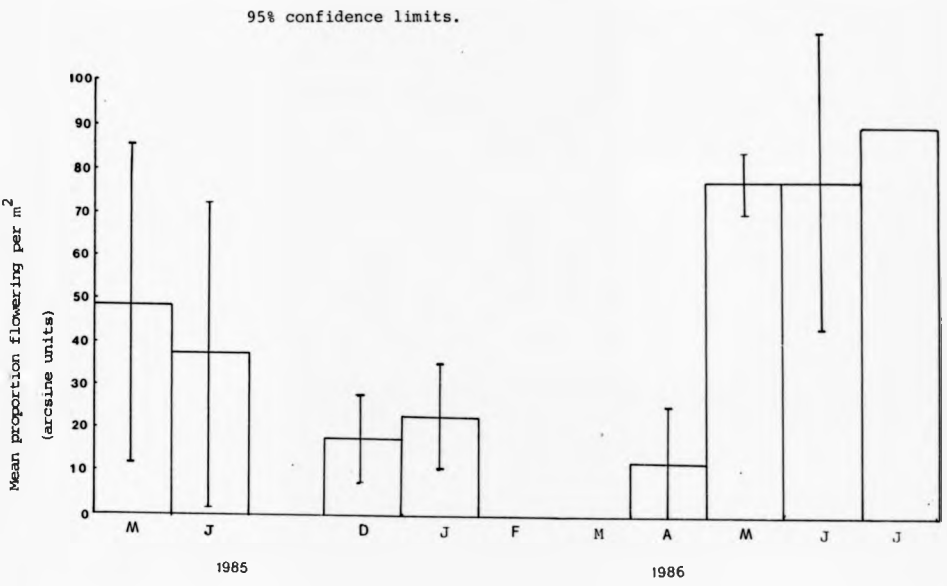
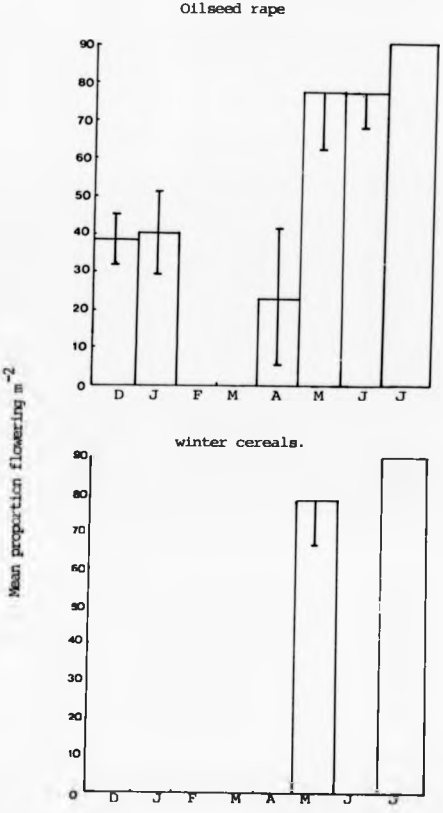


Figure 2.38 The proportion of L.purpureum flowering.

95% confidence limits.



the mean number of seeds per pod (4), the mean number of pods per plant and the mean number of plants per m^2 . Hanf (1985) found 200 seeds could be produced per plant. From plants observed in a greenhouse and in hedgerows, a mean of 210 seeds per plant was estimated (Table 2.8). It was difficult to estimate this from the field. The actual input, in theory, could be estimated by the difference in the October 1985 and July 1986 seedbanks since seed dispersal had occurred by then. However, no significant difference between the seedbanks in July and October was apparent so the actual input could not be calculated (Table 2.4).

Table 2.8

L.purpureum: Mean expected input per plant

Mean number of seeds per pod	= 4
Standard deviation	= 0
n	= 20
Mean number of pods per plant	= 52.6
Standard deviation	= 46.6
n	= 18
Mean number of seeds per plant	= 4 x 52.6 = 210.4

Discussion

1 The seedbank

Infestations of L.purpureum in this area were very low and where populations did occur there was insufficient data to do statistical analysis on the seedbank. Roberts (1958) found only 'occasional' occurrence of L.purpureum in cereal fields and Jensen (1969) found low numbers. Janczak (1982) found low numbers in oilseed rape, though rotation with spring barley caused a slight increase. Chancellor (1985) also found very few seeds in arable seedbanks. Species with low dormancy do not build up large seedbanks (Baskin and Baskin 1985) and since L.purpureum can germinate to a relatively high level when dispersed, many seeds do not enter the seedbank. Furthermore, in situ germination is relatively high (Chapter 3). On the other hand, Baskin and Baskin (1984) refer to its presence in arable seedbanks and Roberts and Stokes (1966) found 16 out of 58 fields contained L.purpureum, four populations exceeding one million seeds per m^2. In general however, infestation in winter cereals in the study area was very low.

Field populations and the seedbanks of V.arvensis were fairly high and allowed statistical analysis of the results. The seedbank density increased as the amount of sand in the soil increased. A high seedbank may be due to reduced germination, or to increased germination and emergence leading to a higher seed input, or to increased longevity of seeds. Sandy soils tend to contain less nitrate than clay soils, being readily leached (Table 2.9). Since nitrate stimulates germination of V.arvensis (Chapter 3), lower levels in sandy soils may reduce germination and thus maintain a high seedbank. However, if

this was true, the proportion of empty seedcoats in the seedbank should be less in sandy soils since in situ germination would be reduced.

Table 2.9 Nitrate nitrogen content of soil used in garden experiments (see Chapter 3)

Soil type	Nitrate nitrogen (mg 100 g^{-1})
Sandy	0.87
Intermediate	2.43
Clay	6.01

No relationship between percentage sand and the proportion of empty seedcoats was found. However, garden experiments comparing emergence in different soil types do tend to support this hypothesis, with less emergence from sandy soils (Chapter 3).

On the other hand, most authors report increased emergence from sandy soils being better aerated and well-drained. Pawlowski (1963) in Jensen (1969) found sandy soils produced more seedlings than alluvial, loess, chernozem and rendzina respectively. No relationship between percentage emergence or mean total emergence and percentage sand was apparent here.

Persistence of V.arvensis seeds may be favoured in sandy soils. Evans (1959) found seeds persisted better in dry conditions. However, conditions favouring persistence varies between species. Sorghum bicolor preferred sandy to silty soils, whilst Polygonum persicaria and

Matricaria inodora were better preserved in peat (Kolk 1978). Many species are better preserved in acid and waterlogged conditions (Egley and Chandler 1978, Schafer and Chilcote 1970) since seeds become more dormant.

Soil type may also influence crop growth and thus competition with weeds. A sandy soil is susceptible to drought as occurred in February and March 1986 and this can damage crops allowing weeds to proliferate and produce more seeds (Bridges and Walker 1985). It may also influence the choice of crops and thus the crop history of the fields which will affect the seedbank density of any particular weed. Heavy soils tend to be sown more to pasture than to arable, whereas lighter soils are more favourable for cereals, any lack of nutrients being supplied by heavy application of fertilizers.

The crop history has an important influence on the composition of the seedbank. Autumn cultivation favours autumn-germinating species and spring cultivation favours spring-germinating species. Many authors have reported changes in total seedbank density under different cultivation regimes (Chapter 1). Shallow autumn cultivation accelerated the decline of Bromus sterilis (Froud-Williams 1983) and the decline of A.fatua was slower in winter barley than in spring barley since no spring cultivation occurred which would coincide with the minimum level of dormancy (Wilson 1985). Chancellor and Froud-Williams (1986) indicated that reduced soil disturbance due to direct drilling has reduced the density of many annual dicotyledonous species but not V.arvensis, though on the light soils in this area direct drilling is not practiced. Chancellor (1985) monitored changes in the weed flora over 20 years of arable cropping after grass. L.purpureum

appeared after 11 years but in very low numbers then disappeared again. V.arvensis showed a trend of increasing seedling density with a periodicity of 2 years, which is explained by the dormancy characteristics of the seeds (Chapter 4). This has been confirmed by several farmers in the study area. Brenchley and Warington (1930, 1933) found populations depended more on the type of cropping and the crop than on the soil type. Fallowing after winter wheat reduced numbers but no decline occurred in spring barley. Roberts (1958) found vegetable cropping reduced seedbank numbers. Jensen (1969) found 34 out of 57 cereal fields contained no Viola spp., though most that did so contained up to 5000 per m^2 (though this is fairly low compared to these results). Viola spp. had one of the highest seed numbers, relative frequency and percentage occurrence of any species.

On the other hand, many authors report its predominance in spring cereals (Ervio 1981, 1982 in Sweden; Janczak 1982 in Poland; Chancellor 1985 in Britain). Janczak (1982) found high densities of plants (25 to 135 per m^2) in winter rape, the numbers depending on density of rape plants to a certain extent and probably reflected competition for light. Rotation with spring barley caused a decline. That V.arvensis predominates in spring cereals in Europe may reflect differences in climate or even dormancy of the seed. But in Britain this is difficult to explain since dormancy is lowest in autumn (Chapter 4).

When the previous crop history of these fields was studied, however, no relationship was apparent between the seedbank density of V.arvensis and the number of years under autumn-sown crops, winter wheat, oilseed rape, or winter cereals if analysed separately. However, there was a

positive relationship between the seedbank and the number of years sown to winter barley. This is difficult to explain since barley is a better competitor than wheat, closing its canopy sooner and competing well with weeds (Orson 1981, Cousens et al. 1985, Douglas et al. 1985) since the roots are shallow like those of the weeds (Pavlychenko and Harrington 1934). It also contradicts the results of Roberts and Neilson (1981) who found most in winter wheat. The relationship actually reflects the fact that winter barley is sown on sandier soils than winter wheat since it is not affected as much by drought during ripening. Whether the relationship between the sandiness of the soil and the seedbank is due to the predominance of winter barley on sandy soils, or whether the relationship is a direct result of the soil type would be difficult to determine. Experiments under controlled conditions (Chapter 3) attempt to uncover the causality of this relationship. Brenchley and Warington (1930) found that V.arvensis densities were higher on light soils irrespective of the crop.

Removing the effect of soil type still produced no relationship with crop history in general and other factors such as herbicide use and its effectiveness must also be taken into account. Detailed experiments in a controlled environment would be required to examine these factors, knowing the complete history of the area under study (Chapter 1).

Seedbank density was not related to the pH of the soil. However, none was expected since pH is not a stable characteristic of arable soils (Chancellor 1986) and is often increased by liming.

It is important to understand the limitations of seedbank sampling if such data is to be used predictively. Roberts (1981) reviewed the

main limitations; one of the major problems is the heterogeneity of the seedbank (Williams 1984). Variation between replicate cores within a row for each sample made variation between quadrats within a field non-significant. The sample size was therefore too small for detailed studies within fields. However, differences between fields were significant and it is this scale which is of practical importance.

2 Emergence

V.arvensis

The seasonal pattern of emergence followed similar trends in 1984-85 and in 1985-86. Peak emergence occurred after autumn cultivation in October and November. The difference between the two months was not significant due to large variation between fields. This variation was partly due to differences in seedbank density and thus potential emergence. When the proportion of the seedbank emerging for each month was plotted, emergence in October was significantly higher in October than in November since most fields were cultivated in October. However, in autumn 1985, the timing of cultivation varied greatly due to poor weather conditions and in many cases peak emergence did not occur until November.

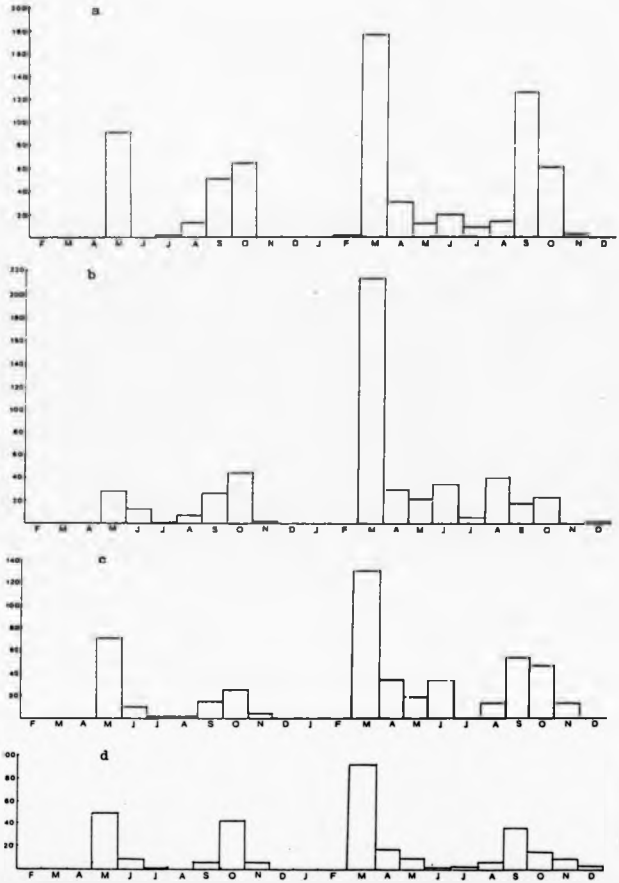
Emergence declined from December and increased again slightly in March 1985 and April 1986. This increase was slightly later in 1986 due to an extended cold period which lasted until April (Figure 2.5). In spring 1985, the peak was extended until June whereas in 1986, emergence had declined again by June. Temperatures were generally warmer in spring 1985 than in 1986 which should have increased dormancy

and decreased emergence of V.arvensis since it prefers cooler temperatures (Chapter 4). Rainfall was similar for both years and so could not have caused this discrepancy. Reasons for the discrepancy are therefore unclear and may involve differences in the average age of seeds in the seedbank and thus their dormancy; differences in the degree of after-ripening experienced in the soil in each year due to climatic differences, or even differences in the initial level of dormancy of the seeds. Suffice it to note that an extended peak in emergence can be expected in some years.

Emergence declined again in July 1985 and in June 1986 as mean daily soil temperatures exceeded 13°C. It is interesting to note that autumn emergence also coincides with a decrease in temperature to below 13°C . Thus, mean daily soil temperature may be important in the control of emergence. Ervio (1981) found low temperatures in early summer in Sweden were correlated with maximum emergence, and Roberts (pers. comm.) found minimal germination at higher temperatures, as was found in this thesis (Chapter 4).

In another study in winter wheat fields in Britain, Brenchley and Warington (1930, 1933) also found an autumn peak in emergence and this is confirmed by farmers reports (pers. comm.). However, Chancellor (1965) found little difference overall between spring and autumn emergence. This probably reflects differences in the timing of cultivation (Figure 2.39) since autumn and spring peaks were equal when cultivation occurred monthly and in the first year of burial for all treatments. However, where cultivation occurred 3 monthly or not at all, peak emergence occurred in the second spring of burial. A spring peak rather than an autumn peak may reflect the timing of burial since

Figure 2.39 Emergence of V. arvensis from soil cultivated a) monthly, b) 3 monthly, c) yearly, d) uncultivated. Data in Chancellor (1965).



here, burial occurred in January and the first cultivation in April. This would not occur in the field so these results may not reflect the behaviour of populations buried in autumn. The effects of differences in the timing of burial are discussed in Chapter 5. Early buried seeds tend to be less dormant so burial in January rather than October may influence dormancy leading to germination the following spring rather than the following autumn, especially since any chilling requirement will not have been fulfilled until the following spring.

On the other hand, temperatures in WRO, Oxford and in the Midlands (Keele and NVRS) are probably quite different, Oxford probably being warmer and allowing more spring germination. In Denmark and Sweden, where the climate is cooler, Jensen (1969) noted that spring emergence exceeded that in autumn, and Ervio (1981) found a summer peak.

Furthermore, genetic differences between the populations may exist. In spring-cereals, seeds may have become adapted to spring germination, whilst in winter cereals, they may have adapted to autumn germination in order to coincide with the timing of cultivation. Jensen (1969) and Ervio (1981) studied emergence in spring cereals and this may have been so for Chancellor's study (1965). Genetic differences in dormancy level are discussed in Chapter 6.

If September and October emergence is totalled in Chancellor's study (1965), spring and autumn emergence are similar, except where cultivated 3-monthly and this reflects the effect of cultivation in releasing the seeds from enforced dormancy. In winter cereal fields, peak emergence occurs in autumn since the soil is cultivated then and seeds are brought to the surface releasing them from dormancy at autumn

temperatures (Chapter 4).

Emergence was not related to the mean soil temperature at 10 cm depth, nor to the mean air temperature range, nor to rainfall per month. However, this does not mean they are not involved in the control of emergence. Soil temperature range is probably more important than air temperature range (but this data was not available), and these factors may interact to stimulate germination. Other soil factors may also be involved. V.arvensis is stimulated to germinate by nitrate (Chapter 3) and peak nitrate concentrations occur in spring and autumn (Chapter 1). Finally, germination and emergence will only occur when germination requirements coincide with prevailing conditions and since dormancy in the light is least in autumn and declines slightly in spring, cultivation then will expose seeds to light and emergence will occur.

The emergence pattern discovered in winter cereal fields reflected the pattern of dormancy changes found from the thermobar during the second year of burial (Chapter 4). This implies that a high proportion of the emergence was from seeds that had been buried for at least one year and was not from the preceding summers input. It also explains why emergence in autumn 1984 and 1985 was not related to the preceding adult population. This has implications for predictions of infestation.

Mean annual emergence per m^2 as a proportion of the seedbank was 0.036 in 1984-85 and 0.033 in 1985-86. The data from July 1984 represented those which had emerged and survived until May, not the total emergence since counting did not begin until May so this was excluded.

The proportion of the seedbank emerging during the year was relatively consistent with 55.6% and 68.2% of quadrats having less than 5% emergence from the seedbank and 72.2% and 91.8%, less than 10% for 1984-85 and 1985-86 respectively. Any differences reflect differences in dormancy level of the seeds due to the age distribution of the seedbank since most emergence would occur from seeds buried 2 years (Roberts and Feast 1972, 1973, Roberts and Boddrell 1983). Phenotypic and genotypic variation in dormancy may also occur between and within fields (Chapter 6).

Variation within and between fields may reflect the microenvironment to which the seeds were exposed, moisture and temperature having large effects on dormancy and emergence (Harper et al. 1965). Blackshaw et al. (1981) indicated that dry, cool soil conditions delayed emergence of Setaria viridis. Such variations may be retained throughout the growth period creating peristent heterogeneity within the seed population. For example, Evans and Young (1982) found that seedbed differences in depth, water retention and temperature persisted throughout the growth period. Harper et al. (1965) found the establishment of Plantago spp. bore little resemblance to laboratory germination capacity due to the effect of heterogeneous soil surfaces. They proposed the degree of protection from water loss to be important, though their use of polythene sheeting to establish this would also have raised the temperature. Pemadasa and Amarasinghe (1982) found higher emergence in hollows than in hummocks for 3 grass species in Sri Lanka. Thus, differences in soil type or soil nutrient levels may be important in determining emergence. Roberts and Hewson (1971) found a finer seedbed allowed greater emergence in several species and they too suggested moisture around the seed was important. In sandy soils

aeration is better than in silty soils and this may be important. However, emergence of V.arvensis was not related to sandiness of the soil in general.

Genetic differences in dormancy levels have been established (Chapter 6) and may have created much of this variation in emergence. Adaptation to a particular soil type, cultivation regime or set of environmental factors over a period of time may have established this variation.

Mean total emergence per m^2 was related to the seedbank per m^2 with more seedlings emerging as the seedbank density increased. Confidence limits at 95% have been calculated to enable prediction of potential infestation levels given the seedbank size per m^2. However, as a proportion of the seedbank, emergence was only related to the seedbank in 1985-86 and then the proportion emerging declined as the seedbank increased. Thus, emergence was controlled by density in 1984-85. Linhart (1976) found that 4 of the 9 weedy species studied were inhibited from germinating at high density, the other weedy species showing little or no effect. Of species from closed communities, 3 out of 5 showed increased germination at higher densities. He reviewed the evidence and proposed firstly that secretions from the seeds stimulated or inhibited germination, and secondly, that groups of seeds together may provide a more or less favourable microenvironment for germination. Inouye (1980) found that a high seedling density in desert annuals delayed germination and suggested high carbon dioxide production or shading was involved and Palmblad (1968) found germination of Silene anglica was reduced at higher sowing densities. Smith (1983) found that germination of Floerkea proserpinacoides was

not affected by seed density.

In an attempt to determine the loss of seeds from the seedbank from *in situ* germination, seasonal changes in the seedbank between October and July were studied. However, no significant differences were apparent due to a high sampling error. Roberts (1981) found no available data for seasonal changes in the seedbank in agricultural systems.

When numbers of non-viable seeds were determined from the seedbank samples, however, a significant difference did exist between October 1985 and July 1986 with 36.1% ± 4.7 (95% confidence limits) and 59.3% ± 5.2 respectively. Thus, the proportion of non-viable seeds increased representing *in situ* germination of about 23% during the year. This figure is relatively low when compared to that found for *V.arvensis* by Roberts and Feast (1973) in incubated soil. They found 7% of the loss from the seedbank was due to *in situ* germination, 55% giving rise to seedlings and 38% remaining viable after 6 years. It is also low compared to other species. Roberts (1981) reviewed the literature and concluded that viability of seeds recovered from the seedbank is usually low (between 6 and 36%) depending on the species. Washitani (1985) found 60% of *Amaranthus patulus* seeds germinated *in situ*, especially during the spring germination season when dormancy was at its lowest. Thill et al. (1985) also found seasonal differences in achene deterioration of *Crupina vulgaris*. However, in this case it was not associated with different dormancy levels or environmental conditions during burial. Possibly predation or decay differed. Schafer and Chilcote (1970) found 85% of the loss from the seedbank of *Lolium perenne* was due to *in situ* germination, whilst only 49% occurred for *L.multiflorum*, the latter being more persistent. Baskin and

Baskin (1985) found 50% in situ germination for Rumex crispus and Baalen (1982) found 30% for Digitalis purpurea.

Seed longevity is generally positively associated with depth of dormancy (Schafer and Chilcote 1970, Taylorson 1970, Bostock 1978,). If buried seeds lose their light requirement they can germinate during burial, providing other environmental factors are favourable. Predation and decay may be important for some species but for V.arvensis these factors are probably not a major cause of loss. The fact that in situ germination was low here reflects the depth of dormancy of V.arvensis and explains why it is a persistent and recurring arable weed.

L.purpureum

As in the case of V.arvensis, peak emergence followed autumn cultivation (Figure 2.9). However, the decline in emergence was very rapid and, unlike V.arvensis, no spring increase occurred. This abrupt decline reflects the requirement for relatively warm temperatures for germination but in 1986, it was partly a result of herbicide application in late autumn. Emergence in March 1986 was partly vegetative rather than from seeds.

Roberts (pers. comm.) found field emergence began in June with a peak in autumn, declining abruptly to zero in December, and Leguizamon and Roberts (1982) found it among the most abundant species in August. However, Ervio (1981) in Sweden and Beuret (1984) in France found a mid-summer peak. Discrepancies between these reports may reflect the temperature of the area since Sweden and France have cooler winters

than the UK and temperatures begin to increase earlier in spring and summer. L.purpureum requires relatively warm temperatures for germination and so would germinate earlier in Sweden and France.

Secondly, the fact that emergence did not begin until October/November in this study simply reflects the cultivation regime, any seedlings being destroyed by autumn cultivation. By early summer, the temperature may be favourable for emergence, but germination beneath a crop is probably prevented by insufficient light. This is supported by the fact that in the Botanical Gardens emergence did begin in late spring/early summer.

Thirdly, discrepancies in emergence patterns may reflect the timing of burial. Roberts and Boddrell (1983) found that L.purpureum seeds sown in July showed an early autumn peak, whilst those sown in November emerged mainly between April and October. This may simply have been due to low winter temperatures enforcing dormancy, but after-ripening would also be slow at November temperatures (Baskin and Baskin 1984). In this study, seeds germinated in autumn and peak flowering time was in May and June so seeds would have been sown in July, producing an autumn peak in emergence. In France and Sweden, spring-germinating populations would be favoured due to the predominance of spring-sown crops. Those populations were therefore adapted to the cultivation regime, germinating and setting seed with the crop. Any seedlings that emerged during summer would have been destroyed by autumn cultivation. However, since growth rate is rapid then, some seeds may be dispersed before autumn. The quadrats used in this study were all at field margins so harvesting would probably have done little damage.

Some seeds were dispersed during winter yet did not germinate in spring. A little emergence would have been expected, (from the thermobar results - Chapter 4), but in the small sample none was found. Possibly, unburied seeds dispersed in winter were more dormant than those dispersed in summer, or winter temperatures may have imposed dormancy which required summer after-ripening to overcome it. The maturation conditions of the seeds can influence dormancy such that spring and autumn germinating populations differ in their behaviour. Roberts (pers. comm.), Baskin and Baskin (1984) and this study used spring-dispersed seeds, whilst Ervio (1981,1982) studied autumn-dispersed seeds.

Taking these factors into consideration, rotations of autumn and spring-germinating crops would reduce infestations where these occur, since autumn dispersed seeds from a spring-germinating crop would emerge the following spring. If an autumn-germinating crop followed the spring-sown crop, those weeds that would have emerged in spring will not produce any crop competition and would probably be prevented from germinating by the shade cast by the crop.

Plants arise from rhizomes as well as from seeds so that they are difficult to eradicate with contact herbicides. Some emergence in March 1986 was from rhizomes of plants damaged by winter frost. However, this did not appear to be the major source of infestation.

In this study, L.purpureum behaved as a strict winter annual, emerging only in autumn with the crop, with only minor emergence in the rest of the year. Mean emergence over the year as a proportion of the seedbank in 1985-86 was 0.03 which is similar to other annual arable weeds

(Chapter 1). The proportion emerging was not related to the seedbank but total emergence during the year was related ($P<0.01$), with emergence increasing as the seedbank increased, as for V.arvensis. The 95% confidence limits have been calculated to enable prediction of potential infestation levels.

Emergence was not related to the amount of sand in the soil, only two fields being used in this study. Neither was there any relationship with rainfall, soil or air temperature, or air temperature range. This is not surprising since L.purpureum like V.arvensis has a seasonal cycle of dormancy which controls germination.

The fields used in 1985-86 were different to those used in 1981-85 so it could not be determined whether emergence in autumn was related to the preceding adult population. Few seeds of L.purpureum were detected in the seedbanks of the fields studied but where they were, no significant difference was found between the seedbank in October 1985 and that in July 1986. Seeds were added to the seedbank during the winter but this would not have been a major input, though it may have been sufficient to hide the loss from the seedbank.

Similarly, no significant difference was found between the October 1985 and July 1986 seedbanks in the proportion of non-viable seeds with 15.7% ± 22.9 in October and 32.8% ± 20.5 in July. These values are similar to that found for V.arvensis despite differences in the depth of dormancy (Chapter 4).

3 Mortality

V.arvensis

Mortality exceeded 10 arcsine units (about 3%) in every month. However peaks were apparent in December and February of all three years and in July 1984 and 1985. The December peak reflected the increasing number of days with ground frost which destroyed many newly emerged seedlings and several fields were sprayed with herbicide which destroyed most newly emerged seedlings. Mortality as a percentage of the adult population decreased during January probably since most seedling mortality had already occurred in December such that those remaining were fairly robust. Furthermore, snow cover may have protected seedlings to some extent in January since the maximum number of days of snow cover occurred in January for 1985 and 1986 (Appendix 2). During February, and into March in 1986, frost again destroyed many seedlings. The longer period of high mortality in 1986 than 1985 was not a result of more ground frost, since this did not differ between years. However snow cover in February and March 1985 protected seedlings to a greater extent than in 1986; the number of days of snow cover being 14 and 2, and 5 and 1 for February and March 1985 and 1986 respectively. Furthermore, a widespread frost drought occurred in February 1986 which damaged crops and weeds alike.

The peak in mortality in July reflected seedset and subsequent death of some adult plants and some deaths due to drought. By August a higher proportion of the plants would have flowered and harvesting would destroy the remainder. However, some of the smaller plants do escape the harvesters and remain to flower in the stubble, though this is only a small proportion and is unlikely to contribute to the seedbank, being

burnt with the stubble. Mortality in July 1986 was lower than in 1984 and 1985, firstly due to inclusion of oilseed rape fields where plants were more mature and so survived drought better and also flowering was delayed by the shading of the crop. Secondly, flowering was delayed in 1986 such that deaths due to reproduction were fewer in July.

Within several of the fields, mechanical damage by tractors destroyed many seedlings and several had been attacked by insects or uprooted by rodents or wind. However, such effects were not very important in terms of overall mortality.

In 1985-86, oilseed rape and winter cereal fields were examined separately. Seasonal patterns of mortality were similar but in winter cereal fields mortality remained high throughout the winter, whilst in oilseed rape fields a decline in mortality occurred in January. Conversely, in April, less mortality occurred in winter cereal fields than in oilseed rape. Oilseed rape fields were cultivated earlier than winter cereal fields such that emergence of V.arvensis seedlings was earlier. During the January drought, plants were therefore better established with deeper roots and so suffered less damage. Conversely, in April, newly emerged seedlings in oilseed rape were shaded out by the dense shade of the crop which was absent in winter cereal fields.

Figure 2.25 shows the increasing density-dependence of mortality. Density-dependent mortality occurred in July 1984 but not in July 1985 or 1986, mortality increasing as density of weed plants increased. At this time, drought was probably extremely important creating some competition for water. In July 1984 there were 226.2 hours of

sunshine and only 24.7 mm of rainfall compared to 157 hours and 54.3 mm of rainfall in July 1985.

In February 1985, density-dependent mortality was also probably due to drought with only 11.5 mm of rainfall and 22 days of frost. In January and March, although there were a few more days of ground frost, there was more rainfall. In April 1985, May 1986 and June 1985 and 1986, density-dependent mortality cannot be explained by the weather. Since emergence increased slightly then, density-dependent mortality probably occurred among weed seedlings which were competing for light with established plants and the crop. Competition for nutrients is unlikely to be the cause, due to the differences in root depth between seedlings, established plants and the crop.

In December 1985 and February 1986, mortality rate decreased as the seedling density increased. Thus, the environment was favourable for newly emerged seedlings and established plants alike. Possibly, soil temperature and soil moisture conditions, together with protection from wind and pests provided good conditions for growth. At this time, a peak in mortality occurred (Figure 2.15). This implies that when conditions were unfavourable for seedling survival they were also unfavourable for seedling establishment and growth. Peaks in mortality at other times were either due to density-dependent mortality, or to climate as discussed above.

In April 1986, the density of all other weeds was determined and a negative relationship between V.arvensis mortality and seedling density of other weeds occurred. Thus, where the environment was favourable for the establishment of V.arvensis, it was also favourable for other

weeds and no density-dependent mortality occurred. Baskin and Baskin (1976) found a similar effect for Phacelia purshii. Watkinson and Harper (1978) also found mortality of Vulpia fasciculata was not density dependent but spikelet production was, and since this was not determined here, there may have been some effect of density on seed production. However, the density of other weeds was important. In general, density-dependent mortality only occurred when the environment was stressful due to drought or shading. Mortality of Vulpia fasciculata was also influenced by desiccation, shading and also wind.

Taking all months and fields into account, survival was negatively related to emergence in 1984-85, indicating density-dependent mortality, but this did not occur in 1985-86. Since the proportion surviving was not related to the final adult population, density-dependent mortality must have occurred among seedlings rather than adults. Sagar and Mortimer (1976) reviewed the available evidence and found between 0% and 60% mortality occurred in seedlings, with some later when the stand closed. Rai and Tripathi (1985) studied the effects of established populations of two weeds on their newly emerged seedling cohorts in pots. Seed germination, survivorship and reproduction were reduced by competition from established plants. For V.arvensis 19.2% and 25.7% of the population survived to reproduce in 1984-85 and 1985-86. Chancellor and Peters (1972) reported 0% to 60% mortality of Avena fatua in cereals and Naylor (1972) found 60% mortality of Alopecurus myosuroides. Thus, mortality of V.arvensis was rather higher than these two species.

Herbicide application did not significantly affect mortality! V.arvensis is only moderately susceptible to herbicides, and then only

at the seedling stage. Field observations revealed only seedlings at the one or two leaf stage were destroyed. Browning of the leaves of older plants occurred but this was not fatal. Furthermore, autumn application only affected those which had already emerged. Many emerged subsequent to spraying. Spring application only affected newly emerged seedlings.

Mortality was probably not just related to drought or competition for nutrients since neither the proportion surviving nor the final population were related to the sandiness of the soil.

The adult population was only related to the seedbank if individual quadrats were used. The mean adult population per field was not significantly related to the seedbank per field so could not be predicted. This reflects the heterogeneity of the seedbank within a field. Detailed study within a particular field would allow prediction of infestation in any particular area but this would not be of much practical use.

L.purpureum

Mortality of L.purpureum generally followed flowering, notably in July and in February and December, 1984. This can be seen by comparing graphs for mortality and flowering where a gradual increase in flowering is paralleled by a gradual increase in mortality. Mortality in February may have been related to the drought caused by frost which was responsible for much V.arvensis mortality. L.purpureum plants

appear to be less robust than V.arvensis and even mature plants suffered, any buds present failing to open. No density-dependent mortality occcurred since populations were very low (see 'Emergence').

Mortality in the oilseed rape field differed to that in the winter cereal field being much higher in February and April. This coincided with periods of flowering. The oilseed rape field was cultivated earlier than the winter cereal field so that emergence, flowering and death occurred earlier, in April rather than June in winter cereals.

The final adult population per m^2 was significantly related to the seedbank (Figure 2.33) unlike that of V.arvensis. This reflects the difference in sampling. Samples for L.purpureum were taken close to the quadrats under study due to localisation of the species. Such a positive relationship within individual quadrats also existed for V.arvensis. Since only two fields were used for L.purpureum no relationship between the mean seedbank per field and the mean adult population could be found. However, the fact that L.purpureum was localised means seedbank sampling within the area of known populations would enable prediction of likely infestations and subsequent seed input from Figure 2.33.

4 Flowering and seed input

V.arvensis

Flowering of V.arvensis began in May, reaching a peak in July with a mean percentage flowering of 56.2% in July 1985 and 35.1% in July 1986. Harvest took place in August which prevented counting then and by this time a high percentage would have been flowering. The percentage

flowering in 1986 was lower than in the previous year due to delayed cultivation in autumn and thus delayed flowering in summer. Thus, the timing of cultivation will affect the summer seed input by influencing the proportion of plants which set seed by harvest time. The mean adult flowering population per m^2 was 19.7 $\pm$ 79 (95% confidence limits) in 1984, 23.1 $\pm$ 91 in 1985 and 14.2 $\pm$ 45 in 1986.

Of the total annual emergence, the mean proportion surviving to reproduce was 19.2% in 1984-85 and 25.7% in 1985-86. This could not be calculated for 1983-84 since annual emergence was underestimated as monitoring did not begin until May. The proportion surviving to reproduce was therefore similar in both years despite differences in the proportion of the population flowering and numbers of flowering adults. The proportion flowering was positively related to the number of sunshine hours and to the mean air temperature, and began above 140 sunshine hours and above 9.5°C with a peak between 156 and 226 sunshine hours and between 15.2°C and 15.9°C.

When populations in oilseed rape and winter cereal fields were studied separately in 1986, there was a significant difference in the proportion flowering in May, June and July. This reflected differences in the average age of the plants. Cultivation was earlier in oilseed rape fields so plants flowered earlier. However, by July, the proportion flowering was the same in both crops unless the less dense oilseed rape crop was considered alone. Where the oilseed rape had been damaged by frost drought, V.arvensis plants were able to flower due to the poor cover. But where little damage had occurred, the dense crop cover inhibited bud-opening. Thus, under normal conditions, the oilseed rape would smother the weeds and prevent

flowering, despite earlier maturation. Input to the seedbank would therefore be low.

The potential input to the seedbank can be calculated from the mean number of seeds produced per plant and the mean number of plants per m^2. In theory, the actual input could be estimated from the difference between the seedbank in July and October. No significant difference in the July and October seedbank was found due to large variation about the mean. In some instances, a decline was found. Due to the heterogeneity of arable seedbanks very detailed sampling would be required to discover the actual input. Any difference between the expected input and the actual input found in the seedbank would indicate the proportion of seeds removed with the crop during harvest. Thurston (1964) estimated that 75% of Avena fatua seeds were removed with the grain and 20% with the straw, only 5% entering the seedbank. The numbers of weed seeds retrieved during grain cleaning attest to this fact. Since only 5% is likely to enter the seedbank, an extremely sensitive sampling procedure would be required to reveal the input.

The relationship observed between seedbank density and the sandiness of the soil may have been due to differences in seed production per plant. V.arvensis shows indeterminate growth such that more seeds could be produced under more favourable conditions (Schaal 1980). However, sandy soils are often subject to drought and nutrient deficiency (especially magnesium). Newman (1967) found that for Aira praecox, the number of seeds per spikelet was only affected if inflorescence emergence was affected. However, Teesdalia nudicaulis, having shallower roots and non-synchronous flowering, was affected by spring

soil water stress. Furthermore, drought may reduce crop growth and thus allow a higher weed seed production as occurred for Cassia obtusifolia (Bridges and Walker 1985).

Newman (1963) found small variation in germination date markedly affected subsequent size and seed production of the adult, and Baskin and Baskin (1976) found Phacelia purshii produced more seeds from those plants which germinated in September and October. Ghersa et al. (1985) found that Johnsongrass produced more seeds per panicle in early summer than in late summer, especially under maize. The cropping system and crop type may therefore be important in determining input to the seedbank. Oilseed rape is sown earlier but the dense shade cast by the plants prevents flower buds opening. Possibly, different cultivars of winter cereals may affect flowering and seed input differently. It would be interesting to determine whether autumn- or spring-emerging plants contributed most to the seedbank. McKeon et al. (1985) found for 2 grassland species that the first wave of emergence produced 80% of the total seedlings and were at a competitive advantage to those emerging later. In winter cereal fields, spring drought in 1986 caused the death of many newly emerged seedlings and those surviving tended to be those which had emerged in autumn. Thus, spring application of herbicides would seem to be unprofitable, especially since established plants are fairly resistant.

From the laboratory experiment it was apparent that V.arvensis seeds are dispersed quite a long way from the parent, with a maximum distance of 399 cm measured. Only 58.6% of the seeds counted fell within 100 cm of the parent. A localised population would therefore rapidly spread throughout a field.

L.purpureum

The main flowering period for L.purpureum is from April to late autumn and often throughout the winter (Hanf 1985). In this study, flowering occurred in May, June and July, with some in December and January. The winter flowering period only applied to the population which had emerged early in autumn along the hedgerow in an oilseed rape field. Those which emerged in November after cultivation did not flower until Spring 1986. Populations in the middle of winter cereal fields would therefore have only one flowering period when they would contribute to the seedbank, in late spring - early summer.

Of the annual emergence, mean survival to reproduce was 67.9% with a mean of 20.5 + 8.1 flowering plants per m^2. The remainder were destroyed as seedlings by drought or herbicides. Any emerging in the crop during summer would be harvested with the crop or, if small enough, may survive to reproduce before burning or cultivation. Those emerging in hedgerows at the field margins would survive and contribute to the seedbank there, but they would not interfere with the crop. L.purpureum rhizomes can survive and some of the plants destroyed above ground by herbicide were able to survive beneath the soil and re-emerge later to produce flowers.

The seedbank in October 1985 was not significantly different to that observed in July 1986. Variation about the mean was high due to the crude sampling methods used (discussed for V.arvensis) and a more detailed study would be required to discover real changes. Furthermore, some input occurred during winter and spring such that some of the input may have emerged immediately since seeds are not

completely dormant when dispersed (Chapter 4).

From plants observed in hedgerows and those grown in a greenhouse, a mean of 210 seeds per plant was estimated.

Conclusions

A summary of the life history of V.arvensis and L.purpureum is presented in Figures 2.40 and 2.41. The seedbank of L.purpureum was much lower than that for V.arvensis and reflects differences in seed production per plant, the relative sizes of the populations (though this is itself a result of differences in seedbank size) and the longevity and dormancy of the seeds (Chapter 4). The proportion of non-viable seeds in the seedbank were similar for both species but V.arvensis seeds tend to survive longer (Chapter 4).

Emergence as a proportion of the seedbank was similar for both species and was similar to that of other species (e.g. Roberts and Dawkins 1967, Carretero 1977, Roberts and Ricketts 1979, Beuret 1984). However, total numbers emerging obviously differed due to the relative sizes of the seedbank.

Survival of seedlings was much higher for L.purpureum than for V.arvensis with 67.9% as opposed to 19.2% - 25.7% such that the numbers of reproducing adults by July were similar, although more V.arvensis plants may have been reproducing by harvest.

Mortality of V.arvensis occurred due to ground frost and the effects of herbicides on newly emerged seedlings, and in summer due to drought and

Figure 2.40 The life cycle of V.arvensis in winter cereal and oilseed rape fields..
(Figures are means per m^2)

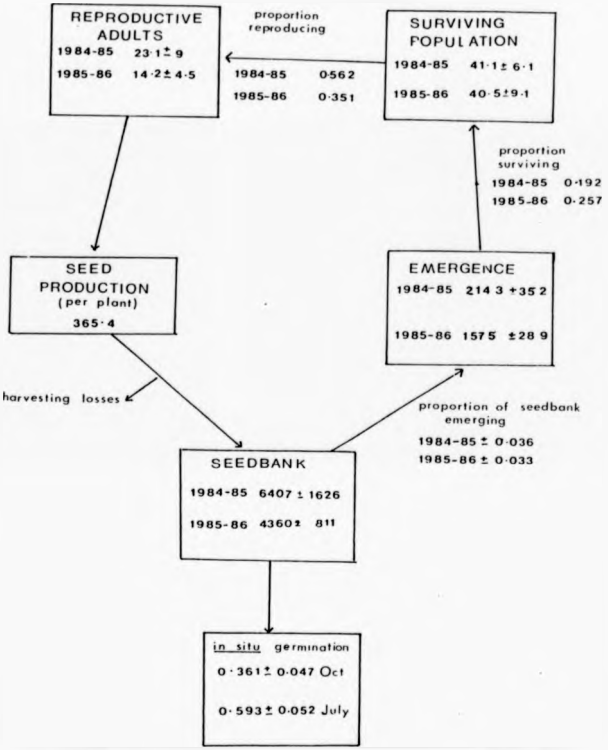
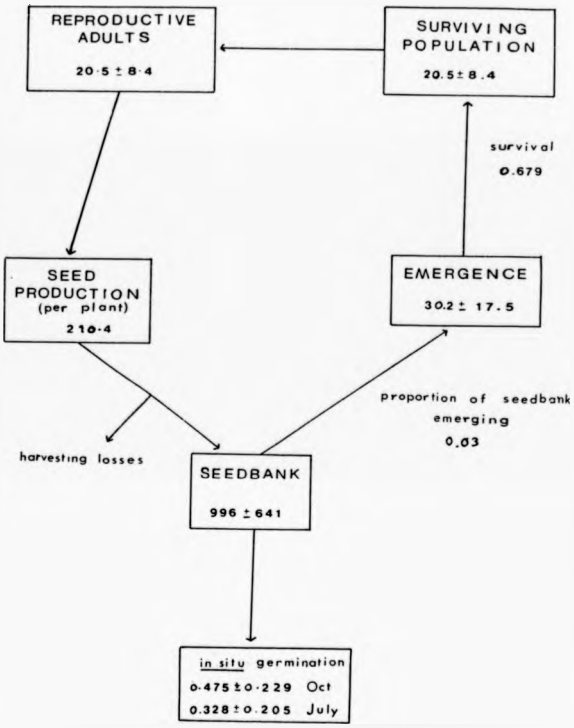


Figure 2.41 The life cycle of L. purpureum in winter cereal and oilseed rape fields.

(Figures are means per m^{-2}).



reproduction (though few had reproduced by July). Density-dependent mortality occurred during periods of environmental stress and, when all months were taken into account, in 1984-85 this was a general phenomenon. Mechanical damage by tractors was also a minor cause of death. Earlier cultivation and emergence in oilseed rape meant that plants were mature during periods of stress and consequently survived better. Enrlier cultivation could therefore reduce natural mortality.

No density-dependent mortality occurred for L.purpureum and most mortality followed reproduction. Frost did kill many established plants and herbicides were also effective on the above ground portions of the plants, though re-establishment could occur from rhizomes.

Flowering and seed dispersal of V.arvensis occurred with the crop so many seeds were removed with the grain. This creates an additional cost of seed cleaning to the farmer since only between 1 and 2% 'trash' is allowed in the grain when sold to the EEC. However, this is not considered the major cost incurred. Some farmers clean the grain anyway to improve drying efficiency and the cost is halved if cleaning is done by the farmer as opposed to a contractor (£1.50 per tonne as opposed to £3.00 per tonne). The major cost is considered to be a depression of grain yield if pansies are not suppressed early on. Once the grain has been harvested, those plants suppressed by the crop and not destroyed by harvesting are able to set seed and this is an additional input to the seedbank. The actual input therefore includes those plants setting seed before harvest, those present at harvest, and those setting seed after harvest, minus those removed with the grain. Determination of the actual seed input would require more detailed sampling than occurred here.

Flowering of L.purpureum occurred during late winter and early spring in this study so all seeds produced entered the seedbank unless they germinated. Thus, although V.arvensis produces more seeds per plant than L.purpureum, fewer may actually enter the seedbank.

L.purpureum populations tended to be localised, whilst V.arvensis populations were widespread throughout the field. This reflects differences in seed dispersal. V.arvensis seeds can be projected up to 400 cm from the plant whilst L.purpureum seeds fall just below the plant (although some are removed by ants). This may be one reason for the spread of V.arvensis in winter cereal fields. If seeds are introduced with the grain, populations may rapidly spread outward from the source region(s).

A significant relationship occurred between the seedbank and emergence for both species and Figures 2.10 and 2.15 could be used to predict emergence in the field within the limits shown. Such information will influence decisions on herbicide application. If infestation levels are likely to be low - especially for V.arvensis - a broad spectrum herbicide can be applied. Conversely, if infestation levels are likely to be high, a specific herbicide against V.arvensis will be required. For L.purpureum, the adult population could also be predicted from the seedbank using Figure 2.33.

The seedbank of V.arvensis was positively related to the sandiness of the soil and to the number of years sown to winter barley. Factors responsible for this relationship will be examined in Chapter 3.

Chapter 3

Experiments in the Botanical Gardens

Introduction

To complement observations in the field and to confirm the data obtained from the thermobar, experiments were set up in the Botanical Gardens and in growth cabinets.

Firstly, an attempt was made to study seasonal patterns of emergence in cylinders of soil buried to ground level in the Botanical Gardens, with soil cultivation once a year in autumn, as fields would be cultivated for winter cereals. In this way, emergence patterns could be studied under controlled conditions with similar soil types and temperatures but with no crop present. However, this experiment had to be abandoned due to a dense moss growth on the soil surface.

Secondly, an experiment was performed to determine the causes of the positive relationship between the seedbank density and the sandiness of the soil observed for V.arvensis (Chapter 2). A large seedbank in sandy soils could be the result of low germination, or of high seed production following high germination, or of greater seed longevity. It was to determine whether germination in sandy soils was stimulated or inhibited, that emergence of seeds buried in 3 different soil types was monitored monthly. Sandy soils tend to be low in nitrates since they are readily leached, while germination of many species is stimulated by nitrate. If these species were stimulated by nitrate then field germination may be inhibited in sandy soils. So an experiment was performed to determine the effect of nitrate on germination.

A dense seedbank might also be due to higher longevity in sandy soils

and this was examined by burying seeds in sachets for 12 months in the three different soil types. Both species were used in these experiments, even though no significant relationship was apparent between the seedbank of L.purpureum and the soil type. This enabled differences in response to soil type to be related to differences in dormancy of the two species.

The reproductive capacity of the species may also vary with soil type and thus influence seed input. However, it would have been difficult to control soil type effects without having differences in nutrient levels and competition so this was not studied.

In order to discover whether V.arvensis and the crop did interact in the field, influencing yields, competition experiments were begun in winter barley fields and in the Botanical Gardens. Different densities of V.arvensis were grown with a standard density of crop plants and the grain and seed production was to be harvested. However, this proved too difficult and time-consuming and was abandoned.

Materials and Methods

1 The effect of nitrate on germination

To determine whether 0.2% KNO_3 solution stimulated germination, two replicates of 100 seeds for V.arvensis and 50 seeds for L.purpureum were placed in incubation tins as used in the thermobar experiments (Chapter 1). Treatments were light with nitrate, light with water, darkness with nitrate, and darkness with water. Seeds were incubated for 2 weeks at 17.9/6.4°C. Light treatments were examined every alternate day and seeds with a protruding radicle were counted and removed. Dark treatments were examined after 14 days. A two-way ANOVA was performed on the results.

2 Nitrate content of soils

The three soil types used for experiments were analysed for nitrate after Allen (1974).

3 Emergence from different soil types

For each species, 8 inch diameter cylinders were sunk to ground level in the Botanical Gardens and filled with either sandy, clay or intermediate soils (Table 3.1) which had been sterilized. The range of percentage sand approximated that found in the field (52.6% to 83.9%). The cylinders were arranged as two blocks of latin squares. In each cylinder 1000 seeds were mixed with the top 3 cm of soil and emergence was monitored monthly, seedlings being removed and the soil cultivated. The cylinders were covered with netting to avoid

predation(Plate 7).

Table 3.1: Soil types used in the emergence experiment. (Percentage sand determined from Allen 1974).

Soil type	Percentage sand
Sand	80.3
Intermediate	69.1
Clay	19.3

4 Longevity in different soil types

In September 1985, 6 replicates of 100 seeds for each species were sealed in nylon mesh sachets and buried 8 cm deep in cylinders containing either sandy, clay or intermediate sterilized soil (Table 3.1). L.purpureum seeds were sealed in the sachets with the appropriate soil, but V.arvensis seeds, being smaller, would have been difficult to retrieve from the soil in the sachets so were sealed into sachets without soil. Soil did enter through the mesh to a certain extent, however.

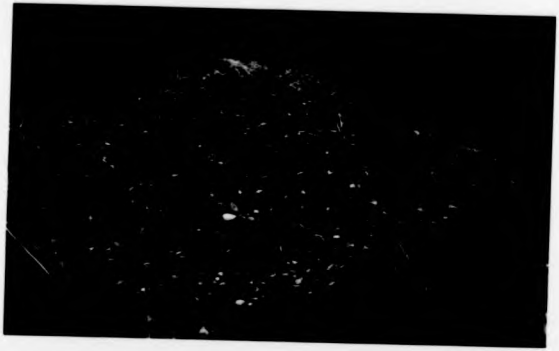
In August 1986, sachets were exhumed and viability determined by incubating in a growth cabinet to allow imbibition. Incubation time were the same as those described for the thermobar (Chapter 1). Viability was determined by applying gentle pressure with forceps. Cylinders used were those used for emergence. A one-way ANOVA was performed on the results.

Plate 7

Burial of seeds in sandy , clay , or intermediate soil

Plate 8

Emergence patterns in the Botanical Gardens



5 Seasonal patterns of emergence

In September 1981 in the Botanical Gardens, 2 replicates of 2000 seeds for each species were sown in sterilized sandy soil taken from a winter cereal field. Pots of 20 cm diameter were used and sunk to ground level. Green bird netting was used to cover the pots to prevent predation. The mesh size was fairly large (approx. 2 cm^2) so it would not interfere with light penetration (Plate 8) The top 1 cm to 6 cm of soil was cultivated in September 1981 when the seeds were initially sown and again in September 1985 to reproduce field cultivation.

However, during the experiment a moss blanket grew on the soil surface since the experimental plot was in a shaded area and the soil became waterlogged. All attempts to remove this failed so the data obtained was not representative of field conditions and the experiment was terminated.

6 Competition experiments

In 2 winter barley fields a latin square design was set up to study the effect of different densities of V.arvensis on crop yields and to determine the effect of the crop on different densities of V.arvensis. Two fields were used with different soil types and in different areas and situations to determine whether the environment would affect any observed relationships. Once the quadrats were marked out with canes and string, V.arvensis plants were thinned to achieve densities representing the range observed in the field. In the Botanical Gardens, a similar experiment was set up for both species such that crop density was constant and more detailed study of growth and

reproduction of the plants could occur.

However, after plots had been weeded of other weeds several times and sprayed with herbicide it was apparent that the experiments would prove too time-consuming. Furthermore, due to variation in crop density and growth, aspect, drainage, etc. in the field and even in the garden plots, the result would not have been very useful. The experiments were terminated.

Results

1 The effect of nitrate on germination

Figures 3.1 and 3.2 show the effect of 0.2% KNO_3 on germination of V.arvensis and L.purpureum. In both species, germination was significantly stimulated by 0.2% KNO_3, both in the light and in darkness (Table 3.2 and Appendix 6). For V.arvensis there was a significant interaction between light and nitrate.

Table 3.2

The effect of nitrate nitrogen on germination

(Figures are arcsine proportions).

(ANOVA tables are presented in Appendix).

L.purpureum

Treatment	Water	Nitrate
Darkness	16.7	33.5
Light	27.3	49.9

V.arvensis

Treatment	Water	Nitrate
Darkness	45.9	69.9
Light	22.5	55.9

Figure 3.1
The effect of 0.2% KNO_3 on germination of Viola arvensis in the light and in the dark. at 17.9/6.4°C.

I 95% confidence limits

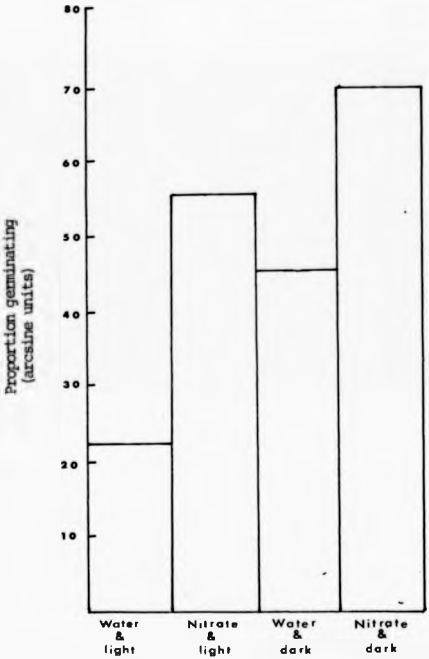
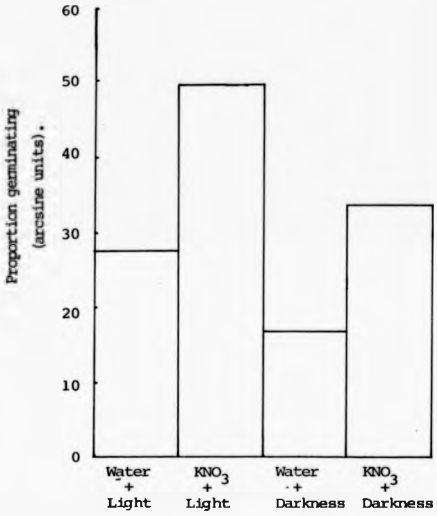


Figure 3.2 The effect of 0.2% KNO_3 on germination of L. purpureum seeds at 17.9, 6.4 °C

I 95% confidence limits.



2 Nitrate content of the 3 soil types

Table 3.3 Nitrate content of the 3 soil types used in emergence and longevity studies.

Soil type	Nitrate ($mg\ 100g^{-1}$)
Sandy	0.87
Intermediate	2.13
Clay	6.04

Sandy soils had the lowest nitrate content and clay soil is the highest (Table 3.3).

3. Emergence from different soil types

Annual emergence as a proportion of the seedbank for V.arvensis was greatest from clay soils and least from intermediate soils (Figure 3.3). However, a significant difference between soil types in the proportion emerging on a monthly basis only occurred in September, April, May and June (Figure 3.4). Emergence from clay soils only exceeded that from sandy soils in September and June. In April and May, emergence from sandy soils exceeded that from clay soils. In September and April emergence from sandy soils exceeded that from intermediate soils but in June the reverse occurred and in May and June emergence from intermediate soils exceeded that from clay.

For L.purpureum, annual emergence as a proportion of the seedbank was greatest from sandy soils, with clay soils having the least (Figure

Figure 3.3. The proportion of the seedbank emerging from sandy, clay and intermediate soil for *Viola arvensis* and *Lamium purpureum*.

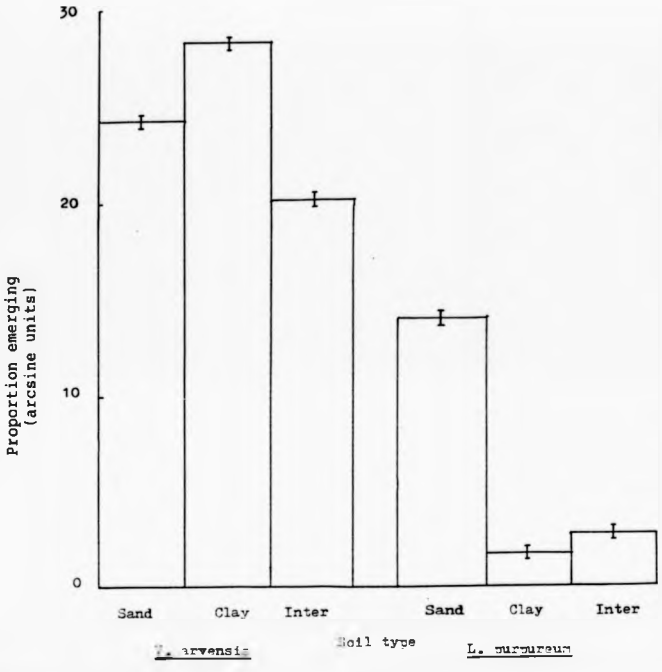
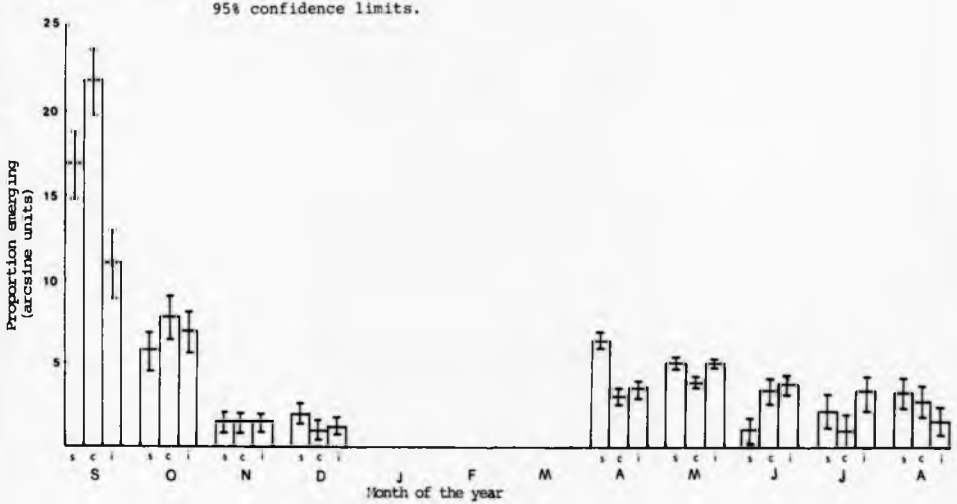


Figure 3.4 The proportion of the seedbank emerging per month in sandy, clay, or intermediate soils of V.arvensis.



3.3). On a monthly basis, emergence was always greatest from sandy soils, with no significant difference between clay and intermediate soils (Figure 3.5). Data is shown in Appendix 7 and 8 for V.arvensis and L.purpureum respectively.

The seasonal pattern of emergence for both species reflected that observed in winter cereal and oilseed rape fields (Chapter 2) even though the soil was cultivated monthly. The pattern also confirmed that expected from observed changes in dormancy level of the seeds (Chapter 1).

1 Longevity in different soil types

There was no significant difference between soil types in the proportion of seeds remaining viable after 11 months burial in sachets for either species (Table 3.4 and Figure 3.6). Neither was there any significant relationship between the proportion of non-viable seeds in the seedbank of the fields studied and the amount of sand in the soil (Appendix 9).

Figure 3.5 Proportion of the seedbank emerging per month in sand, clay, and intermediate soils for L.purpureum.

95% confidence limits.

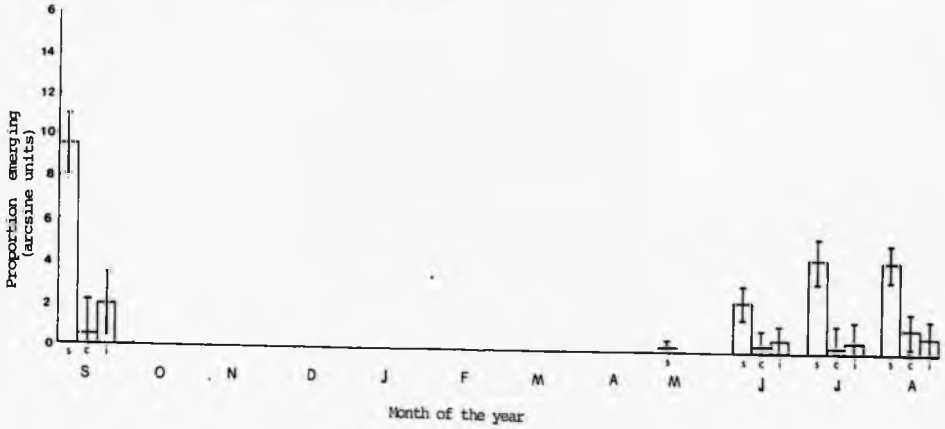


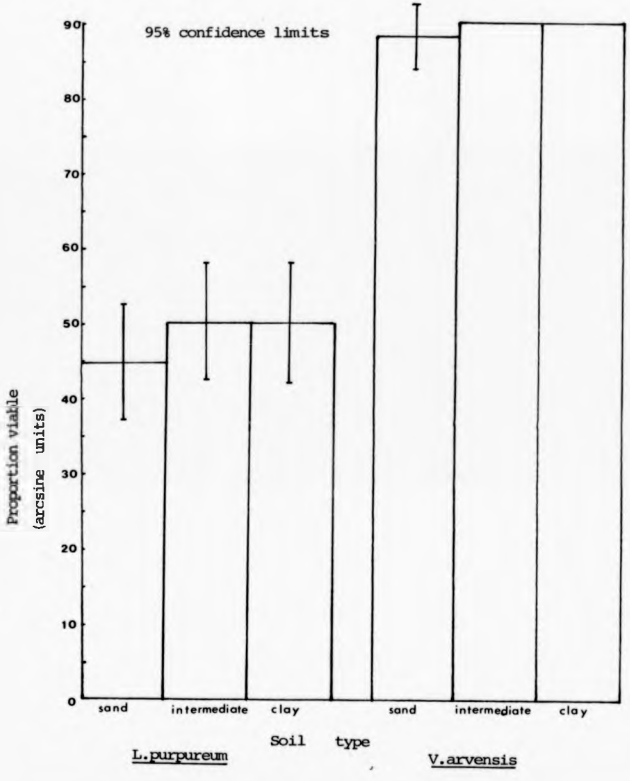
Table 3.1 Longevity of seeds of V.arvensis and L.purpureum buried in different soil types for 11 months.

Figures are arcsine transformed proportions.

Replicates of 100 seeds were used.

Species	L.purpureum						V.arvensis					
Replicate	1	2	3	4	5	6	1	2	3	4	5	6
Treatment												
Sand	35.3	37.0	52.5	35.9	56.3	50.3	90.0	90.0	80.0	90.0	90.0	90.0
Clay	19.0	55.6	42.8	51.9			90.0	90.0	90.0	90.0	90.0	90.0
Intermediate	59.8	39.5	53.0	10.6	57.7	17.0	90.0	90.0	90.0	90.0	90.0	90.0

Figure 3.6 Longevity of V.arvensis and L.purpureum seeds stored in sandy, intermediate, or clay soils for one year.



Discussion

Factors involved in the positive relationship between the seedbank and the sandiness of the soil.

In both species, germination was stimulated by 0.2% KNO_3 in the light and in darkness. For V.arvensis there was a positive interaction between light and nitrate, with germination being stimulated more by nitrate in the light. Fresh seeds of V.arvensis (used here) are inhibited by light so the greatest effect of nitrate occurred under the least favourable conditions. Such an effect has been found for several species (Chapter 1).

Analysis of the three soils used in emergence experiments revealed that the sandy soils had the least nitrate nitrogen and the clay soil had the most. Thus, there was a negative relationship between the amount of sand in the soil and the nitrate nitrogen content. Sandy soils are readily leached, whilst clay adsorbs salts and prevents leaching.

In view of these results, most emergence would be expected from clay soil and least from sandy soil if the nitrate nitrogen content of the soil was the only factor involved. For V.arvensis, annual emergence was greatest from clay soil as anticipated, but least occurred from intermediate soil rather than from sandy soil. Thus, for V.arvensis, nitrate content was not the only factor involved in differences in emergence. Sandy soils are more porous and are therefore better drained and aerated. Pawlowski (1963 in Jensen, 1969) found sandy soils produced more seedlings than alluvial, loess, chernozem and rendzina respectively, though this may act indirectly by influencing

the crop and cropping system. The intermediate soil type, having both a moderate nitrate content and a moderate level of drainage, had the lowest emergence.

However, on a monthly basis, emergence of V.arvensis from clay soil exceeded that from sandy soil only in September and June. In April and May, the reverse occurred and may have resulted from the difference in temperature of the soils. Being more porous, sandy soil warms and cools more rapidly and so temperature fluctuation will be greater, and may have stimulated emergence. This hypothesis is supported by the fact that emergence from intermediate soil was also higher than that from clay in May when temperature fluctuation was fairly high. In June, sandy soil had least emergence, probably due to drought since sandy soils dry out quicker.

Since annual emergence from sandy soil was higher than from intermediate soil, it is unlikely that a high seedbank density in sandy soils results from inhibition of germination due to low nitrate levels.

Longevity of the seeds over 11 months did not differ significantly between soil types. However, over a longer time period, differences in longevity may occur since loss of dormancy may differ in different soil types. Champness and Morris (1948) found L.purpureum seeds were more prevalent in lowland pastures than in arable soils since seeds were better preserved in the damp acid conditions but

Brenchley (1918) found the reverse. Dormancy of the seeds is also important and may cause such discrepancies. Egley and Duke (1985) found high soil temperatures caused a loss of viability. Predation may also vary between soil types but this would be difficult to examine and is probably of only minor importance. Nitrate stimulated germination in darkness, so in situ germination may be higher in clay soils. However, from seedbank data, there was no relationship between the proportion of non-viable seeds in the seedbank and the sandiness of the soil.

The conditions experienced by the seeds in this experiment did not exactly replicate those in the field. In a field situation, clay soils easily become waterlogged. Here, however, cultivation of the soil monthly and with a depth of only 30 cm meant that little compaction and waterlogging occurred. Waterlogging may inhibit germination (though in tins, seeds were able to germinate even if they had fallen into the reservoir of water), or even increase fungal attack.

The positive relationship between the seedbank density and sandiness of the soil may not be due to the effects of the soil factors on the seeds themselves. The relationship also reflects crop history since clay soils are less favourable for winter cereals and are used more for pasture and winter barley tends to be grown more on sandy soils. This has been discussed in Chapter 2. Nitrate fertilizer can be added to remove this deficiency in sandy soils. If heavy clay soils are ignored on the grounds of difference in crop history, the fact that emergence from sandy soils exceeds that from intermediate soils suggests that higher emergence in sandy soils is an important factor in

The soil type may exert its effect on the plants themselves rather than the seeds. The more rapid heating of sandy soils in the summer may affect the reproductive capacity of the plants. It is important to remember that the seed input is largely determined by the number of seeds dispersed before harvest since many undispersed seeds are harvested with the crop such that earlier flowering may increase the input. Flowering is related to temperature (Chapter 2) so the more rapid heating of sandy soils may lead to earlier flowering. Such a relationship could not be studied in the field since variation in the time of cultivation also affected the time of flowering.

L.purpureum germination was also stimulated by nitrate but most emergence occurred from nitrate-poor sandy soil. Thus, nitrate levels did not seem to affect emergence in the field. Very little emergence occurred from clay or intermediate soils.

L.purpureum germination is favoured by warmer temperatures (Chapter 1 and Figure 3.5) and since sandy soils will heat up more rapidly as discussed earlier, this may stimulate emergence. Alternation of temperature will also be greater. Published information on the relationship of L.purpureum to soil type refers to plant growth, not the seedbank, and it is reported to prefer nutrient-rich soils (Chapter 1). These results suggest that this is unlikely to be due to any effects on seed germination.

Since clay soils do not tend to be used for winter cereals in this area, most soils belonging to an 'intermediate' category, the most interesting finding is that emergence in sandy soils exceeded that in intermediate soils for both species so this may be an important factor

in the relationship between the seedbank and the sandiness of the soil.

The seasonal pattern of emergence

The seasonal pattern of emergence from the three soil types for V.arvensis was similar to the observed pattern in the field (Chapter 2), except that in the gardens no emergence occurred from January to March. This may reflect differences in dormancy of the seeds since the seeds in the field were a mixed age population, whilst in the gardens they were less than one year old and V.arvensis seeds are relatively dormant in the first year of burial (Chapter 4). On the other hand, a severe drought occurred throughout much of this period during which time the soil was permanently frozen in the gardens. Soil in the field may not have been frozen to such an extent, being deeper and protected by the crop, such that emergence was possible.

For L.purpureum, the pattern of emergence in the gardens was again similar to that observed in the field (Chapter 2) except that the peak observed in September in the gardens was later in the field due to the timing of cultivation. Also, there was no late spring - early summer peak in the field, possibly reflecting the effect of cultivation in the gardens. A slight increase did occur in the field in early spring 1986 but this was mainly from freshly dispersed seeds and from rhizomes.

Thus, for both species, emergence patterns were similar in the gardens to that observed in the field and confirmed thermobar results on the dormancy status of the seeds (Chapter 4).

CHAPTER 4

Seasonal Changes in Dormancy

Introduction

Many species undergo seasonal changes in germination requirements during burial, enabling germination at the time most favourable for completion of the life cycle (Chapter 1.3). In order to monitor seasonal changes in germination requirements of V.arvensis and L.purpureum, seeds were buried in August 1984 and exhumed monthly for two years. The temperature and light requirements for germination were then tested on a thermogradient bar at seven temperature regimes representing particular times of the year (Fig 4.1). These results will be used to explain emergence patterns in the field in terms of prevailing temperatures and light conditions. Seasonal changes in the proportion of non-viable seeds were also determined from this data.

Materials and Methods

1 Seed collection

Viola arvensis seeds were collected from one field of winter cereals in August 1984 (Canal field - 9 on map p.60). Open pods containing ripe seeds were taken and dried inside paper bags since the seeds dehisce explosively (Plate 6). In 1985, seeds had to be collected from several winter cereal fields since cool, wet conditions delayed dehiscence and made ripe seeds scarce (Canal field and Shebdon - 9 - and Hill, - 3 on map p.60). Some ripe but unopened pods had to be collected additionally in order to obtain sufficient numbers. Any differences between the behaviour of the two seed lots must take this difference in collection into account.

Lamium purpureum plants with ripe seeds were collected from hedgerow populations along a roadside in May and June 1984 (shown on map p.60)and from populations at the edge of an oilseed rape field in 1985 (Bank field - 3 on map p.60). Again, these differences in origin of the seeds may be reflected in their germination behaviour. The plants were allowed to dry until all ripe seeds had been released. All seeds were dried in the light in a desiccator for 14 days.

2 Burial

Lots of 50 (L.purpureum) or 100 (V.arvensis) seeds were sealed in nylon mesh sachets (250 nm mesh size) using a heat sealer (Plates 9 and 10).

On 19th August 1984, 14 sachets for each species were buried 8 cm deep in 8 inch diameter cylinders with open ends, in sterilized sandy soil taken from a winter cereal field (Mills - 7 on map p.60). Forty eight cylinders were sunk into a border at the Botanical Gardens, Keele, with the soil surfaces flush. They were arranged in two replicate blocks. Two cylinders - one from each block - were exhumed each month. These two replicate cylinders were kept separate as replicates for each temperature regime on the thermogradient bar. The two species shared cylinders (Plate 11).

In 1985, seeds were buried earlier, on 1st July for L.purpureum and one week later on 26th August for V.arvensis to determine, by comparison with the results of the previous burial, whether observed changes were due to the month of burial or the length of time buried. The two species were in different cylinders. Altogether a further 48 cylinders were sunk.

An attempt was made to monitor soil temperatures but the equipment was unreliable and soil temperatures from the Keele meteorological station were used.

3 The thermogradient bar

The thermogradient bar (Plate 12) consisted of an aluminium plate 4 cm

Plate 9

Sachet used in burial experiment

Plate 10

Seeds of *Lamium purpureum* & *Viola arvensis*

Plate 11

Plot used for burial of seeds

Plate 12

The thermogradient bar

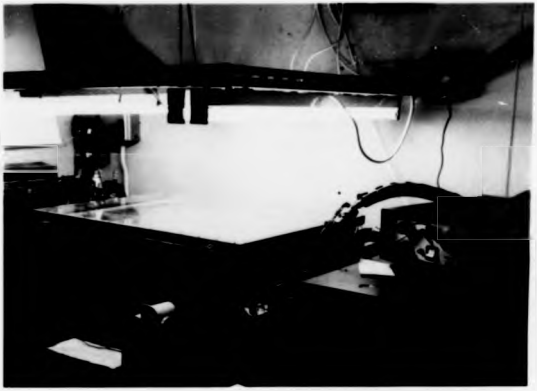
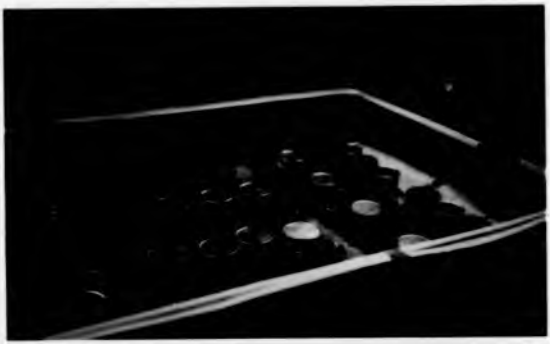


Plate 13

Arrangement of pots on the thermogradient bar
(numbers are explained in the text)



thick. At either end, antifreeze at a controlled temperature was pumped through the plate. The equipment at both ends could maintain 2 alternative temperatures, which were alternated on a 12 hour cycle by a clock. Although one end ('winter') was always cooler than the other ('summer'), with a gradient between, the ends alternated temperatures in synchrony to simulate a 12 hour day (warm) and a 12 hour night (cool) at every point along the gradient. Temperatures were set at either end to produce winter temperatures at position 7 and an extreme summer temperature at position 1 (Plate 13). Between these two, a range of temperatures representative of the mean and ranges experienced at particular months existed. The plate was insulated from external temperatures by a polystyrene covering around the sides and beneath the plate. It was covered by a double layer perspex lid. The light source was provided by four 60 watt fluorescent tubes suspended above the bar, arranged to give uniform light intensity across the plate. An attempt to produce uniform but realistic red/far-red wavelengths using a mixture of tungsten bulbs and fluorescent tubes was unsuccessful and was abandoned. The fluorescent tubes gave a high red/far red ratio.

Figure 4.1 shows monthly averages of daily mean temperatures and diurnal ranges of surface soil temperatures between 1952 and 1962 at Keele. These were calculated from air temperatures and the formula from Walker and Barnes (1981) and a regression line fitted. The temperature means and ranges on the thermogradient bar were matched to this regression (Table 4.1 and Figure 4.1). Ideally, temperatures representing each month would have been used but this is impossible on a thermobar, which must be represented by a straight line on a graph such as Figure 4.1.

Table 4.1

Temperature means and ranges produced on the thermogradient bar

Station	Temperatures (°C)	Mean	Range	Months represented
1	28.5/12.6	20.6	16.0	Extreme summer
2	24.1/ 9.2	17.2	13.9	June, July, August
3	22.1/ 9.0	15.6	13.1	September
4	19.8/ 7.7	13.8	12.1	May
5	17.9/ 6.4	11.2	11.5	October
6	13.6/ 3.6	8.6	10.0	November/March
7	9.1/-0.1	4.7	9.2	December-February

4 Experimental procedure

Two replicate cylinders were exhumed monthly. They were first taken to a dark room in order to set up dark treatments without exposing seeds to light. A green lamp was used to transfer seeds from sachets to tins only exposing seeds to about 30 seconds of the green light. This was found to have no effect on germination (Appendix 10). Seeds were placed on filter paper supported by glass beads over a reservoir of 4 mls of water in aluminium tins of 4.5 cm diameter (Plate 11). Once the dark treatments had been prepared with light-tight lids, the room light was switched on and light treatment tins were prepared, with polythene covers held by elastic bands. Tins were placed on the thermogradient bar at the 7 different positions.

Germinated seeds in light treatments were counted and removed on

Figure 4.1 Mean soil surface temperatures 1952-1962 at Keele

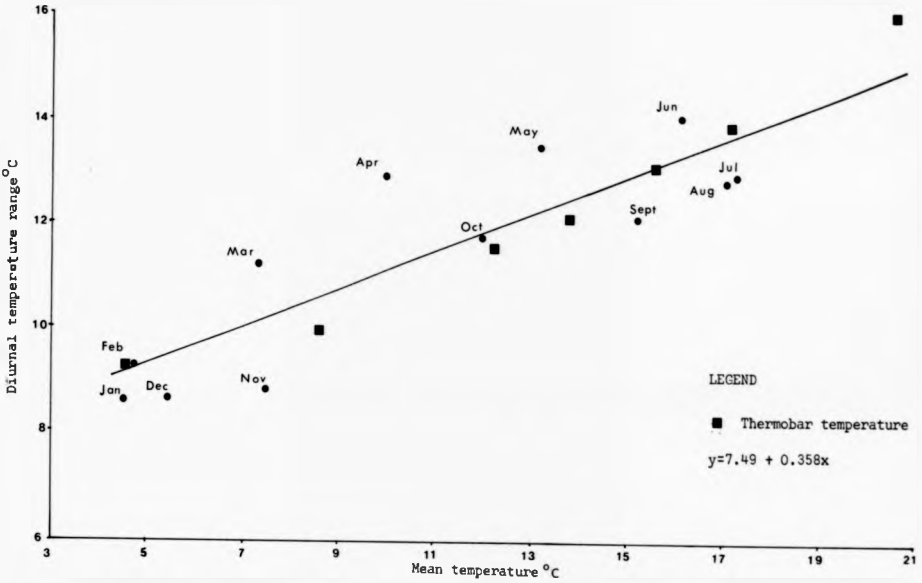


Plate 14

Pots used for seed germination

alternate days. Germination was taken as the protrusion of the radicle from the seed coat. Initially, lids from dark treatments were removed inside a photographic dark bag to allow gas exchange equivalent to that experienced by the light treatments. However, this procedure was found to have no effect on germination and so was terminated. The incubations continued for each tin for 14 days, or until no further germination was apparent, at which point that tin and its dark equivalent were removed and the germination in the dark was counted. Numbers of viable and non-viable seeds were counted by applying slight pressure to the seeds with forceps.

Data was transformed to arcsine square root of the proportion germinating. The proportion of non-viable seeds was also determined for each month. If slight pressure caused exudation of the embryo, the seed was counted as decayed.

5 An additional experiment to confirm the effect of burial on the acquisition of a light requirement in V.arvensis.

It was discovered that V. arvensis seeds were inhibited by light until buried, when they gained a net light requirement. A garden experiment was performed to determine whether burial itself or just contact with the soil produced this effect (Plate 15).

Three treatments were set up as follows:

(a) Four replicates of 500 seeds were mixed with the top 6 cm of sandy soil in 15 cm diameter cylinders sunk to ground level in the Botanical Gardens. Seedlings were counted and removed, and the

Plate 15

Viola arvensis - the effect of burial & soil contact on the release of seeds from dormancy

soil mixed monthly.

(b) Four replicates of 500 seeds were scattered on soil in a tray and placed outside at ground level in the Botanical Gardens. Seedlings were counted and removed monthly.

(c) Four replicates of 500 seeds were scattered on the surface of filter paper in trays at ground level in the Botanical Gardens. Seedlings were counted and removed monthly.

All treatments were covered with netting against predation.

6 Attempts to break down dormancy of V.arvensis

For each treatment, light treatments were exposed to light every alternate day at counting and dark treatments were counted after 14 days.

Chilling

Two replicates of 100 seeds, prepared as for the thermobar, were placed in a refrigerator at 4°C for two weeks and then incubated on the thermobar at 17.9/6.4°C.

Scarification

Seeds were scarified between 2 layers of sand paper until the seedcoat was obviously roughened. Two replicates of 100 seeds were then incubated in a refrigerator since this gave similar germination to the

thermobar in darkness and germination was monitored.

Heating

Dry seeds were placed in an oven at 50°C for 5 days and then incubated in tins as for the thermobar. Two replicates for light and dark treatments were placed in a refrigerator for two weeks and germination monitored.

Treatment with solvents

Seeds were soaked in 'Tween' for a few minutes until the mucous layer was obviously dissolving. Seeds were then washed thoroughly in water and placed imbibed in tins as for the thermobar in the light and in darkness in the fridge for two weeks.

Results.

V. arvensis

The graphs shown in Figure 4.2 a-g show germination at each particular temperature regime. Each regime corresponds approximately to particular months in the year, which are indicated by arrows on the horizontal axis. Where germination occurred at the month corresponding to the temperature regime experienced, emergence would occur in the field if other conditions were similar. Figure 4.3 represents germination at the appropriate field temperatures for each month using data from Figure 4.2 and indicates when germination would be expected in the field. The dashed lines indicate seeds buried in the second year of the experiment.

Fresh unburied 1984 seeds were relatively dormant, only exceeding 10% germination in the light at 22.1/ 9°C (4.2 c) and in darkness at the lower temperatures (Figure 4.2 d-f), and exceeding 30% in darkness at 9.1/-0.1°C (Figure 4.2 g).

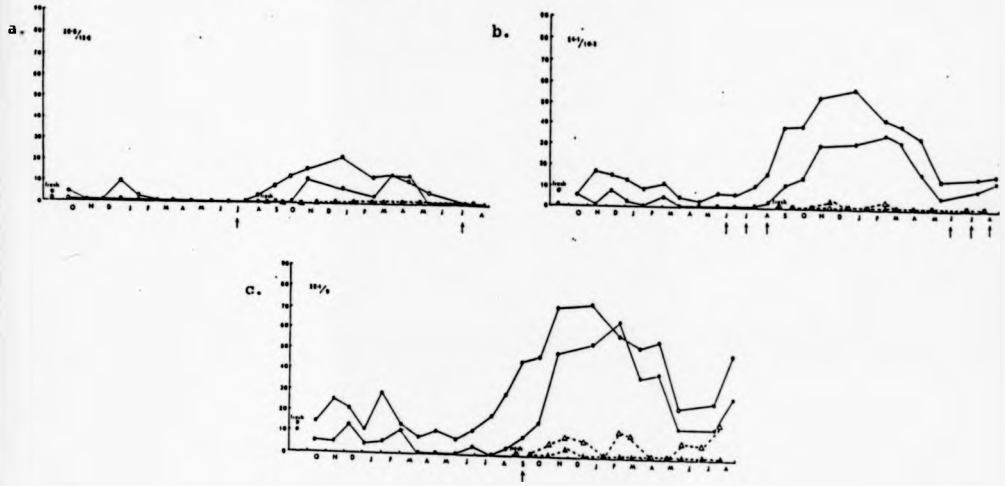
Where light and dark germination differed, light inhibited germination of unburied seeds, but germination of buried seeds was generally stimulated by light.

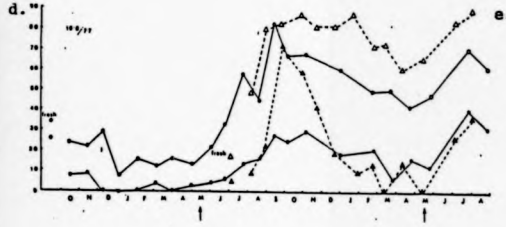
Germination in the first autumn was relatively low at autumn temperatures (Figure 4.2 e) so little emergence would be expected. This low level of germination extended into winter (Figure 4.2 g)

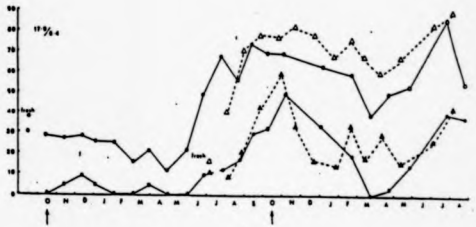
During the first year burial, seeds were least dormant at autumn,

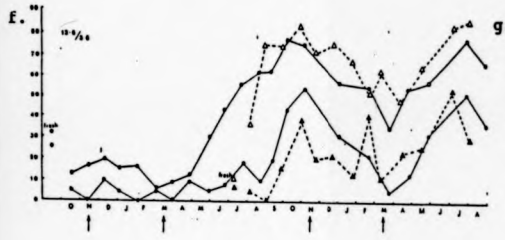
Figure 4.2 Germination of V. arvensis seeds on the thermogradient bar exhumed monthly and tested at 7 temperature regimes. Figures are arcsine proportions. Open symbols are light treatments, triangles are 1985 seeds.

↑ Month corresponding to test temperature.




d.
O N D J F M A M J J A S O N D J F M A M J J A


e.
O N D J F M A M J J A S O N D J F M A M J J A


f.
O N D J F M A M J J A S O N D J F M A M J J A

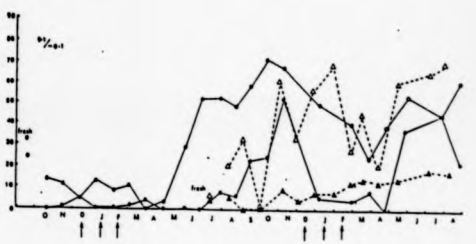
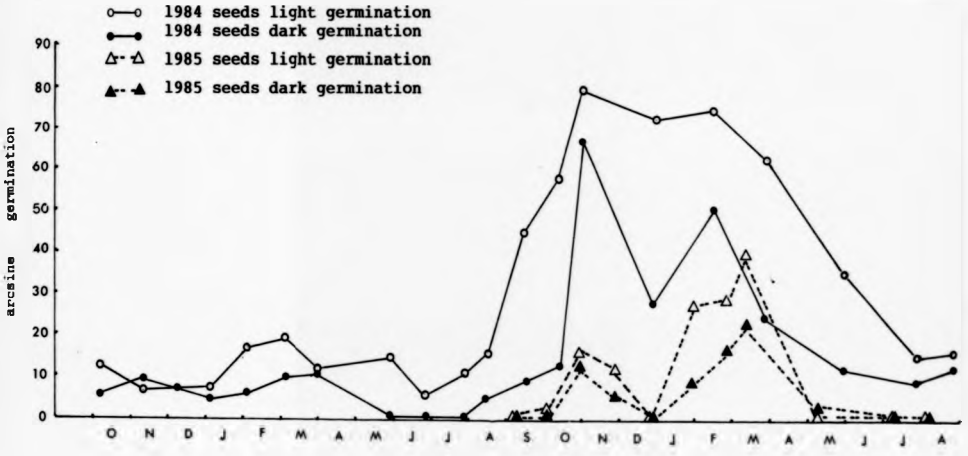

g.
O N D J F M A M J J A S O N D J F M A M J J A

Figure 4.8 Viola arvensis arcsine germination at prevailing field temperatures



winter and spring temperatures (Figure 4.2 d, e, f and g). During summer seeds were unable to germinate at summer temperatures (Figure 4.2 a and b). During the second autumn and winter of burial, dormancy was low at all but the warmest temperatures. At 9.1/-0.1°C in the light and dark and 19.8/7.7°C in the dark, dormancy increased in December but decreased again thereafter. In 1985 seeds, a similar trend was apparent with the seeds having similar dormancy levels.

The decline in germination observed during the second year of the experiment in December at 9.1/-0.1°C and 19.8/7.7°C was observed in 1985 seeds and here was evident at all but the warmest temperature regimes. This implies that conditions experienced by the seeds during burial increased dormancy during December. Figure 4.3 reveals this pattern clearly. Dormancy at prevailing field temperatures was high until February - April, when it declined then increased again so there would be little germination in June, July or early August. Dormancy at prevailing field temperatures then declined rapidly to reach a minimum in October and November of the second year of burial. In the light, this peak in germination prevailed into April, but in the dark a sharp increase in dormancy occurred in December, decreasing in February, and increasing again thereafter to produce low germination in July and August.

The 1985 seeds showed the same trend as 1984 seeds which had been in the soil one year except the former were more dormant. They did follow a similar trend to that of 1984 seeds in their first seasons burial but October germination was higher, as was that in January, February and March. Thus, the second year seeds appeared to be less

dormant. Alternatively, conditions were more favourable in 1985-86 than in 1984-85 for the release of dormancy. Germination was not correlated with rainfall, mean monthly soil temperature range, nor with mean monthly soil temperature.

In the experiment set up to determine reasons for the effect of burial on light inhibition of germination, it was found that most germination occurred when seeds were mixed with the soil (Figure 4.4 and Table 4.2). No germination occurred on filter paper. Only in May did emergence occur from seeds scattered on the soil surface when it almost exceeded that from seeds mixed in with soil.

Neither chilling, scarification, heating nor soaking seeds in solvents to remove the mucus layer affected germination; the seeds remained completely dormant.

Figure 4.4 The mean proportion emerging of V.arvensis seeds:
a) mixed with soil and cultivated monthly; b) scattered on the soil surface; c) scattered on filter paper. (Treatments were outside in the botanical gardens and consisted of 4 replicates of 500 seeds).

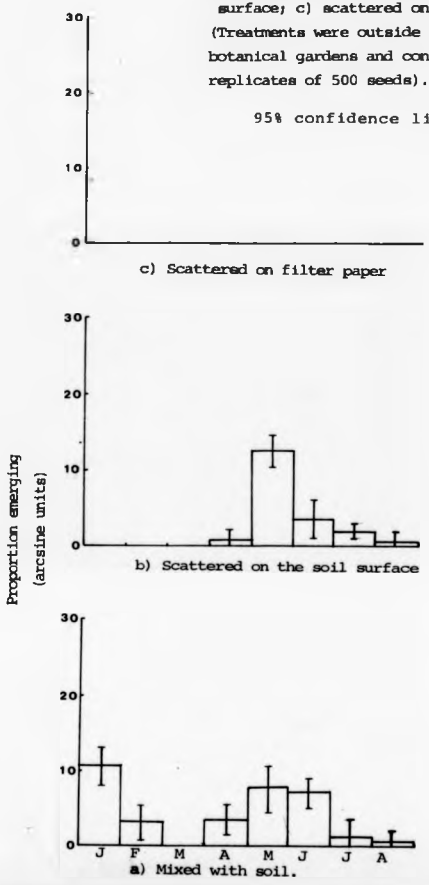


Table 4.2

Arcsine proportions of germination of V. arvensis from
(a) Seeds mixed with soil monthly
(b) Seeds on the soil surface
(c) Seeds on filter paper

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
	Replicates								
(a) Mixed with	1	8.5	5.8	0	5.2	6.9	6.5	0	0
soil	2	7.7	3.7	0	2.6	5.2	8.7	2.6	2.6
	3	11.8	0	0	0	11.4	4.7	3.9	0
	4	13.4	2.6	0	5.3	7.0	8.5	0	0
Mean		10.4	3.0	0	3.3	7.6	7.1	1.6	0.7
St.Dev		2.7	2.41	0	2.51	2.64	1.88	1.95	1.3
(b) On soil	1	0	0	0	2.6	14.4	0	2.7	0
Surface	2	0	0	0	0	9.6	4.5	2.6	2.6
	3	0	0	0	0	12.9	5.8	2.6	0
	4	0	0	0	0	13.2	3.8	0	0
Mean		0	0	0	0.7	12.5	3.5	2.0	0.7
St.Dev		0	0	0	1.30	2.05	2.49	1.31	1.30
(c) On filter	1	0	0	0	0	0	0	0	0
paper	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
Mean		0	0	0	0	0	0	0	0
St.Dev		0	0	0	0	0	0	0	0

L. purpureum

At most temperatures, L. purpureum seeds had 20 to 40 arcsine units of germination when dispersed in 1984, but burial induced further dormancy, especially in the dark (Figure 4.5 a to g). Light germination exceeded dark germination in all treatments. Germination was low at all temperatures until June and it gradually reached a peak during the second autumn (August to November). Dormancy gradually increased again during December to give minimum germination in May. In the second spring of burial seeds were less dormant and germination began to increase from May, earlier than the previous season.

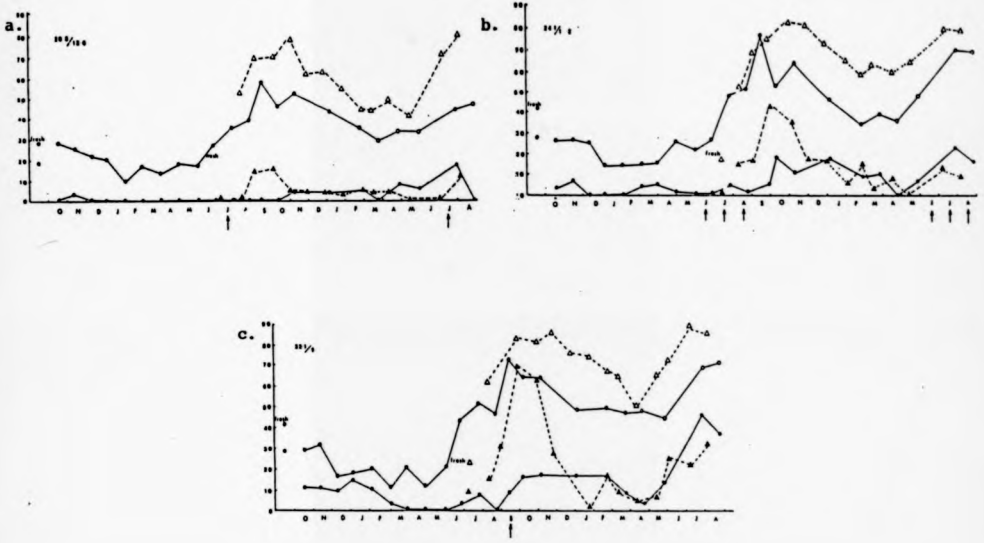
The 1985 seeds behaved similarly but burial did not induce dormancy at any temperature. Seeds were gradually released from dormancy and behaved the same as seeds which had been buried one year. Thus, both seed lots responded to the environment in the same way, irrespective of duration of burial and differences in origin. In fact, recently buried seeds were less dormant than those buried for one year.

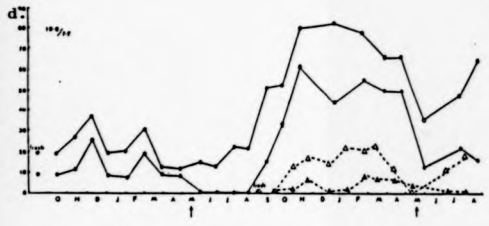
In both years, dark germination was less than that in the light but was parallel in responses, and any increase or decrease in dormancy was more rapid in darkness.

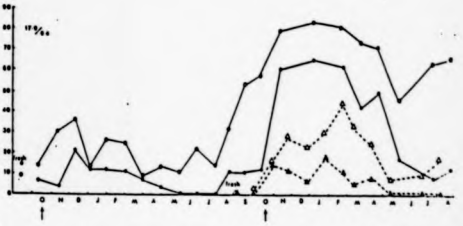
Figure 4.6 shows germination at prevailing field temperatures and illustrates these trends clearly. At prevailing field temperatures in the light, seeds were initially relatively non-dormant but burial induced dormancy in 1984 seeds, such that by December in the first winter of burial very little germination would occur in the field. A small amount of germination occurred from January to April but not to

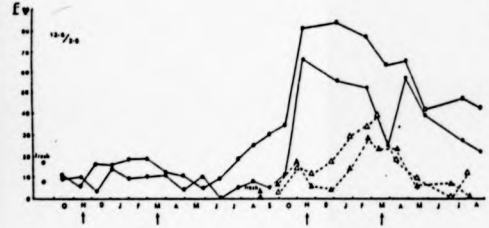
Figure 4.5 Germination of L. purpureum seeds on the thermogradient bar exhumed monthly and tested at 7 temperature regimes. Figures are arcsine proportions. Open symbols are light treatments, triangles are 1985 seeds.

↑ Month corresponding to test temperature.




d.
O N D J F M A M J J A S O N D J F M A M J J A


e.
O N D J F M A M J J A S O N D J F M A M J J A


f.
O N D J F M A M J J A S O N D J F M A M J J A

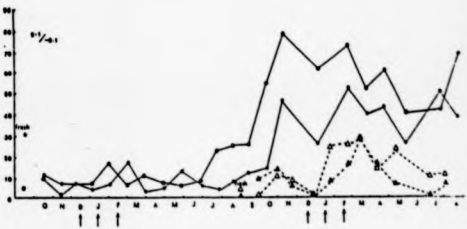
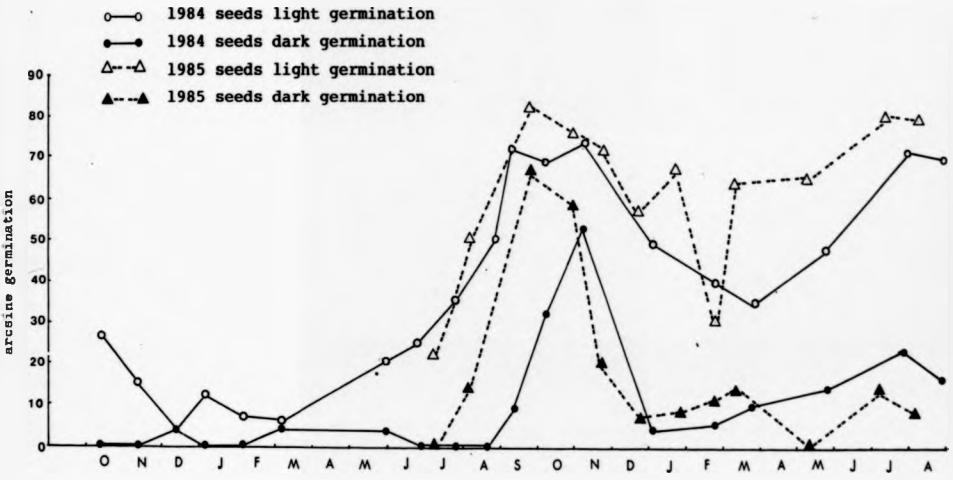

g.
O N D J F M A M J J A S O N D J F M A M J J A

Figure 4.6 Lamium purpureum arcsine germination at prevailing field temperatures



any great extent until late May. There was then a gradual decline in dormancy until peak germination occurred in August and September during the second year of burial. Dormancy then increased again gradually to a maximum in March during the second spring of burial, though never did it reach the level of the previous winter. Dormancy then decreased again during late spring to early summer. The 1985 seeds reflected the behaviour of seeds which had been buried one year and were never induced into dormancy to the same extent as 1984 seeds were in the first year of burial.

Dark germination was negligible at field temperatures in 1984 until the second autumn of burial when it increased rapidly, declining again during winter to a low level. Dark germination increased to a certain extent during the second spring. The 1985 seeds were less dormant and only in the first month of burial and again in the following May did germination become negligible in darkness.

Thus, peak emergence would be expected in the second autumn for 1984 seeds and in the first autumn for 1985 seeds. By autumn 1986, germination of both seed lots reached a similar level to that of autumn 1985. The duration of burial did not therefore affect dormancy.

Seasonal changes in the proportion of non-viable seeds

Only one year's data was used in this experiment. The proportion of non-viable seeds in each tin on the thermobar was calculated and a mean value determined for each month. Monitoring began in August 1985 and ended in August 1986. However, seeds had been buried for different lengths of time. One population had been buried between 1 and 14

months and one between 11 and 24 months.

For V.arvensis, Figure 4.7 shows that in most cases less than 3 arcsine units of the seeds were empty until 10 months burial. The proportion of empty seeds increased after 10 months burial and fluctuated around a high level up to 23 months. Those seeds which had been buried 11 months by July 1985 contained significantly more non-viable seeds than those which had been buried 11 months by May 1986. Very few seeds were found to be decaying.

For L.purpureum, the proportion of non-viable seeds gradually increased with time to reach 15.5 arcsine units after 12 months burial and a maximum of 25.0 arcsine units after 24 months. Seeds buried 12 months by August 1985 contained significantly more non-viable seeds than those buried 12 months by June 1986. Some L.purpureum seeds were found to be decaying but this amounted to less than 3 arcsine unit generally and showed no seasonal trend (Figure 4.8b).

Figure 4.7 Seasonal changes in the proportion of non-viable seeds of V.arvensis in sachets buried 8cm deep in soil and exhumed monthly.
(Data is taken from the thermobar experiment).

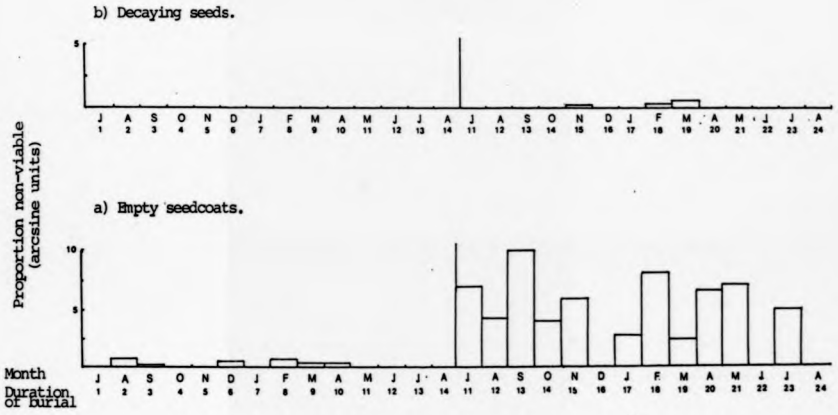
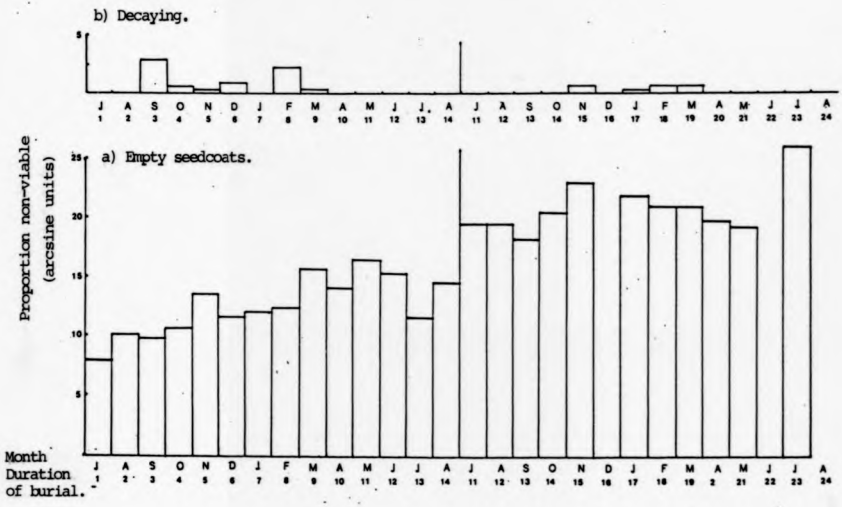


Figure 4.8 Seasonal changes in the proportion of non-viable seeds of L. purpureum in sachets buried 8cm deep in soil and exhumed monthly.
(Data is taken from the thermobar experiment).



Discussion

V.arvensis

Fresh seeds of V.arvensis were not completely dormant, as found by H A Roberts (pers.comm.) and shown in Figure 4.9. Light inhibited germination at cooler temperatures initially but burial reduced this inhibition and induced a light requirement for germination in some seeds (Wesson and Wareing 1969). Such light inhibition in fresh seeds would prevent germination of seeds on the plant or on the soil surface after dispersal. Seedlings which emerged then would be exposed to drought and to autumn cultivation. Furthermore, induction of a light requirement by burial ensures that emergence only occurs after autumn cultivation.

This light inhibition in fresh seeds has been reported elsewhere (Bewley and Black 1982, Froud-Williams et al. 1984, Bliss and Smith 1985). Fresh seeds of Avena fatua (Hsaio and Simpson 1971), and Avena sterilis and Avena ludoviciana (Froud-Williams 1985) are inhibited by light. Such inhibition only occurs at lower temperatures in lettuce (Milthorpe 1950, in Bewley and Black 1982), Senecio vulgaris (Popay and Roberts 1970) and V.arvensis (Froud-Williams et al. 1984, and here).

It has been suggested that, at higher temperatures, dark germination is inhibited by thermal reversion of Pfr in darkness and this can be seen here. It is also probable that germination in the light is inhibited in fresh seeds by rapid cycling of phytochrome, produced by high irradiance (Chapter 1). Roberts (pers. comm.) used intermittent light and found no light inhibition in fresh V.arvensis seeds. This

provides further support for the hypothesis that light inhibition is a result of continuous excitation of phytochrome (Bewley and Black 1982).

Light inhibition of germination declines with age in Avena ludoviciana seeds (Froud-Williams 1985) as seeds lose dormancy. Thus, in some instances, induction of a light-requirement by burial may simply be due to ageing in soil and the changing dormancy status of the seed. However, in this study seeds stored in a Stevenson Screen or fridge, despite losing dormancy, remained light-inhibited, suggesting an effect of soil burial which was absent from storage in the screen or fridge (Chapter 5). Similarly, seeds on the soil surface were generally inhibited from germinating compared to those mixed with soil (Figure 4.4) Froud-Williams et al. (1984) found that most emergence of V.arvensis occurred from seeds which had been deeply sown rather than surface sown, even if the surface sown seeds were shallowly cultivated. Only when the soil was thoroughly mixed, burying seeds, was emergence similar to the deeply sown seeds (Table 4.3)

However, by spring, germination from seeds on the soil surface was not significantly different from those mixed into the soil. Either contact with soil had reduced light inhibition, or rainsplash had buried some seeds which were then able to germinate. If contact with soil had reduced light inhibition, nitrates may have been involved since 0.2% KNO_3 stimulated germination of V.arvensis on filter paper (Chapter 3). No germination occurred from seeds on filter paper either because they did not have the required soil contact, or because the seeds dried out frequently and were unable to imbibe.

Table 4.3

The response of V.arvensis to burial (after Froud-Williams et al. 1984).

Depth of sowing	Cultivation	Percentage emergence
Surface sown:	No cultivation	1
	Shallow cultivation	0
	Inversion and reinversion	12
Shallow sown:	No cultivation	0
Deeply sown	Autumnal inversion	16
	Spring inversion	4
	Summer inversion	0
	Autumn inversion	20

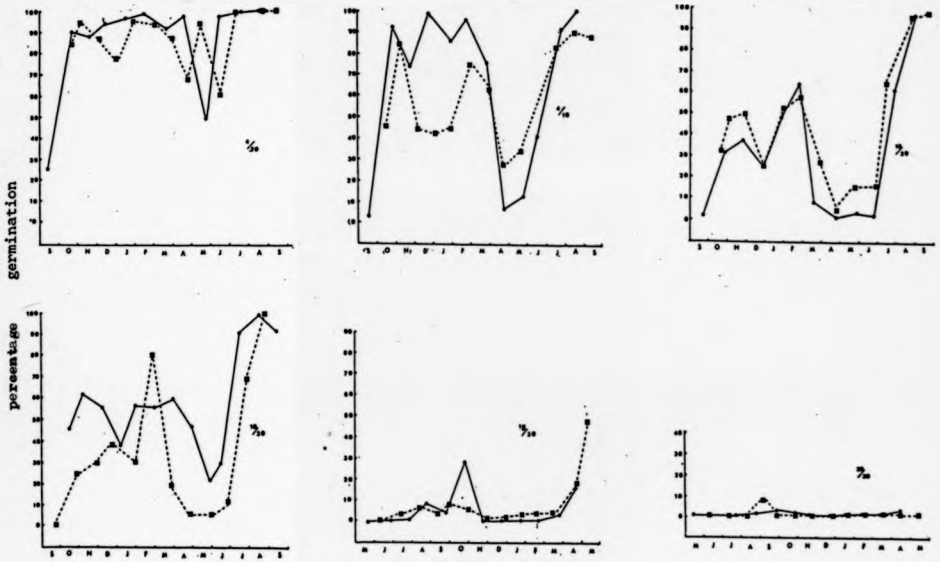
Little germination was observed during the first year of burial. Only a small percentage germinated in October-November and January-February when dormancy was released at the prevailing field temperatures (Figure 4.3) especially at 17.9/6.4°C (Figure 4.2 e). Roberts' seeds germinated to a far greater extent in the first season than occurred here, with relatively high germination from October to March (Figure 4.9). As mentioned above, Roberts used intermittent rather than continuous light and this may have provided a more favourable light environment for germination. However, since several authors and farmers have reported most emergence in the second year of burial (Roberts and Neilson 1982, Baskin and Baskin 1984), any discrepancies between the experiments probably reflects differences in the dormancy

status of the seed lots. Such discrepancies have also been reported for Torilis japonica (Roberts 1979, Baskin and Baskin 1983) and for several grass species (Froud-Williams 1985).

V.arvensis seeds were conditionally dormant during summer, germinating substantially at all temperatures but very little at those temperatures prevailing in the field, (Figures 4.2 and 4.3). Dormancy was gradually released, first at the coolest temperatures and then at warmer temperatures so peak emergence would occur after cultivation during the second autumn of burial. Release of dormancy also occurred in darkness at this time, so if no other factors were inhibiting germination, uncovered seeds would germinate in situ. During summer (Figures 4.2 a and b) germination was prevented since this would expose seedlings to drought and competition from established crop plants and also to autumn cultivation. During the second autumn of burial, Roberts (pers.comm.) also found release of dormancy at slightly warmer temperatures (10/20°C and 10/30°C) so germination could occur from late summer (Figure 4.9). During the second winter of burial, germination remained high at all but the warmest and coolest temperatures, thus preventing germination in an environment too cold for survival. This was especially marked in December.

The 1985 seeds repeated the behaviour of 1984 seeds but were generally less dormant at cooler temperatures. Roberts (pers. comm.) also found a difference between seeds of successive years, especially at 4/10°C in spring and at 10/20°C (Figure 4.9). This may have reflected the length of time buried since 1983 seeds were buried one month later than 1982 seeds, or it may reflect the environment experienced by the seeds during ripening (Chapter 1).

Figure 4.9 Seasonal germination patterns for Viola arvensis in intermittent light. Seeds were buried 23.8.82 (•——•) and 15.9.83(•- - -•) and exhumed each month. No data is available for tests in darkness (After H.A.Roberts unpubl.)



The pattern of release from dormancy at prevailing temperatures (Figure 4.3) indicates peak emergence would be expected during the second autumn of burial. This is supported by Roberts and Feast (1972, 1973) and Roberts and Boddrell (1983). Minimal emergence would be expected during June and July, a small peak also occurring in the first spring. A similar pattern was observed in emergence experiments in the Botanical Gardens (Chapter 3) and in field data (Chapter 2). Since temperature and light were the only field conditions represented on the thermobar, and the thermobar data was confirmed by field data, it can be concluded that these two factors are of major importance in the control of dormancy of V.arvensis.

High dark germination during the second autumn of burial (Figure 4.3) would cause high in situ germination and death unless the seedlings were just below the soil surface and were able to emerge. However, since V.arvensis builds up persistent seedbanks this in situ germination cannot be a major loss from the seedbank. Many non-viable seeds were found (Chapter 2) but the high dark germination seen here may not occur in the soil since the gaseous environment and other factors may enforce dormancy.

Germination on a monthly basis was not correlated with rainfall, with mean soil temperatures at 10 cm depth nor with the mean temperature range prevailing in the field.

V.arvensis thus behaved as a winter annual, germinating during autumn and most of the winter and early spring. There appeared to be a slight increase in dormancy during the winter (December) such that an early spring peak was also evident at 17.9/6.4°C, 19.8/7.7°C and

22.1/9°C during the first year of burial (Figure 4.2). Roberts (pers. comm.) found a similar effect in his second years seeds at 4/10 C and in all seeds at 10/20 C and 10/30°C. Thus, a proportion of the seeds were not induced into dormancy by cool winter temperatures and could germinate in spring. For 1984 seeds, this effect occurred only in darkness but for 1985 seeds it was apparent in the light and in darkness.

Peak germination occurred during the second autumn of burial and this may be due to a requirement for prolonged after-ripening. Vegis (1964) found that after-ripening extended the range of germination for V.arvensis. Sequential temperature changes may also be involved in this effect. Grime et al. (1981) and Froud-Williams et al. (1984) found chilling stimulated germination but no such effect was observed here, though cold dry storage did lead to a gradual release of dormancy (Chapter 5). Neither heating to 50°C for five days, nor scarification reduced dormancy of fresh seeds.

For V.arvensis, changes in the seed coat during burial may be as important as physiological changes, fresh seeds having a mucus coating which may inhibit germination, possibly by interfering with gas exchange. Seeds which had been buried one month lose this mucus layer and after one years burial the seed coat is much rougher, darker and more fragile. This mucus layer may also be involved in light inhibition of fresh seeds, possibly influencing the R/FR ratio reaching the embryo. Attempts to examine the effect of removal of this mucus layer using solvents implied no effect on germination but the solvents used themselves may have inhibited germination as much as the mucus.

Such prolonged dormancy in V.arvensis allows the build up of a substantial seedbank (Chapter 2) and if populations are allowed to become established each year, some germination will occur each autumn. In order to substantially reduce the seedbank, the adult population and seed input must be controlled for several years. V.arvensis is therefore well-adapted to be a weed of winter-sown crops and to some extent, early spring-sown crops. Cultivation in autumn or early spring allows germination of seeds brought into the light which then become established in the crop.

L.purpureum

Both seed lots followed similar trends in dormancy (Figure 4.5 a-g). The 1984 seeds were tested fresh in September when they germinated to between 20 and 40 arcsine units. Subsequently they became more dormant to give minimum germination in December. Germination then began to increase from May to reach a peak from August to October after which it began to decrease again. This pattern was similar for all temperatures but with slightly less germination at the cooler temperatures and with the period of high germination being extended such that germination could extend into February. Dark germination was always very low but reflected germination in the light. Most dark germination occurred at the warmer temperatures during the first winter of burial but at the cooler temperatures during the second winter of burial (Figure 4.5). Thus, dark germination in the field would be most likely during the second autumn/early winter of burial (Figure 4.6).

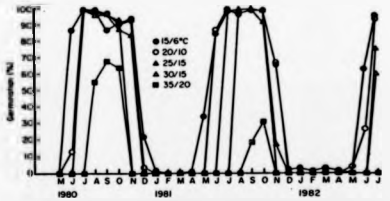
The 1985 seeds were tested fresh in July, at the time when germination began to increase in the 1984 seeds which had been buried one year, and

followed similar tends. The two seed lots therefore responded similarly to ambient temperatures in spite of differences in the duration of burial. The duration of burial did not, therefore, affect dormancy except that the trend in dark germination during summer in 1984 seeds seemed to lag behind that of 1985 seeds which had been buried earlier. However, this may reflect inherent differences in the two seed lots or differences in the temperatures experienced during burial, since 1985 seeds appeared to be generally less dormant, especially in the dark, and did not become as dormant in spring as 1984 seeds. Both seed lots followed the same trend in autumn 1986 and germinated to the same extent as in autumn 1985.

These results confirm those of Baskin and Baskin (1984) and Roberts (pers. comm.) shown in Figures 4.10 and 4.11. Roberts, however, did find the duration of burial to be important, since seeds buried two months later in the second year repeated the pattern of the first years seeds but with a two month lag. Roberts results also lag behind the results presented here, having been buried later. Baskin and Baskin (1984) found slightly different behaviour with a more abrupt decline and increase in germination, leading to zero germination from December to April. They also found that autumn-produced seeds could germinate in spring, being conditionally dormant, similar to 1985 seeds here. Such differences probably reflect differences in climate between the UK and the USA, and also the time of dispersal, since seeds used here were spring-dispersed.

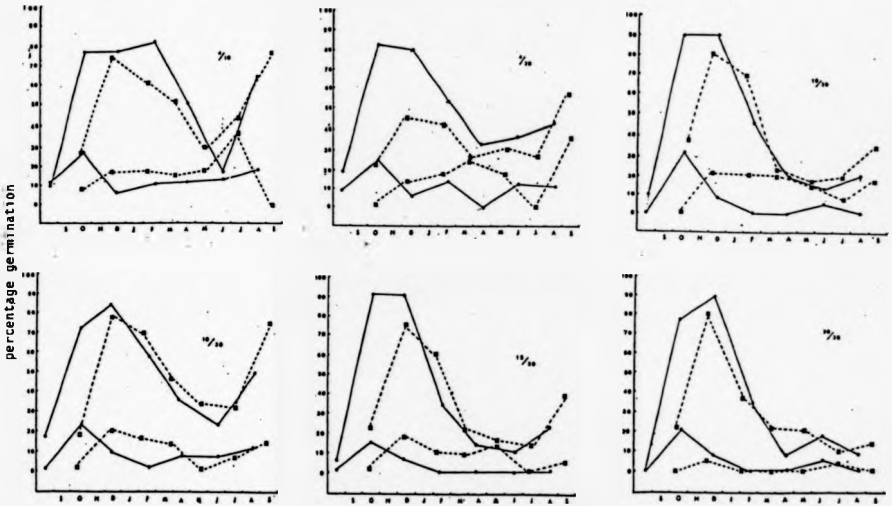
Maximum germination occurred in autumn as seeds became completely non-dormant, germinating over a wide range of temperatures. This period of high germination tended to extend into winter at lower

Figure 4.10 Seasonal changes in seed dormancy of L.purpureum. (after Baskin and Baskin 1984)



Germination percentages (mean ± s.e., if ≥ 5%) of *Lamium purpureum* seeds incubated at a 14-h photoperiod following 0-26 months of burial. Seeds were buried on 13 May 1980 and exhumed on the 1st day of each subsequent month.

Figure 4.11 Seasonal germination patterns of Lamium purpureum in intermittent light and in darkness (lower lines). Seed was collected from overwintered plants on 20.5.82 (●——●) and 18.7.83 (■····■). After H.A. Roberts unpublished.)



temperatures. Thus, as for other winter annuals (Chapter 1), dormancy increased first at warmer temperatures (Baskin and Baskin 1984). Baskin and Baskin (1984) found 5°C induced dormancy in L.purpureum as for other winter annuals.

During winter 1985-86, germination was relatively high for both seed lots suggesting that environmental conditions were more favourable than in winter 1984-85 and had the same effect on both seed lots. However, it is conceivable that the two seed lots were different in their response relative to their age. The 1985 seeds may have been less dormant than the 1984 seeds were when dispersed. This may have been due to greater after-ripening of the 1985 seeds, having been buried in July and at warmer temperatures than 1984 seeds, which therefore only received high temperature after-ripening during the second summer. Baskin and Baskin (1984) found that seeds of L.purpureum could after-ripen over a range of 5 to 35/20°C, so exposure to high summer temperatures was not an absolute requirement for release of dormancy. But the degree of after-ripening was important in determining the time of germination and emergence in the field. Fresh seeds buried and kept at late spring/summer temperatures during late spring and summer gained the ability to germinate to 100% at September and October temperatures in September and October. On the other hand, seeds kept at 5°C during this period only gained the ability to germinate at November temperatures (15/6°C). Many winter annuals show higher germination during the second year of burial (Chapter 1) probably reflecting the requirement for prolonged high temperature after-ripening. Baskin and Baskin (1984) found autumn germination of L.purpureum was identical for three seasons. However, 1984 seeds were more dormant in autumn 1984 than in autumn 1985, here.

Secondly, differences in the level of dormancy relative to the age of the seeds may be due to differences in the seed source. Froud-Williams (1985) found a hedgerow population of Galium aparine to be less dormant than a field population. However, for L.purpureum the field population was the least dormant.

High dark germination in autumn 1985 would entail a considerable loss from the population. In the region of this study, L.purpureum was not a particularly troublesome weed and very few seeds were found in the seedbanks of arable fields (Chapter 2). This high dark germination partly explains this. However, Roberts (pers.comm.) and Baskin and Baskin (1984) found little dark germination and a persistent seedbank. It was thought that the green lamp used to set up dark treatments may have stimulated germination to a certain extent but an experiment set up to examine this found no such stimulation. Thus, differences in the dormancy of the seeds or environmental conditions must have created these differences.

L.purpureum, therefore behaved as a winter annual with some germination during the first or second spring of burial for 1985 and 1984 seeds respectively. Winter temperatures induced dormancy to a certain extent and dormancy was gradually released as temperatures increased during late spring and early summer to reach peak germination in autumn.

Since this pattern in germination was reflected by field data (Chapter 2) and by experiments in the Botanical Gardens (Chapter 3), temperature and light do seem to be the major factors influencing germination. Germination on a monthly basis was not correlated with mean soil

temperature at 10 cm depth (data from Keele Meteorological Station), mean monthly air temperature, mean monthly soil temperature range, nor with rainfall. So the seasonal cycle of dormancy must be considered important.

Both L.purpureum and V.arvensis behave as winter annuals, germinating in autumn after cultivation brings seeds into the light. V.arvensis may have a slight increase in germination during spring, declining again until August when germination increases to a maximum in the second year of burial. L.purpureum, however, has one extended peak in germination, beginning to increase in May and continuing into December and March for 1984 and 1985 seeds respectively. L.purpureum is characterized by complete dormancy during winter, becoming completely non-dormant during the rest of the year, the proportion germinating being similar for all temperatures, except at very low temperatures where there is less germination. V.arvensis germinates little at warmer temperatures, with maximum germination at autumn temperatures. The fact that germination is relatively low in the first year of burial ensures an accumulation of seeds in the soil and this presents a problem to the farmer. L.purpureum seeds are able to germinate immediately when dispersed, though a peak occurs in the first autumn, provided the seeds have experienced sufficient warm temperature after-ripening. Thus, few seeds accumulate in the soil and the existing population can be eradicated relatively easily with herbicides.

A comparison of the proportion of non-viable seeds reflected the level of dark germination to a certain extent. L.purpureum germinated to a relatively high level in darkness during early autumn irrespective of

the length of time buried. A relatively high level of dark germination did not occur until the second autumn of burial for V.arvensis. However, the proportion of non-viable seeds found did not equal the level of dark germination expected, so in the soil other factors were enforcing dormancy. These have been discussed in Chapter 1. Since dark germination in autumn 1985, for 1984 seeds, was similar for both species, the proportion of non-viable seeds would be expected to be similar but this was not the case and L.purpureum seeds were less inhibited from germinating in the soil than V.arvensis seeds. This may involve differences in the seed coat. The mucus layer and relatively smooth seed coat of V.arvensis may isolate the embryo from external factors to a certain extent (Plate 16). The seedcoat of L.purpureum is much more pitted and has many pores and cracks which would expose the embryo to microorganisms and other soil factors, accelerating ageing (Plate 17).

The two seed lots in both species behaved slightly differently in the proportion germinating in situ with time and this may reflect differences in the burial environment between the two years, or differences in dormancy of the seed lots, or an interaction between the two. For V.arvensis, 1985 seeds were less dormant than 1984 seeds, yet after 10 months burial, fewer were non-viable. A similar effect was apparent for L.purpureum. Since seeds were buried at different times in 1984 and 1985 they were exposed to slightly different conditions and this may have affected in situ germination and decay. Such a gradual increase in the proportion dying during burial was noted for three Ranunculus species by Sarukhan (1974). He also found the proportion non-viable was related to the depth of dormancy. Such differences in germination in situ is probably an important factor

Plate 16

An electron micrograph of a seed of *Viola arvensis* x 100

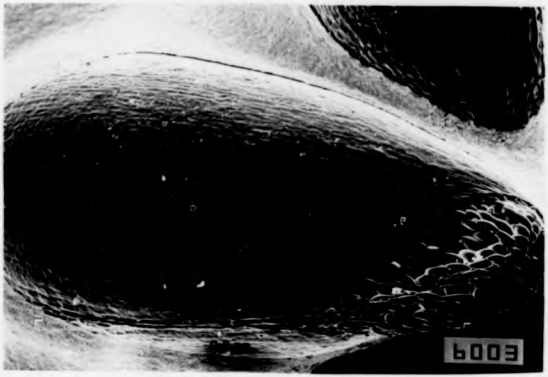


Plate 17

Lamium purpureum x 50

leading to the difference in the seedbank between the two species.

Chapter 5

Further factors affecting dormancy characteristics of buried seeds.

Introduction

Dormancy characteristics of any seed lot do not necessarily reflect that of the species as a whole, or in every year, or under all conditions of storage. Differences between populations are discussed in Chapter 1. In this chapter, experiments investigating differences between collection dates of the seeds, differences in the time of burial, and the effects of storage outside of a soil atmosphere at ambient temperatures, or at constant temperatures will be discussed.

1 Collection date

Variation in dormancy between collection dates may be due to different stages of maturity, since dormancy may develop during the later stages of development (Froud-Williams 1985). Thus, various cohorts of seed production will have different periodicities of germination. It has been suggested that a polymorphic response to temperature fluctuation may account for the variability in establishment of weed infestations (Thompson and Grime 1983). Baskin and Baskin (1979c) found that Aster pilosus seeds could after-ripen on the plant during winter so the longer they remained on the plant, the lower was their dormancy. Various authors have observed differences between early and late collections (Chapter 1). In the field L.purpureum and V.arvensis set seed over a period of about four months and thus the seeds mature under a variety of conditions (Chapter 1.5). To observe any differences, seeds were collected early and late in the season and kept separate.

2 Time of burial

The duration of burial may influence the response to prevailing temperatures by affecting the dormancy level of the seeds. Early collected seeds were buried both earlier and later to produce differences in the duration of burial and differences in soil conditions experienced by the seeds, since soil conditions vary seasonally.

3 Effects of burial

To isolate the effects of burial and the soil environment from the effects of temperature, seeds were stored in darkness in a Stevenson Screen exposed to ambient temperatures but not to a soil environment.

4 Endogenous control of dormancy

To isolate seeds from all environmental influences, seeds were stored at a constant 4°C in a fridge. H.A.Roberts (pers. comm.) found a seasonal cycle of dormancy in dry storage for V.arvensis as did Froud-Williams et al. (1986) for Poa trivialis. However, these seeds were kept in a laboratory where temperatures were not constant and this may have exerted some effect on the seeds.

Various comparisons between these treatments should clarify the important factors determining dormancy. From these results, any differences in dormancy between early and late dispersed seed would imply that date of collection is important. Any difference between burial date would imply that duration and/or time of burial is important. If behaviour in the screen is similar to that in the soil,

then specifically soil factors are unimportant. If behaviour in the screen is similar to that in the fridge, then temperature is unimportant.

Materials and methods

1 Seed collection

L.purpureum seeds were collected from the edge of an oilseed rape field on 1/5/85 and were labelled 'early-dispersed' seeds,and on 1/6/85, 'late-dispersed' seeds. Plants were left to dry in the laboratory until ripe seeds had been released. Debris was then sieved and winnowed away and seeds dried in a desiccator for two weeks.

V.arvensis seeds were collected on 6/8/85 (early-dispersed) and 23/8/85 (late-dispersed) seeds. Heads which had opened and were presenting shiny brown ripe seeds were collected as far as possible but due to cool, wet weather, many ripe pods remained closed. These were collected and left to dry in paper bags in the laboratory until the seeds had been released. It is possible that such seeds were not fully ripe but since harvest was imminent, they had to be used. Seeds were dried in a desiccator for two weeks.

2 Burial

Burial experiments were set up as for the thermogradient bar except that 12 sachets per replicate cylinder were used. For L.purpureum, 'early-dispersed' seed was buried on 13/6/85 - early burial - and both 'early-dispersed' and 'late-dispersed' seed was buried on 1/7/85 - late burial. For V.arvensis, 'early-dispersed' seed was buried on 26/8/85 - early burial - and both 'early-dispersed' and 'late-dispersed' seed was buried on 16/9/85 - late burial.

3 Stevenson Screen (Plate 18)

Mesh sachets were placed in labelled brown paper bags and placed in a Stevenson Screen on 1/7/85 for 'late-dispersed' L.purpureum seeds and 16/9/85 for 'early-dispersed' V.arvensis seeds.

4 Refrigerator

Sachets were placed in brown paper bags in a fridge at 4°C on 1/7/85 and 16/9/85 for L.purpureum and V.arvensis respectively.

5 Incubation

Since only one controlled environment cabinet was available, and both species differ in their temperature requirements for optimum germination, monthly testing was not possible. So, each species was tested every alternate month in light and darkness at the most appropriate alternating temperature (determined from the thermogradient bar).

Results for 'late-dispersed' L.purpureum and 'early-dispersed' V.arvensis buried early were taken from the thermogradient bar results (Chapter 4). Experimental techniques are described in Chapter 4.

6 Analysis

Within months global error mean square was used in partitioning the sums of squares in various comparisons. This avoided the problem of heterogeneous variances between months and allowed the data to be analysed as it became available.

Plate 18

The Stevenson Screen

To summarize, the treatments were:

1 Early dispersed seeds buried early;

2 Early dispersed seeds buried late;

3 Late dispersed seeds buried late;

4 Seeds stored in a Stevenson Screen;

5 Seeds stored in the fridge.

Results

V.arvensis

Germination data of V.arvensis in each treatment are in Appendix II, and are represented graphically in Figure 5.1 and 5.2. Table 5.1 indicates significant differences between treatments.

1 The effect of light on germination

In general, light had no effect on germination. However, Figures 5.1 and 5.2 reveal sigificant differences in a few cases between light and dark germination. Dark germination exceeded that in light in November for late seeds buried late, screen-stored and fridge-stored seeds;in January for fridge-stored seeds; in March for early seeds buried late; and in July for screen-stored seeds. However, light stimulated germination in May and July for early seeds buried early.

2 Time of seed collection

Where there was a significant difference, in March, early-dispersed seeds were less dormant than late dispersed seeds. This is evident from Figure 5.2a and b where the seasonal pattern of dormancy changes between early dispersed seeds and late dispersed seeds, buried at the same time, were similar but late dispersed seeds were always more dormant.

3 Time of burial

Where there was a significant difference (in January and May) early

Figure 5.1 A comparison of Viola arvensis dormancy of seeds 1) dispersed early and buried late; 2) dispersed late and buried late; 3) dispersed early and buried early; 4) dispersed early and stored in a Stevenson Screen; 5) dispersed early and stored in a fridge.

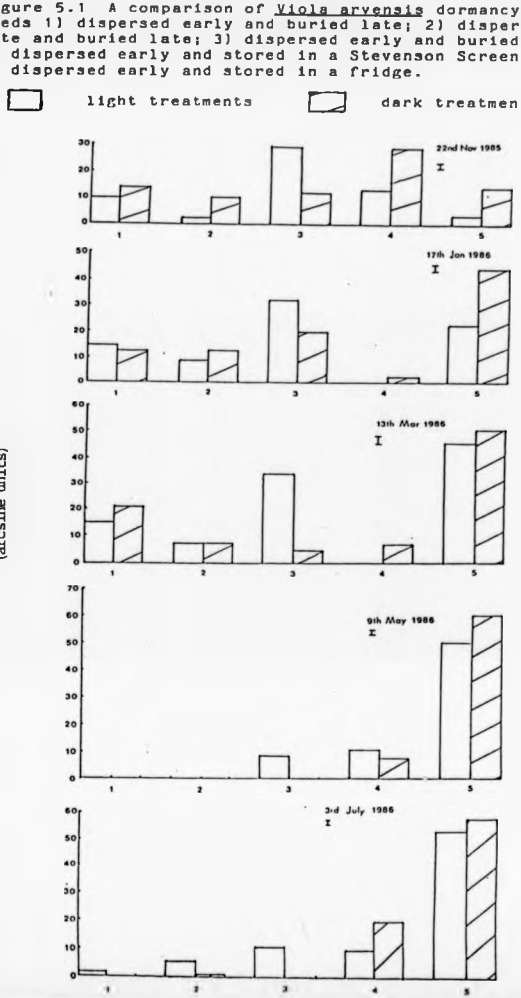
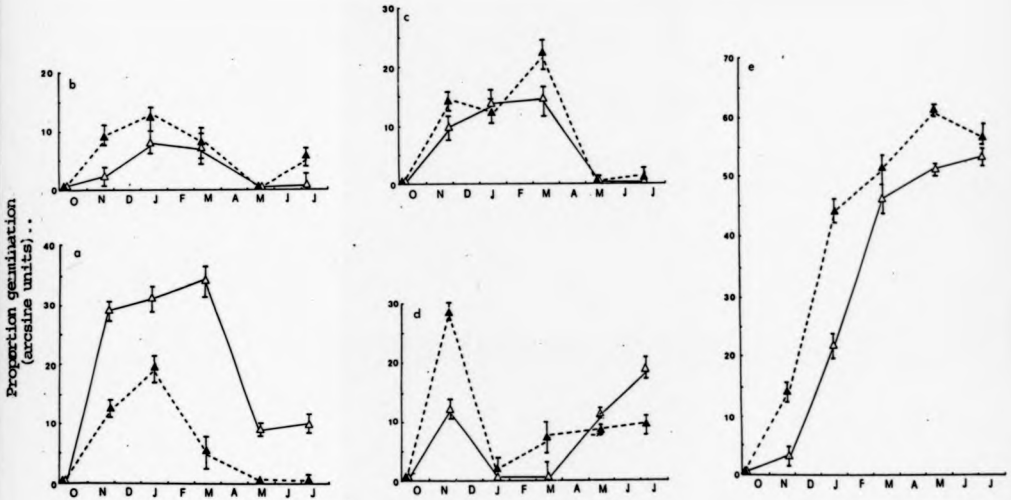


Figure 5.2 Seasonal changes in dormancy of V.arvensis a) dispersed early and buried early; b) dispersed late and buried late; c) dispersed early and buried late; d) dispersed early and stored in a Stevensen Screen; e) dispersed early and stored in a fridge.
95% confidence limits.



buried seeds were less dormant than those buried late.

4 Effects of burial

In November, buried seeds were more dormant than non-buried seeds in the screen but in January, and March, buried seeds were less dormant as screen-stored seeds became dormant. In May and July, screen-stored seeds came out of dormancy whilst buried seeds became dormant, such that buried seeds were more dormant than screen-stored seeds.

5 The role of temperature during storage

During the first two months, seeds stored in the screen were less dormant than those in the fridge. However, fridge-stored seeds gradually lost their dormancy and from December onwards they were always less dormant than those in the screen.

Table 5.1

V.arvensis — Factors affecting seeds during burial

Results were compared using a one-way ANOVA, and comparisons between treatments using an F test on means (after Sokal and Rohlf 1969)

Date	22.11.85	17.1.86	13.3.86	9.5.86	3.7.86
Difference between light and dark germination	NS	NS	NS	NS	NS
Time of dispersal	NS	NS	P<0.001 Early less dormant than late	NS	NS
Time of burial	NS	P < 0.01 F = 9.151 Early less dormant	NS	P<0.05 Early less dormant than late	NS
Early buried vs screen	P<0.001 Buried more dormant than screen	P<0.001 Buried less dormant than screen	P<0.001 Buried less dormant than screen	P<0.001 Buried more dormant	P<0.001 Buried more dormant
Screen vs fridge	P<0.001 Screen less dormant than fridge	P<0.001 Screen more dormant than fridge	P<0.001 Screen more dormant than fridge	P<0.001 Screen more dormant	P<0.001 Screen more dormant than fridge

L.purpureum

Germination data for L.purpureum in each treatment are in Appendix 12, and are represented graphically in Figure 5.3 and 5.4. Table 5.2 indicates significant differences between treatments.

1 The effect of light on germination

Light stimulated germination in all treatments.

2 Time of seed collection

The time of seed collection had no effect on dormancy, except by August 1986 when early dispersed seeds were less dormant in darkness than late dispersed seeds.

3 Time of burial

The time of burial had no effect on dormancy.

4 The effects of burial

Burial only affected dormancy in October, April and August, when buried seeds were less dormant than screen-stored seeds, though this effect is only apparent in darkness in April.

Figure 5.3 A comparison of L. purpureum dormancy of seeds 1) dispersed early and buried late; 2) dispersed late and buried late; 3) dispersed early and buried early; 4)dispersed late and stored in a Stevensen Screen; 5) dispersed late and stored in a fridge.

95 % confidence limits

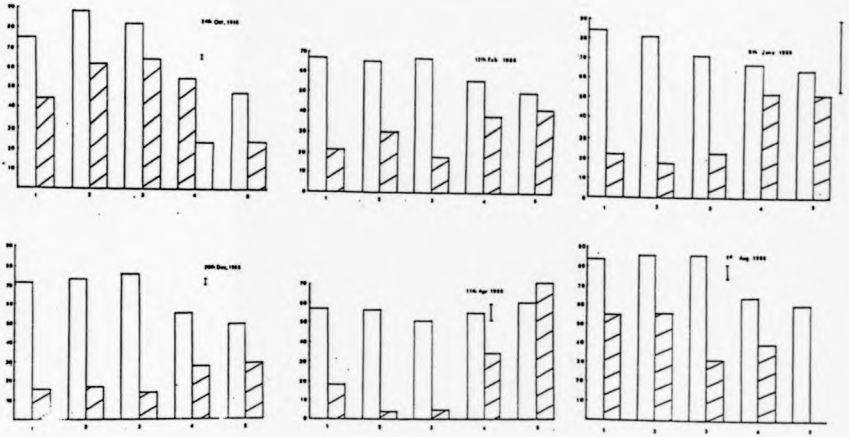
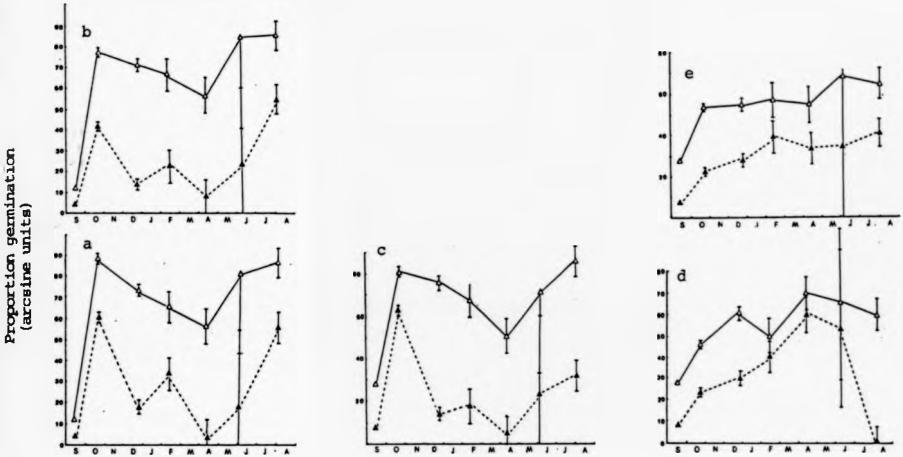


Figure 5.4 Seasonal changes in dormancy of L.purpureum seeds a) dispersed early and buried early; b) dispersed late and buried late; c) dispersed early and buried late; d) dispersed early and stored in a Stevenson Screen; e) dispersed early and stored in a fridge.

95% confidence limits.



5 The role of temperature during storage

There was no significant difference in germination between seeds stored outside in a Stevenson Screen or those stored at a constant 4°C in a refrigerator.

Table 5.2

L. purpureum — Factors affecting seeds during burial

Results were compared using a one-way ANOVA and comparisons between treatments using an F test on means (after Sokal and Rohlf 1969)

Date	24.10.85	20.12.85	12.2.86	11.4.86	6.6.86	1.8.86
Difference between light and dark germination	P<0.01 light greater than dark	P<0.001 light greater than dark	P<0.05 light greater than dark	P<0.001 light greater than dark	P<0.001 light greater than dark	P<0.001 light greater than dark
Time of seed dispersal	NS	NS	NS	NS	NS	P<0.001 Early less dormant in darkness
Time of burial	NS	NS	NS	NS	NS	NS
Buried vs non-buried (late seeds)	P<0.001 Buried less dormant than non-buried	NS	NS	P<0.05	NS	P<0.01 Buried less dormant
Screen vs fridge	NS	NS	NS	NS	NS	NS

Discussion

1 The effect of light on germination

V.arvensis

Overall, light had no effect on germination but significant differences did exist occasionally: In November for late seeds buried late, and unburied seeds; in January for fridge-stored seeds; in March for early seeds buried late and in May and July for early seeds buried early. In all cases, except early seeds buried early, light inhibited germination. Late seeds stored in the screen lost this light inhibition by May, and in January, light and dark germination were equal for screen-stored seeds and for early seeds buried late.

This implies that either the duration of burial, or environmental conditions experienced during burial are important. Early burial coincided with warmer, drier conditions such that pre-existing Pfr in the seeds would decay more rapidly creating a light-requirement for germination. Light inhibition of germination has been discussed in Chapters 1 and 4.

L.purpureum

Light stimulated germination of L.purpureum in all treatments as found by Baskin and Baskin (1984), although they only found a maximum of 4% dark germination.

Seasonal changes in dormancy differed in the light and in darkness. Loss

of dark germination as seeds became dormant after November, was more rapid than loss of light germination and probably reflects decay of Pfr such that seeds became increasingly light-requiring. Thus, the difference between light and dark germination increased. In February, dark germination increased slightly in all treatments before decreasing again. This secondary germination peak in darkness implies release from phytochrome-controlled dormancy to a certain extent. Possibly, temperature becomes more important at this time in controlling dormancy. The decline in dark germination after this peak in February reflected the rate of decline in the light and possibly indicates the status of Pfr within the seeds which gradually decays during burial. In screen-stored seeds, dark germination continued to increase after February until in April dark germination exceeded that in the light. This suggests that soil factors which are absent from the screen induced dormancy. The decline in dark germination is, however, at least partly endogenous since it occurred in fridge-stored seeds.

Differences in the response of V.arvensis and L.purpureum seeds to light can be explained in terms of the status of phytochrome within the seeds. Where light stimulated germination, little Pfr was present in the seed. Thus, either little light reached the seed during maturation, or decay of Pfr in darkness was rapid. L.purpureum seeds mature within green capsules, and are shaded by taller plants, so little light reaches the seeds during drying such that little Pfr would be present (see Grime 1979, and Chapter 1). Where light inhibited germination, a high irradiance reaction (HIR) is probably involved (discussed in Chapter 1) whereby there is sufficient Pfr in the seed but rapid cycling prevents its action. V.arvensis seeds experience high irradiation during drying. The pods are lifted out of the surrounding crop plants, they

are only a translucent yellow colour allowing light to reach the seeds, and once the pods open, the seeds are exposed to full daylight. However, it is interesting that the seed coat is a shiny, dark brown which would reflect light and thus little would be expected to penetrate the seed coat (Plate 6). Production of Pfr, therefore, probably occurs before the seeds are ripe when light still reaches the embryo. From the thermobar tests (Chapter 4) it was discovered that only at the temperature used in this experiment (17.9/6.4°C) did light inhibit germination. At warmer temperatures and after burial, it seems likely that thermal decay of Pfr occurs in darkness and the HIR is inoperative.

In terms of field behaviour, these differences between the two species mean that L.purpureum seeds will germinate on the soil surface immediately they are dispersed whereas V.arvensis seeds require burial. Thus, L.purpureum is easily controlled by autumn cultivation which destroys seedlings, whilst V.arvensis seedlings will not emerge until after cultivation.

2 The effect of the time of seed collection on dormancy (treatments 2 and 3).

V.arvensis

Early dispersed seeds were significantly less dormant than late dispersed seeds until May when germination ceased. Rorison (1973) found similar differences between collections of Scabiosa columbaria, with September seeds being heavier and less dormant than October/November seeds, and Froud-Williams (1985) found the same for Alopecurus myosuroides. However, the reverse was true for Poa annua and

Froud-Williams (1985) also found differences in the optimum temperature for germination, which was not examined here.

Warmer conditions experienced during the maturation of early collected seeds may have increased their rate of maturation such that a high proportion of the seeds were relatively non-dormant when dispersed. However, these differences only appeared after two months burial so it is more likely that early dispersed seeds, being more mature and less dormant, were able to respond more rapidly to changing soil conditions.

These results suggest that somatic polymorphism occurs in V.arvensis such that seeds produced by any single population germinate discontinuously. They also indicate the dangers of ascribing a single germination response to any one species or population.

L.purpureum

The time of seed dispersal only affected the response to burial in August 1986 when early dispersed seeds were less dormant in darkness than late dispersed seeds. This would have little effect on emergence but may influence in situ germination and lead to a more rapid decline in the seedbank of seeds dispersed earlier after one years burial. However, in general the time of dispersal did not affect the response of seeds to burial so, either conditions during development of the seeds had no effect on dormancy, or these conditions were uniform throughout the collecting season. Froud-Williams et al. (1986) collected Poa trivialis seed early-season, mid-season and late-season and he also found no difference in germination at any temperature. However, there were only three weeks between early-dispersed and late-dispersed seeds

in the L.purpureum collections whereas in the field seeds can be dispersed over several months and thus are exposed to a range of environmental conditions during maturation. Also, only one temperature regime was used and there may have been differences in germination at other temperatures. Furthermore, both collections were dried in desiccators for 14 days under uniform conditions whereas, in the field, seeds would dry on the plant or soil surface under a variety of conditions, both in terms of air temperature, moisture levels and degree of shading. If moisture content varied at the time of burial this would affect dormancy and the status of phytochrome within the seed.

If these results do reflect field behaviour and there are no differences in dormancy between different seed lots, L.purpureum seed dormancy is not influenced by conditions experienced during maturation. Thus, results obtained in one year can be applied to any year within the same population.

3 The effect of burial time on dormancy (treatments 1, 2 and 3).

V.arvensis

The time of burial did affect the level of dormancy, except in March and July. Early seeds buried early were less dormant than early seeds buried late. Early seeds buried early were generally stimulated to germinate by light whilst those buried later showed no significant differences between light and dark germination, except in March where germination was slightly inhibited by light.

It is interesting that although late seeds buried late (treatment 3)

were much more dormant than early seeds buried early (treatment 1), the seasonal pattern of changing dormancy was similar. Where early seeds were buried late (treatment 2), the pattern was also similar but the dormancy level was intermediate between treatments 1 and 3. Where light inhibition (in late seeds buried late) or light stimulation (in early seeds buried early) reached a peak, in January, early seeds buried late showed no difference between light and dark germination. This implies that the combined effects (in treatment 2) on dormancy of early or late dispersal and early or late burial are balanced.

These results cast doubt on the validity of the thermobar results at this temperature since the period of burial affected the dormancy of the seeds and whether light inhibited or stimulated germination. If early seeds buried late had been used on the thermobar, germination at 17.9/6.4°C would have been lower and would not have been light inhibited, when fresh.

Since it was the early dispersed seeds buried early which were light stimulated when buried, seeds germinating in the first autumn after burial would be those which were dispersed and buried earlier and had experienced soil conditions and darkness for a longer period. This has implications for weed control. If harvest is delayed, a higher proportion of later dispersed seeds will enter the seedbank and thus the proportion of the expected seed input which germinates in the first autumn will be lower. The earlier the harvest, the higher will be the proportion of that years input which germinates in autumn and which can then be eradicated.

L.purpureum

The time of burial had no effect on dormancy of L.purpureum seeds. Thus, duration of burial had no effect. This hypothesis is confirmed by the thermogradient bar experiments. Here, although 1985 seeds were buried earlier than 1984 seeds, germination patterns were similar, i.e., there was no lag, though 1985 seeds tended to be less dormant. This difference in dormancy level here however, is probably related to the different origins of the seed lots since dispersal time had no effect on dormancy and early buried seeds were initially more dormant than later buried seeds.

4 The effects of burial on dormancy
(comparing treatments 1 and 2 with 4)

V.arvensis

Buried seeds were generally more dormant than non-buried seeds in November and in January. Seeds stored in the screen were exposed to ambient temperatures and moisture levels and dormancy here was seasonal as in buried seeds. However, changes were more abrupt in the screen, with a greater increase in germination in November, decreasing again rapidly in January and increasing again gradually thereafter as temperatures increased.

The discrepancy between screen-stored seeds and buried seeds is probably a result of greater fluctuating temperatures experienced in the screen than at 8 cm deep in the soil, where air and moisture act as buffers and the soil heats and cools more slowly. However, other soil factors,

such as nitrates and the soil atmosphere may also be important. Induction of dormancy generally follows inhibition of germination for extended periods. Seeds in a less favourable environment are more likely to be induced into dormancy. Thus, screen-stored seeds, being isolated from the soil atmosphere and being exposed to a less humid environment were in a less favourable environment than buried seeds so were induced into dormancy to a greater extent. This further implies that temperature is not the only factor involved in the control of dormancy of buried seeds. However, screen temperatures were not equivalent to those 8 cm deep in soil and this must be considered.

Wesson and Wareing (1969 a and b) found that many light-inhibited or light-insensitive species became light-requiring during burial and this occurs here to a certain extent. Seeds which were not buried were always light-inhibited at these temperatures, whilst buried seeds became light-sensitive (early seeds buried early) or light insensitive (late seeds buried late). However, early seeds buried late did not show this effect.

L.purpureum (comparing treatments 3 and 5)

Only in the October, April and August did burial affect dormancy. Buried seeds were then less dormant than those stored in the Stevenson Screen. Cheam (1985) also found that dormancy of wild radish declined more in soil than at surface. However, Salisbury (1965) found loss of dormancy in Plantago major was faster in air than in soil. This is only evident for dark germination in the screen here.

These results confirm the hypothesis that length of time buried is less

important than the season of burial, since burial itself decreases dormancy, whilst seeds buried earlier and longer were more dormant. However, these results should be treated with caution since screen-stored seeds became infested with a fungus and very few were viable.

5 The role of temperature during burial on dormancy (comparing treatments 4 and 5).

V.arvensis

The fridge environment was a constant 4°C and under such conditions seeds gradually lost their dormancy as they aged. No seasonal cycle was apparent. Thill et al. (1985) found a similar effect for Crupina vulgaris. Since no cycle was apparent in fridge-stored seeds at a constant 4°C yet was apparent in screen-stored seeds, and since temperature was the only factor differing markedly between the two, it must have an important influence on seasonal dormancy changes during burial. This is supported by Vanlerburghe and van Assche (1986) for Verbascum thapsus.

Initially, seeds lost dormancy faster in the screen, since they were exposed to ambient alternating temperatures and probably to a higher humidity. Probert et al. (1985) found a similar effect for Dactylis glomerata. Several authors have found that release from dormancy is greater in seeds in the soil than in dry-stored seeds in the laboratory or fridge (Roberts and Lockett 1975, Chadoeuf-Hannel 1985) and the effects are generally attributed to phytochrome changes. But the soil environment and probably the screen environment can also affect

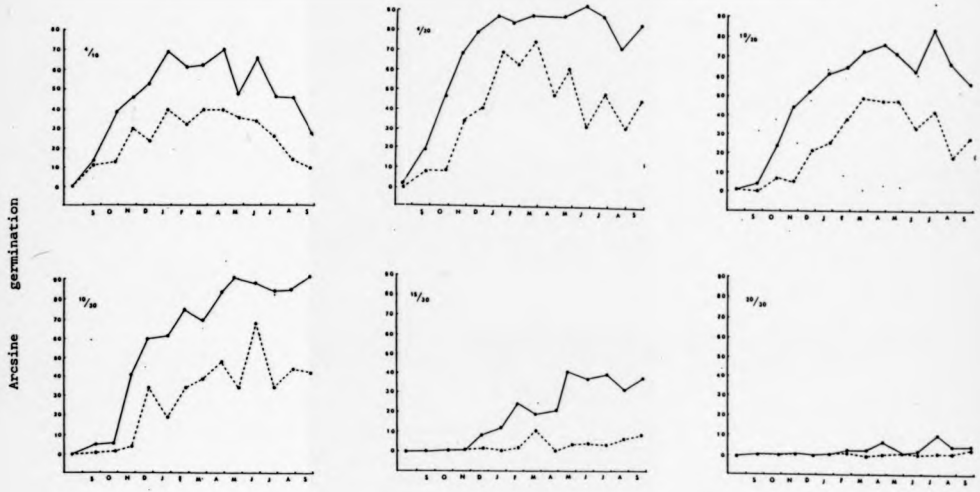
structures around and within the embryo leading to a breakdown of barriers to imbibition, oxygen diffusion, R/FR perception, or those acting as reservoirs for germination inhibitors (Chadoeuf-Hannel 1985). In the screen, as in the soil, the mucus surrounding the seed gradually disappears with age, whilst in the fridge this does not occur.

Roberts and Boddrell (1983) and Roberts (pers.comm.) also found that laboratory-stored V.arvensis seeds were gradually released from dormancy (Figure 5.5). Roberts tested seeds at different temperatures and found that dormancy was released first at the coolest temperatures, as expected for winter annuals (Chapter 1). He also found the temperature range was important for germination of dry-stored seeds, dormancy at 10/30°C and 4/20°C being lower than at 10/20°C and 4/10°C. Loss of dormancy was much slower than occurred in this experiment and probably reflected the fact that seeds were stored at laboratory temperatures, whereas in the fridge part of the chilling requirement may have been fulfilled. This is supported by Froud-Williams et al. (1986) for Poa trivialis, though in others, high temperatures released dormancy better than chilling.

Roberts found a seasonal pattern in dormancy changes for dry-stored seeds tested at 4/10°C and in darkness at 4/20°C and 10/20°C implying some endogenous control (Figure 5.5), though laboratory temperatures are not constant and may reflect ambient temperatures to a certain extent. However, Froud-Williams et al. (1986) found evidence of some endogenous control in Poa trivialis even at 4°C storage temperature.

Roberts also found that light stimulated germination in dry-stored seeds which contradicts these results. In his experiment, seeds were only

Figure 5.5 Seasonal germination patterns for dry-stored Viola arvensis in the light (⟵⟶) and in darkness (⟵ - - ⟶)
Seeds were obtained from spring-germinated plants and the experiment began 19.9.82.
(After H.A.Roberts)unpubl).



exposed to intermittent light so the HIR would not have been operative (Chapter 1). However, in the field, seeds do require burial before they will germinate in the light (Chapter 3), so the HIR must be operative here.

L.purpureum

Seeds stored in the Stevenson Screen, experiencing ambient temperatures, behaved differently to buried seeds and gradually lost dormancy until December. At this point, light germination declined as it had done in buried seeds in November. This decline thus reflects that of the buried seeds but was delayed two months. Furthermore, peak germination was never as high as that for buried seeds. Light germination increased again from February to April which was not apparent for buried seeds. Dark germination in the screen continued to increase and after February the rate of increase rose until dark germination exceeded that in the light in April. However, these results must be treated with caution since a fungal infection destroyed many seeds so seed numbers were very low. The fungal spores could enter the pitted seedcoat of L.purpureum but not that of V.arvensis which was smooth and coated with mucus (Chapter 4).

Late seeds stored in the fridge also behaved differently to buried seeds and after two months storage, dormancy remained relatively stable in the light. This suggests that temperature is involved in changing dormancy levels during burial, since no periodicity is apparent at constant 4°C. However, the loss of dormancy did reflect that of the other treatments, though to a lesser degree. Froud-Williams et al. (1986) found loss of dormancy in Poa trivialis was similar at 4°C and at ambient

temperatures.

Dark germination, however, increases to a peak in February as with buried seeds. This then appears to represent an endogenous rhythm within the seed since it is evident in all buried seeds and in seeds stored in fridge. Karssen (1980/81) suggested no cyclic changes occurred in dry storage but Froud-Williams et al. (1986) did find seasonal periodicity in Poa trivialis with minimum dormancy in autumn and maximum in summer as occurs here. The relative amount of dormancy was influenced by storage temperatures.

Temperature was not the only factor affecting buried seeds since fridge-stored seeds germinated to the same extent as those in the screen at ambient temperatures. Furthermore, seeds from the screen did not reflect the behaviour of buried seeds. The soil atmosphere or nitrate levels may also be important. Alternating temperatures are unlikely to be the predominant cause of ageing since they are likely to be greater in the screen than 8cm below the soil surface, so buried seeds would have been more dormant than non-buried seeds. In fact, the monthly mean temperatures in the atmosphere and at 10 cm deep in the soil are relatively similar (Table 5.3). Degree of imbibition may have been important since seeds in sachets buried in soil would have a higher moisture content than those in the fridge or sceen and thus changes in dormancy, especially phytochrome, could occur to a greater extent in buried seeds. Probably, an interaction between alternating temperatures, moisture, nitrate and the soil atmosphere accelerated ageing in soil.

Table 5.3 A comparison of mean air and soil temperatures at Keele

Soil temperatures were taken at 10 cm depth and all data was obtained from Keele Geography Department.

Month	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Air temp(°C)	13.3	13.8	10.3	3.2	5.2	2.4	-1.1	4.7	5.0	10.2	14.0	14.5
Soil temp(°C) at 10 cm depth	14.6	14.3	10.6	3.6	5.1	1.3	-0.5	3.3	5.7	10.9	15.6	17.1

It is important to realise that these results only apply to the test temperature used. Baskin and Baskin (1984) maintained buried seeds at different temperatures. They moved seeds from a non-temperature controlled greenhouse and kept them at 5 different temperature regimes. Differences in response to different test temperature regimes were apparent. The thermogradient bar results (Chapter 4) indicate a similar effect.

In summary, L.purpureum showed no difference between dormancy of seeds stored in the fridge or screen, whilst V.arvensis seeds from the screen were initially less dormant than fridge-stored seeds but then became more dormant than the fridge-stored seeds as the latter were released from dormancy.

6 Patterns of dormancy changes

If the patterns of changing dormancy are compared both species showed similar trends. During burial, both species first lost dormancy fairly rapidly during autumn and were then induced into dormancy again from late winter to early spring. For L.purpureum, the decline in germination was fairly rapid from December to May, whereas for V.arvensis, the peak in germination was extended from November to March before declining rapidly.

L.purpureum was generally less dormant than V.arvensis, so even though the decline in germination was more rapid for L.purpureum, numbers germinating were still high for an extended period. V.arvensis maintained a constant low level of germination throughout this winter period.

Fridge-stored seeds also behaved similarly between the species. Both were gradually released from dormancy. However, this release was gradual for V.arvensis, whereas for L.purpureum an initial rapid increase in germination was followed by a plateau at about 55% germination in the light. It is possible that such a plateau would be reached by V.arvensis seeds after a longer period since at its peak in May only 51% germinated in the light. Froud-Williams (1985) found a similar loss of dormancy during storage in a laboratory for Avena fatua, though Alopecurus myosuroides was induced into dormancy.

Seeds stored in the screen behaved very differently between the two species. L.purpureum seeds gradually lost dormancy whilst V.arvensis seeds exhibited periodicity similar to buried seeds. Thus, V.arvensis

seeds seem to be more sensitive to environmental effects than L.purpureum seeds. However, most L.purpureum seeds were destroyed by a fungal infection in the screen so the results must be treated with caution.

L.purpureum seed dormancy was not affected by the period of burial or the timing of seed dispersal but it was controlled by environmental factors acting on the seeds during burial. This is unlikely to involve temperature alone since screen-stored seeds did not reflect the pattern observed in buried seeds. However, the fungal infection of these screen-stored seeds may have affected the value of these results.

V.arvensis seeds were generally more dormant and the timing of seed dispersal and burial did affect dormancy. V.arvensis seeds are therefore more responsive to environmental conditions.

Chapter 6

Intraspecific variation in dormancy

Introduction

The characteristics of dormancy in many species can be variable both in time - between seasons - and in space - between populations, between individuals within a population and between seeds on a plant. Such variability and its causes has been discussed in detail in Chapter 1. If dormancy in a species is very variable, then results from one season or from one population cannot be applied to the species as a whole. Variation in dormancy characteristics between seasons has been studied in Chapter 4. Here, variability between populations and between individuals during one season will be examined in order to determine applicability of the results presented in this thesis to the species as a whole.

There are two sources of variation in seed dormancy at dispersal. Firstly, phenotypic variation due to effects on the seed of maturation and drying conditions. Secondly, genotypic variation resulting from variation in the parental genotype and this may result in genetically distinct populations. There are many reports of combined phenotypic and genotypic variation in wild seeds (Chapter 1) but few have isolated the two. Garbutt and Witcombe (1986) reviewed the literature on genetic control of dormancy.

The genetic component of dormancy has only been studied for a few weed species since it is difficult to distinguish genetic and non-genetic components (Harper 1977, Jain 1982). Apart from hybrids of *Papaver*, Harper and McNaughton (1960) discovered a predominance of maternal characteristics in seed dormancy, as opposed to possible paternal effects through the embryo or endosperm genotypes. In *Avena fatua*, the

heritability of dormancy studied between 4 populations was about 50% (Jana et al, 1979), whilst in A.barbata and Bromus mollis it was very weak (Jain 1982). The expression of genetic origin of dormancy may differ between populations and can be strongly affected by the environment (Jain 1979). Naylor (1983) found the expression of genotypes which confer long term seed dormancy in A. fatua was highly sensitive to temperature and drought stress experienced during seed development. Heritability is the amount of variation in seed dormancy which is not produced by the environment and is given by:

$$h = \frac{Vg}{Vg + Ve}$$

where Vg is the genetic variation and Ve is the environmental variation.

The experimental design used here was taken from Sparke and Bostock (1985). Replicate plants were taken from several fields and transferred to a uniform environment in a greenhouse where seeds were collected. These 'wild seeds' were then incubated in uniform conditions to determine variation in dormancy between fields and between plants within a field. Such variation included genotypic and phenotypic effects. As seeds germinated in the growth cabinet they were removed, labelled and grown to maturity in uniform conditions in a greenhouse. This removed the effects of differences in maturation conditions on the next generation of seeds. Seeds from these transplants were then incubated in uniform conditions. Variation in these 'transplant seeds' between fields, between plants and between sibs from these plants was then determined. Since phenotypic variation had been removed, this variation was genotypic.

Sparke and Bostock (1985) found that incubation conditions were important in revealing variability since they affected not only the mean percentage germination but also the variation in percentage germination between seed lots. If the mean germination across all seed lots (or the germination of a pooled seed lot) is 50% the variance will be maximised. As the mean approaches 0% or 100% the variance declines to zero. This is to be expected because germination is binomially distributed, but it has also been demonstrated experimentally (Sparke and Bostock, (pers. comm.). To produce about 50% germination, seed lots were left in the laboratory to after-ripen until a pooled seed lot gave at least 50% germination in optimal light and temperature conditions.

Comparisons of the wild and transplant seed germination can provide estimates of the degree of genetic determination or broad sense heritability. Although parent-progeny regression is the traditional method, Frey and Horner (1957) demonstrated that with characters whose range could vary from year to year a correlation coefficient (rather than a regression coefficient) provides a more realistic estimate of broad sense heritability. Seed dormancy exhibits this feature and so correlation coefficients were used. As it is being assumed that there is no paternal contribution to these characters, the correlation coefficient needs no further adjustment to estimate heritability.

Materials and Methods

1 Variation in wild seeds within and between populations.

L.purpureum

Three plants were collected from each of four fields and grown to maturity in uniform conditions in a greenhouse in order to make seed collection practicable. As far as possible, plants were of a similar size when transplanted. Each plant was labelled and the pots placed in plastic trays to collect seed as it was shed. Where the flower heads could not be contained within the tray, photographic negative bags, approximately 6 cm^2 were stapled over the heads. Any effects of such treatment on the seeds would apply equally to all plants (Plate 19).

Seeds were dried for two weeks in a desiccator and then stored in envelopes in the laboratory until dormancy had declined sufficiently to allow 50% germination of a bulked sample, at 22/9°C in the light, these being the optimum conditions. For each of the 12 seed lots, 2 to 4 replicates of 30 seeds were placed on filter paper in aluminium tins containing glass beads which gave a reservoir of water. They were then incubated at 22/9°C for two weeks in an incubator, counting germination every two days until it ceased. Variation between fields and between plants was then calculated using a 2 level nested ANOVA.

V.arvensis

Three plants were collected from each of seven fields and grown to maturity in the greenhouse. Since Viola seeds dehisce explosively, photographic negative bags were stapled over flower heads as they opened

Plate 19

Collecting seeds for testing variability in dormancy

Lamium purpureum

Plate 20

Viola arvensis

(Plate 20). Seeds were dried in a desiccator for two weeks and then in envelopes in the laboratory to age them since they were completely dormant.

Germination tests on bulked samples were performed periodically to assess the dormancy level using 0.2% KNO_3 in darkness at 18/6.5°C, these being the optimum conditions for germination. When germination exceeded 50% tests on all 21 seed lots were performed as for L.purpureum, except that replicates of 100 seeds were used and counting was done only once after two weeks to prevent exposure to light. Variation between fields and between plants was described using a 2 level nested ANOVA.

2 Genotypic variation in transplant seeds

In both species, germinated seeds from the above experiments were transferred on the filter papers to pots of compost in covered trays, providing a humid atmosphere for the seedlings. Each seedling was labelled. At the cotyledon stage, they were transferred to garden soil in pots and grown to maturity.

Four sibs for each L.purpureum plant and three for each V.arvensis plant were used and seeds were collected as before. Cross-pollination was avoided as far as possible by bagging flower heads as soon as they opened but this was difficult for L.purpureum due to the position of the flowers on the stems. However, plants were well spaced out and insect pollination, if any, would have been low. In any case, paternal influence can be assumed to be low, as discussed above, so cross-pollination would be unimportant.

Incubation experiments were then carried out as before and a 3 level nested ANOVA performed on the results.

Results

L.purpureum

Analysis of variance on wild seeds showed a significant difference in germination between fields and between plants ($P < 0.05$) with 49.1% and 30% of the variation respectively being described. (Table 6.1 and Figure 6.1).

The analysis of variance for transplant seeds lumped sibs with replicates as representing variation within maternal plants. There was a significant difference only between plants within a field ($P < 0.025$), not between fields, (Table 6.2 and figure 6.2). The correlation coefficient between first and second generation plants was 0.781 ($P < 0.001$).

V.arvensis

Analysis of variance on wild seeds showed no significant difference in germination between fields but between plants there was a significant difference ($P < 0.001$) and described 24.8% of the variation (Table 6.3 and Figure 6.3).

The analysis of variance for transplant seeds lumped sibs with replicates and revealed a significant difference between plants ($P < 0.001$), accounting for 13.2% of the variation but there was also a significant difference between fields ($P < 0.001$). The correlation coefficient between first and second generation plants was 0.641 ($P<0.01$). This is shown in Table 6.4.

TABLE 6.1 Variation in wild seeds of L.purpureum

FIELD	PLANT	GERMINATION (arcsine transformed)				Mean
BANK	1	24.5	21.8	24.5	27.1	24.5
	2	15.0	10.5	24.1	28.9	19.6
	3	33.2	25.0	30.0	18.4	26.7
ROE	1	30.6	27.6	31.7	21.4	27.8
	2	46.2	36.1			41.2
	3	50.8	42.0			46.4
BULL	1	38.3	34.5	47.0	50.3	42.5
	2	28.9	28.9	30.6	24.1	28.1
MILL	1	18.8	0.	10.7	10.5	10.0
	2	18.4	21.8	21.8	23.1	21.3
	3	15.2	15.8	18.4	18.4	17.0

Nested analysis of variance

Level	SS	DF	MF	FS	P
Fields	2715.5	3	905.2	4.648	<0.05
Plants	1313.4	69	194.7	6.1234	<0.05
Reps	888.6	29	30.6		

Variance components

Level	%
Fields	49.1
Plants	30.0
Reps	20.9

Figure 6.1. Phenotypic variation in germination of Lamium purpureum seeds at 22,9°C in the light.

- between fields $p < 0.05$ 3,7 DF
- between plants $p < 0.01$ 7,29 DF

95 % confidence limits

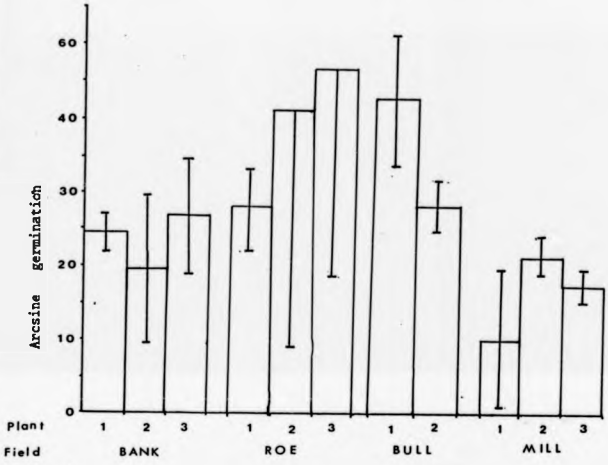


TABLE 6.2 Genotypic variation in transplant seeds of L.purpureum

FIELD	PLANT	SIB	GERMINATION (Arcsine)			Mean	Mean per plant
BANK	1	A	25.8	43.8	45.0	38.2	
		B	63.4	55.9	65.6	61.6	
		C	46.8	44.4	47.4	46.2	24.5
		D	72.0	71.0	75.0	72.7	54.7
	2	A	46.1	42.7	41.6	43.5	
		B	60.0	54.3	59.2	57.8	
		C	62.0	56.8	68.5	62.4	19.6
		D	63.8	49.6	54.3	55.9	54.9
	3	A	71.2	61.5	63.4	65.4	
		B	64.9	68.3	62.5	65.2	
		C	47.2	51.8	48.5	49.2	26.7
		D	49.1	63.4	58.1	56.9	59.2
ROE	1	A	62.8	66.4	81.4	70.2	
		B	62.5	59.0	75.4	65.6	
		C	60.7	57.9	62.0	60.2	27.8
		D	68.8	63.1	59.0	63.6	64.9
	2	A	63.1	68.8	57.9	63.3	
		B	90.0	72.5	69.5	77.3	41.2
		C	50.8	51.2	45.0	49.0	63.2
	3	A	81.5	73.4	78.1	77.7	
		B	57.7	57.7	67.3	60.9	46.4
		C	64.3	70.1	62.6	65.7	68.1
BULL	1	A	73.6	71.8	71.6	72.3	
		B	71.4	66.2	67.8	68.5	
		C	64.0	64.6	61.1	63.2	42.5
		D	68.0	69.5	67.3	68.3	68.1
	2	A	53.9	64.3	62.0	60.1	
		B	63.4	59.3	51.5	58.1	28.1
		C	55.1	59.3	63.1	59.2	59.1
MILL	2	A	61.1	60.3	53.0	58.1	
		B	40.4	26.6	34.4	33.8	
		C	58.6	56.8	62.3	59.2	21.3
		D	56.4	50.8	54.3	53.8	51.2
	3	A	55.5	53.5	53.9	54.3	
		B	67.8	81.5	73.0	74.1	
		C	73.3	62.5	66.4	67.4	17.0
		D	55.2	64.0	62.8	60.7	60.7

Table 6.2 (cont'd)

Nested analysis of variance

The analysis lumped sibs with replicates as representing variation within maternal plants.

level	SS	DF	MS	FS	P
Fields	1839.043	3	613.0142	2.194	NS
Plants	1671.259	5.9	281.9453	3.0431	<0.001
Reps	9244.752	101	91.5322		

Variance components

level	%
Fields	10.0
Plants	14.1
Reps	75.9

Figure 6.2

Lamium purpureum genotypic variation in germination

between field variation NS

between plants within field variation NS

between sib variation $P < 0.001$ $F = 11.4724$ 28, 76 df

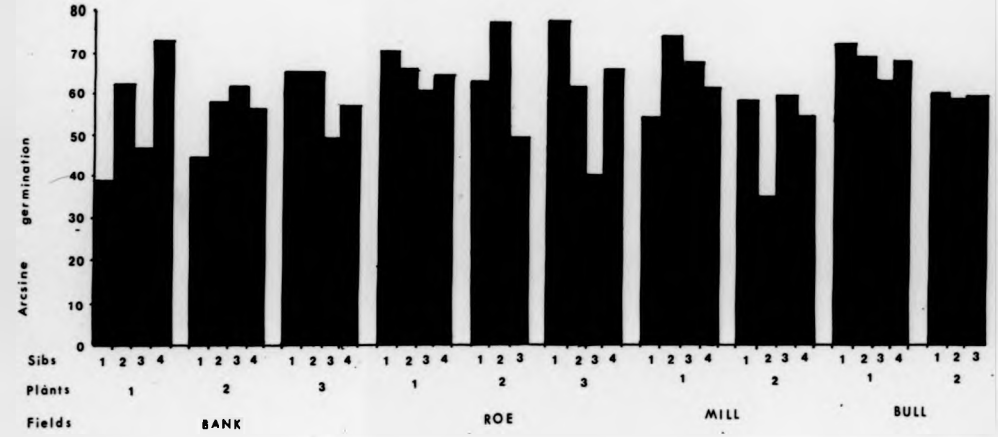


TABLE 6.3

Variations in wild seed of V.arvensis

GERMINATION(arcsine transformed)

FIELD	PLANT	REPLICATES				Mean
Mill	1	69.3	77.1	71.6	67.2	71.3
	2	77.1	90.0	77.1	71.6	79.0
	3	90.0	77.1	67.2	77.1	78.9
Sandy	1	90.0	77.1	90.0	77.1	83.6
	2	90.0	74.1			82.1
	3	74.1	69.3			71.7
Canal 1	1	55.2	45.0	53.7	52.2	51.5
	2	71.6	80.9			76.3
Canal 2	1	74.1	80.9	90.0		81.7
	2	77.1	71.6	71.6		73.4
	3	80.9	90.0	90.0	80.9	85.5
Bank	1	80.9	90.0	67.2	80.9	79.8
	2	90.0	80.9	90.0	77.1	84.5
	3	90.0	80.9	71.6	90.0	83.1
Eaches	1	77.1	90.0	77.1	74.1	79.6
	2	90.0	90.0	77.1	80.9	84.5
	3	71.9	71.9	74.1	90.0	77.0
Bull	2	77.1	90.0	90.0	77.1	83.6
	3	74.1	71.9			73.0

Nested analysis of variance

level	SS	DF	MS	FS	P	
Fields	2482.8	6	413.8	2.818		NS
Plants	1712.7	11.6	142.7	2.7471		<0.001
Reps	2441.9	47	51.95			

Variance components

level	%
Fields	26.7
Plants	24.8
Reps	48.5

Figure 6.3. Phenotypic variation in germination of *Viola arvensis* seeds at 18,6.4°C in 0.2% KNO_3 in darkness.

- between fields NS.
- between plants $p < 0.001$ 2,47 DF

95 % confidence limits

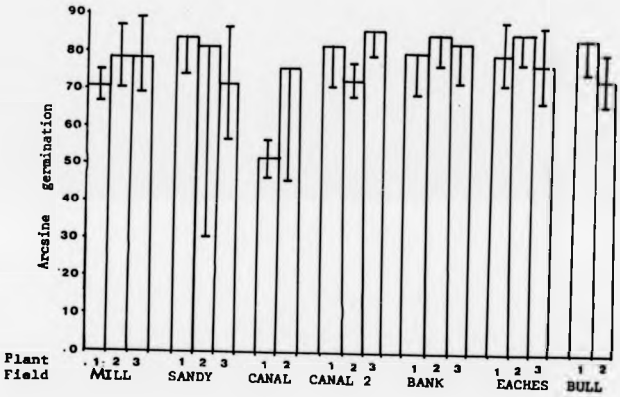


TABLE 6.4

Genotypic variation in transplant seeds of V.arvensis

FIELD	PLANT	SIB	REPLICATE		FIELD	PLANT	SIB	REPLICATE	
Bank	1	a	78.5	81.9	Canal2	1	a	36.9	36.9
		b	78.5	78.5			b	71.6	90.0
		c	73.6	75.8			c	63.4	62.0
	2	a	55.6	60.7		2	a	64.9	69.7
		b	69.7	63.4			b	50.8	55.6
		c	78.5	69.7			c	58.1	68.0
	3	a	90.0	75.8		3	a	62.0	69.7
		b	55.6	47.3			b	81.9	81.9
		c	66.4	59.3			c	81.9	78.5
Mill	1	a	90.0	78.5	Mills1	1	a	81.9	78.5
		b	64.9	71.6			b	90.0	81.9
		c	68.0	81.9			c	90.0	75.8
	2	b	81.9	78.5		3	a	90.0	81.9
		c	71.6	71.6			b	73.6	78.5
	3	a	90.0	90.0			c	73.6	90.0
		b	75.8	73.6	Eaches	1	a	90.0	90.0
		c	90.0	90.0			b	75.8	90.0
Bull	2	a	40.4	31.9			c	90.0	90.0
		b	60.7	78.5		2	a	81.9	78.5
		c	51.9	64.9			b	90.0	75.8
	3	a	56.8	62.0			c	90.0	90.0
		b	82.0	81.9		3	a	62.0	81.9
		c	69.7	68.0			b	71.6	78.5
Canal1	1	a	36.9	41.6			c	75.8	81.9
		b	22.0	31.9	Sandy	1	a	69.7	73.6
		c	26.6	22.0			b	68.0	62.0
Canal1	2	a	51.9	48.4			c	63.4	75.8
		b	45.0	42.7		2	a	75.8	78.5
		c	40.4	38.1			b	81.9	90.0
							c	73.6	75.8
						3	a	81.9	66.4
							b	75.8	90.0
							c	90.0	90.0

Nested analysis of variance

Sibs were lumped with replicates as representing variation within maternal plants.

level	SS	DF	MS	FS	P
Fields	20551.767	7	2935.97	8.9555	p<0.001
Plants	4234.473	12.9	327.8413	3.5455	p<0.001
Reps	9462.843	103	91.8723		

Variance components

level	%
Fields	56.2
Plants	13.2
Reps	30.6

The correlation coefficient between wild and transplant seed germination was 0.641 ($P < 0.01$)

Discussion

L. purpureum

Dormancy in wild seeds of L.purpureum plants collected from four different fields differed significantly ($P < 0.05$) and significant differences were also apparent between plants within a field ($P < 0.001$), describing 49.1% and 30% of the variation respectively. When seeds derived from these plants were grown under uniform conditions, significant variation between fields disappeared but variation between plants was still significant ($P < 0.025$) and described 14.1% of the variation. It thus appears that any between field differences were purely phenotypic effects resulting from differences in the environment affecting the seeds. However, differences between plants within a field were partly genotypic and heritable with 78.1% heritability.

The phenotypic component of this variation in dormancy is an underestimate of that existing in the field since seeds were shed from plants brought into a uniform environment. The causes of such variation were discussed in Chapter 1 and may involve differences in temperature, light or nutrient levels between fields and within fields. For example, plants collected from Bullfield were from beneath an oak tree so grew initially in shaded and cooler conditions. The other fields were close together on the same farm and in similar positions so factors other than light and temperature were probably involved. Possibly, variation in the age of the plants when they were transplanted was important, resulting from differences in emergence times due to differences in the timing of cultivation between fields. This influenced the time of seed dispersal and variation in the proportions

of early and late-dispersed seed may have influenced the overall dormancy level (Chapter 5).

The genetic component of dormancy reflected in differences between plants within a field is interesting, especially since it is very high (78.1%). This reveals a large potential for adaptation to any particular factor, such as herbicide application or cultivation regime. It also acts as an insurance element since this variation ensures that germination does not occur simultaneously, risking death of the population after herbicide application or cultivation.

Germination of wild seeds ranged from 10 to 46.4 arcsine units at 22.1/9°C in the light, which is a wide range in dormancy level. Thus, germination in any bulked seed sample from any one field cannot be taken as representative of the species as a whole. This is important in terms of predicting the proportion of the seedbank which is likely to emerge in any one season in order to propose control measures.

V.arvensis

Dormancy in wild seeds of V.arvensis varied significantly between plants - ($P < 0.001$) but not between fields. However, in transplant seeds there was significant variation both between plants and between fields ($P < 0.001$) accounting for 13.2% and 56.3% of the variation respectively. This effect suggests that phenotypic and genotypic variation combined in the first generation seeds was so great between plants that no significant differences between fields were apparent. However, removal of the phenotypic factor revealed significant genetic differences between fields as well as between plants within a field with 64.1%

heritability.

Phenotypic variation is a result of factors experienced by the parent during seed maturation and these have been discussed in Chapter 1. Soil type may be an important factor here since the seedbank of V.arvensis is also related to soil type. Nutrient and moisture levels, susceptibility to drought and temperature can all influence seed dormancy. Phenotypic effects may also result from time of emergence in different fields which will affect the temperatures experienced by the seed. Differences in the time of emergence may result from variation in the date of cultivation.

Genotypic variation between plants within a field indicates the variability which can exist within a population and acts as an insurance element against adverse conditions. This may explain the extended germination period seen in the field. Combined with phenotypic effects, dormancy can vary greatly. Furthermore, such genetic variation will allow adaptation and the development of herbicide resistance and may explain why V.arvensis is so difficult to eradicate with herbicides and the appearance of large plants in recent years in cereal crops.

The existence of genetic variation between fields has been noted previously by Drabble (1929), Fothergill (1944) and Pettet (1961). However, they described differences in characteristics of the plants. It is possible that the differences between fields in seed dormancy reflect the existence of different races. Genetic differences between fields may result from adaptation to a particular soil type or cultivation regime and may be one reason for the variation in the

proportion of the seedbank emerging each year (Chapter 2). The amount of sand in the soil affects the seedbank and may do so by determining which genotype grows there and its dormancy.

Dormancy in wild seeds ranges from 51.5 to 85.5 arcsine units and since this is the variation which is present in fresh seeds, results from any bulk sample must obviously be treated with caution. Furthermore, this is an underestimate of the variation that exists, since not only were plants brought into uniform conditions during seed ripening but the incubation conditions produced over 50% germination on a bulk sample by the time the experiment was set up, thus reducing the variance as discussed earlier. Thus, thermobar results must be treated with caution and should only be treated in a qualitative way. Differences in dormancy level between seasons and between populations should be expected.

Fryxell (1957) suggested that little genetic variation would be expected in principally self-fertilizing species such as V.arvensis and L.purpureum. However, in both species, significant genetic variation existed between plants within a field and for V.arvensis between fields. Thus, cross-pollination must occur. The existence of both phenotypic and genotypic variation in dormancy means that quantitative differences in dormancy level should be expected both between populations and between seasons.

Chapter 7

Discussion

The experiments described in this thesis have been of three types: those performed in the fields of winter cereal and oilseed rape ; those performed in the Botanical Gardens to help interpretation of field results; and those performed in controlled conditions on a thermogradient bar and in growth cabinets to describe seed dormancy in the hope of explaining the field emergence patterns observed. The aim of these experiments was to provide a comprehensive view of the life cycle of V.arvensis and L.purpureum in order to understand the mechanisms that regulate the size of the weed population in the crop environment. Such information is important to achieve success and economic control (Mortimer et al. 1978, Doyle et al. 1986).

Field observations (Chapter 2) involved permanent 1 m^2 quadrats set up in winter cereal fields. In 1985-86, the same fields were used, but four of which now grew oilseed rape, allowing a comparison of behaviour in different winter-sown crops. Observations included the seedbank size, survival to reproduction, and seed production together with some factors regulating population size such as mortality of seedlings and in situ decay of seeds.

Details of the life cycle for each species have been presented in Chapter 2 . The seedbank for V.arvensis was much larger than that for L.purpureum and reflected not only differences in population size but also differences in seed dormancy between the two species. This is discussed later. Mean annual emergence as a proportion of the seedbank was similar for both species but producing vastly different seedling densities due to differences in seedbank size. However, survival to reproduction was far greater for L.purpureum than for V.arvensis such that numbers of flowering adults by July were very similar.

L.purpureum had about 20 plants per m^2 and V.arvensis between 14 and 23 plants per m^2. Since the difference in potential seed production per plant was small, differences in seedbank size may reflect past population size or the longevity of seeds in the seedbank. This will also be discussed later.

Input of seeds to the seedbank was not effectively studied and requires further research. Doyle et al. (1986) assumed density-dependent seed production but this was not studied here. They assumed a proportion was lost or destroyed by small mammals, birds and fungal infection, whilst some were destroyed by straw burning and only a proportion was viable. These assumptions can also be made for these species but the major source of loss is probably due to harvesting. The timing of harvest in relation to seed set will therefore be important in determining seed input. This is influenced by the weather but also by the crop. For example, oilseed rape is generally harvested before winter cereals. Such effects could be studied in detail. Viola arvensis plants which have been suppressed by the crop can grow rapidly once the crop has been harvested and this provides a further seed input if they set seed before the stubble is burnt.

From field observations, several practically useful relationships were discovered. For both species, total annual emergence was positively related to the seedbank. Using Figures 2.10 and 2.15, annual emergence could be predicted. Knowing the proportion of seedlings likely to survive as adults and to reproduce, the benefits and costs of control could be weighed up. If only low infestations were likely, a more specific spray could be used against other weeds, whilst if a V.arvensis density of 100 per m^2 was expected, a herbicide specific for

V.arvensis could be used. For L.purpureum. the potential adult population could also be estimated from the seedbank using Figure 2.33.

The incorporation of oilseed rape fields in 1985-86 enabled comparisons of the behaviour of the two species under different crop types. The earlier cultivation of oilseed rape fields ensured greater survival of the plants since they were more mature during times of environmental stress. Furthermore, had the canopy cover not inhibited flowering of V.arvensis, dispersal would have occurred earlier and may have increased seed input to the seedbank. This has implications for the timing of cultivation since earlier cultivation is likely to increase seed input of V.arvensis, both due to increased survival and earlier flowering. However, if harvest is also earlier, this effect may be offset somewhat. In the case of L.purpureum, late summer and early autumn germination in oilseed rape fields allowed two seed inputs during the year; one in December and a further one in late spring - early summer. Where populations are higher than here, this may significantly increase the seedbank.

For arable weeds, the seedbank is the major problem to the farmer (Roberts 1981, Chancellor and Froud-Williams 1986). Dormancy characteristics of seeds in the soil will affect the long-term implications for control and will determine the length of time required before the weed population can be completely eradicated. Doyle et al. (1986) found that increasing the initial seed populations simply increased the proportion of years in which spraying was required. Persistent species are those with extended seed dormancy.

Seedbank studies of V.arvensis in the field (Chapter 2) initially

involved sampling in 65 winter cereal fields, taking five cores from each and bulking them. Emergence from these soil cores was monitored initially but subsequently the soil was sieved and the seeds extracted. Several fields were then chosen for more detailed study and smaller cores were taken along a transect for each of the five permanent quadrats set up for population studies. Replicate samples were bulked for each quadrat and the seeds extracted. However, variation between replicate cores was so large that variation between quadrats proved non-significant. This was not suprising since replicate cores were taken from as far as 40 m from the quadrat. Samples were not, therefore, representative of the seedbank for any particular quadrat and the mean seedbank per field was used in statistical analysis. Since this is the value of most practical use, more detailed sampling was not considered necessary. These results confirmed the suggested heterogeneity of the seedbank and thus the necessity for several samples to estimate the seedbank density per m^2 for any field (Roberts 1981).

For L.purpureum, detailed studies only began in autumn 1985 since no appropriate-sized population was found in 1984. Only two populations were studied, both along hedgerows, one in an oilseed rape field and one in a winter cereal field. Since the populations were localized, the seedbank was sampled around the area of each quadrat. Therefore, statistical analysis of the seedbank used individual quadrats as only two fields were available. Relationships between the seedbank and soil type or crop history could not be studied.

It is important to determine causes for the presence of large populations of a particular weed. Many authors have found the crop history of a particular field to affect the seedbank size of V.arvensis.

(Brenchley and Warington 1930, 1933, Roberts 1958, Chancellor 1985) and of L.purpureum (Chancellor 1985). A study of the previous crop history since 1979 found the only significant relationship to be with the number of years sown to winter barley. Detailed information for all fields was not available beyond this, though the number of years since the land had been down to permanent pasture was studied and no relationship was found. The lack of any further significant relationship was not surprising considering the variability between fields in terms of soil type, aspect, herbicide usage and effectiveness (which may be influenced by soil type), differences in situation and past management practices. The seedbank would have to be monitored in detail for several years in order to determine effects of cropping and management (Chancellor 1985). Winter barley is a better competitor than winter wheat so a negative relationship with the seedbank would have been expected rather than the positive relationship observed.

V.arvensis has been reported to prefer light soils (Brenchley and Warington 1930). When this was examined here a positive relationship was apparent between the amount of sand in the soil and the seedbank size. Furthermore, it was interesting to learn that winter barley tends to be sown on lighter soils than winter wheat since it is able to withstand summer drought to a greater extent. Thus, since both the seedbank and the frequency with which the land had been sown to winter barley was related to the sandiness of the soil, factors likely to be involved in this phenomenon were studied in the experiments in the Botanical Gardens (Chapter 3).

The presence of a large seedbank for V.arvensis in sandy soils could be due either to a high seed input or to low output. A high seed input

may be the result of high emergence and survival to reproduction, or a higher reproductive capacity in sandy soils. A low output may be related to low emergence or a greater longevity of seeds in sandy soils. There was no relationship of survival, or the adult population size with the sandiness of the soil. In the Botanical Garden experiments, differences in emergence and longevity of both species were studied in three soil types representative of the range of sandiness observed in the fields (see below).

One variable which may lead to differences in emergence between soil types is inorganic nitrate, which stimulates germination of many arable weeds (Lyne 1985). The effect of 0.2% KNO_3 on germination of fresh seeds of both species was studied. Both were stimulated to germinate by nitrate, both in the light and in darkness, at field temperatures for October (17.9/6.4°C), which is when peak emergence is observed. Analysis of the three soils used indicated that clay soils contained most nitrate nitrogen and sandy soils the least. If emergence is simply related to nitrate levels, most emergence would have been expected from clay soils and least from sandy soils. However, emergence in the gardens was more complex; clay soils did produce most emergence in V.arvensis but sandy soils produced more than intermediate soils (Figure 3.3). For L.purpureum, sandy soil produced most emergence with little from intermediate or clay soil.

The large V.arvensis seedbank in sandy soils is therefore unlikely to be due to lower emergence as a result of low nitrate levels. From these results it is difficult to explain the small seedbank of V.arvensis in clay soils. Possibly, a greater emergence from clay soils and in situ germination below the surface layer, leading to death, prevents the

build up of a larger seedbank. Viability of buried seeds did not differ between soil types for either species in the course of one year, though this may not reflect the long-term situation. However, no significant relationship was apparent between sandiness and the proportion of non-viable seeds in the soil in 1985-86, though no very clay soils were present in this analysis. Clay soils tend to be less used for winter cereals and in this study only four fields had less than 50% sand. The relationship observed between sandiness and the seedbank does not therefore include many clay soils and referred mainly to the difference between sandy and intermediate soils.

Since emergence from sandy soils exceeded that from intermediate soils, the effect of nitrate on germination is probably not involved. Sandy soils are better drained than intermediate soils and temperature changes will be more rapid and severe which may have stimulated germination and emergence since there is often a positive relationship between germination and the level of temperature alternation (Vincent 1974, Grime and Thompson 1976, Totterdell and Roberts 1980, Thompson and Whatley 1984, Probert et al. 1986,). This hypothesis is supported by the fact that, for V.arvensis. emergence from clay soil only exceeded that from sandy soil in September when field nitrate levels would have been high (Lyne 1985) - and in June when sandy soils would have been subject to drought. In April and May sandy soil produced more seedlings probably reflecting a greater temperature alternation and generally warmer temperatures. However, it is also possible that the least dormant fraction of the seed population had already germinated in the clay soil.

The fact that L.purpureum emergence was greatest from sandy soil may be

due to a requirement for relatively warm temperatures and large temperature alternations for germination (Chapter 4) which were only present in sandy soil when seeds were least dormant.

These experiments therefore suggest that a high seedbank in sandy soils results from higher emergence and consequently a higher seed input returned from mature plants. 'Clay' soils tend to be used less for winter cereals and few were used in this analysis. The relationship observed, therefore, refers mainly to sandy and intermediate soils. However, if clay soils were to be used, most emergence would be expected from these soils and also most long-term *in situ* germination. Longevity experiments in controlled conditions would need to be conducted over several years to examine this. Conversely when the relationship between sandiness and total emergence was studied from field data no significant relationship was apparent. The fields used for population studies varied between 50 - 87.5% sand so little significant variation would be expected. Also, other environmental factors may interact with sandiness to affect field emergence. For example, nitrate fertilizers would have been added; variation in aspect and situation may influence temperatures experienced by the seeds; and the timing of cultivation in relation to the dormancy level of the seeds varied.

It is possible that seed input also varies between soil types as a result of differences in reproductive capacity. Warmer soil temperatures may increase growth and stimulate a greater reproductive input in sandy soils, or may lead to earlier flowering, allowing a higher input before harvest.

The second possibly crucial stage in the life history is emergence from the seedbank (Chapter 2). For L.purpureum, 3% emerged during the year and for V.arvensis, between 3.3% and 3.6%. These values were similar to those observed for several other annual arable weeds (eg. Roberts and Dawkins 1967, Beuret 1984). Annual emergence was related to the seedbank for both species, as discussed earlier.

A study of emergence patterns (Chapter 2) revealed maximum emergence after autumn cultivation for both species. The peak occurred immediately after cultivation, whether in September or October as shown by the September peak in the gardens. V.arvensis continued emerging throughout the year with a small increase in spring. For L.purpureum, there was little emergence throughout the rest of the year and only a slight spring increase was apparent. Patterns of emergence were similar both in oilseed rape and in winter cereal fields, except that emergence would have occurred earlier in oilseed rape fields as a result of earlier cultivation.

Emergence patterns from the gardens (Chapter 3) were similar to those observed in the field, despite cultivation each month. Chancellor (1965) observed a similar effect for V.arvensis: an increase in the frequency of cultivation simply increasing the proportion emerging, as occurred here. However, in the gardens no emergence of V.arvensis occurred in January, February and March, whereas it did generally occur in the field (except in March 1986). Similarly, for L.purpureum, a secondary increase in emergence occurred between June and August in the gardens which was absent from the field. In the case of V.arvensis, this may have been due to the age of the seeds. In the field the average age of the seed population would have exceeded that in the

gardens and the seed population would therefore have been less dormant. Furthermore, monthly cultivation of the soil may have stimulated germination of the least dormant seeds such that none germinated in March. For L.purpureum, the summer increase observed in the gardens has been reported by others (Leguizamon and Roberts 1982, Baskin and Baskin 1984, Beuret 1984). The fact that it was not observed in the field may reflect lack of cultivation at this time, so non-dormant seeds were not exposed to light. On the other hand, the presence of a dense crop canopy may have inhibited germination by decreasing the amount of light reaching the soil. Furthermore, observation in the field became less accurate as the crop canopy became more dense and, since populations were small, some emergence may have been missed.

An experiment was set up to study emergence under a field cultivation regime but this was abandoned since the soil surface became covered with moss, which may have affected emergence.

The thermogradient bar allowed a study of seasonal changes in the germination requirements of buried seeds and enabled interpretation of emergence patterns in terms of seed dormancy. Seven temperature regimes were provided representing means and ranges prevalent at particular times of the year. Germination of buried and recovered seeds at each of these temperatures was examined each month. Since emergence patterns could be explained by these results, temperature and light (being the only factors provided by the thermobar) can be assumed to be the two most important factors controlling emergence in the field as is often the case in annual weeds (discussed in Chapter 1).

Figures 7.1 and 7.2 show emergence in the field and gardens, together

Figure 7.1. A comparison of Viola arvensis germination at prevailing field temperatures ●——●1984-85 ●- - - - -●1985-86 with emergence in the fields ▲- - - - -▲and in the Botanical Gardens in sandy soil □——□

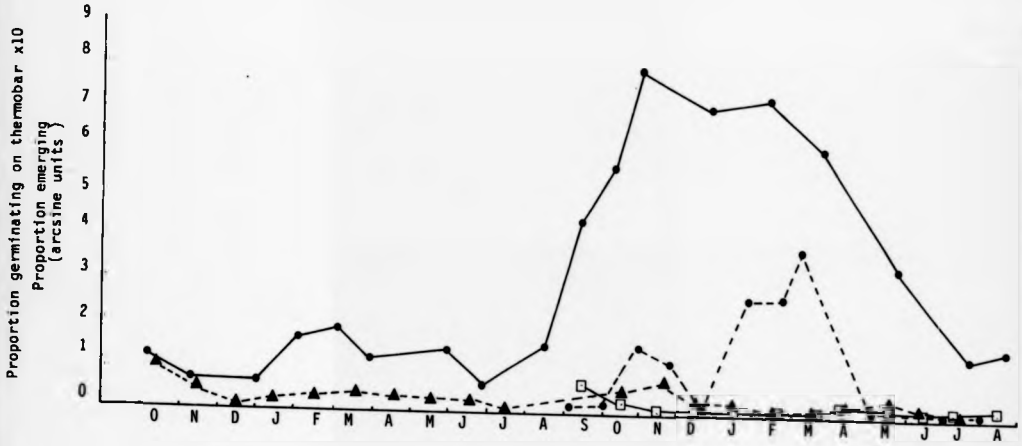
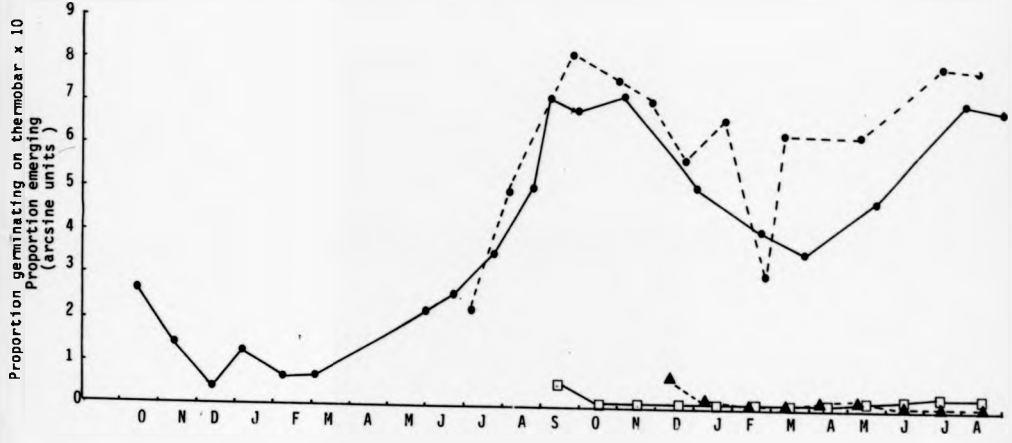


Figure 7.2. A comparison of Lamium purpureum at prevailing field temperatures ●——●——● 1984-85 ●- - - - - -● 1985-86 with emergence in the fields ▲- - - - - -▲ and in the Botanical Gardens in sandy soil □——□



with germination at prevailing field temperatures throughout the year. V.arvensis was relatively dormant during the first year of burial with a slight increase in germination in spring. Maximum germination occurred during the second autumn of burial and this explains the two year periodicity observed in winter cereal fields by farmers and by Chancellor (1985). The proportion emerging in the gardens in the first autumn of burial for V.arvensis is very similar to that expected from thermobar results. However, in spring, actual emergence is much less than potential emergence as displayed on the thermobar. By June, actual emergence again reflected potential emergence. For L.purpureum, actual emergence was always less than potential emergence. This discrepancy probably results from enforced dormancy in a poportion of the seed population due to lack of light or even an unfavourable CO_2/O_2 ratio in the soil. Some dark germination was possible for both species but this would have entailed death of seeds rather than emergence if germination occurred at depth.

Dark germination was high in the second autumn of burial for V.arvensis and relatively high in the first spring for 1985 seeds. For L.purpureum, dark germination was high in the second autumn of burial for 1984 seeds and in the first autumn of burial for 1985 seeds. Such dark germination would entail a loss from the seedbank. For L.purpureum this loss could have been between 50 and 65 arcsine units (59% and 82%) in autumn 1985 and for V.arvensis, about 70 arcsine units (88%) for seeds buried one year. However, from the thermobar results, few V.arvensis seeds were actually empty, indicating that the average age of the seedbank seeds was greater than 2 years and a maximum of 26 arcsine units (ca.19%) of L.purpureum seeds were empty by July 1986. From seedbank studies, between 36% of the seedbank for V.arvensis were

non-viable in October and 59% in July, 23% therefore being lost throughout the year. For L.purpureum between 16% and 33% were non-viable with no significant increase during the year. Thus, for both species, the observed in situ germination was much less than expected on the basis of dark germination from the thermobar. But the thermobar represented surface temperatures and seeds in the dark in the soil experience different temperatures than seeds on the surface with much less temperature fluctuation (Lyne 1985) and an unfavourable gaseous environment may also inhibit germination at depth.

The higher level of dormancy during the first year for V.arvensis was reflected by a much lower proportion of non-viable seeds from the thermobar results. This phenomenon may help to explain the build-up of large seedbanks. The higher proportion of non-viable seeds from the seedbank studies was probably a result of the average age of seeds in the seedbank being above two years. L.purpureum seeds lose viability much more rapidly and so it does not build up a persistent seedbank, being generally less dormant during the first year of burial than V.arvensis. A small proportion of L.purpureum seeds were also found to be decaying from the seeds recovered for thermobar experiments. From the seedbank data the proportion of non-viable seeds was similar for both species since the average age of the seeds was greater than that of the seeds used for thermobar experiments.

Thermobar results indicated variation in dormancy level between seed lots and this may affect emergence from the seedbank. For V.arvensis. germination in the first autumn and spring for 1985 seeds was higher than for 1984 seeds but for L.purpureum. 1985 seeds germinated to the same extent as 1984 seeds in autumn 1985. However, this may have

resulted from the timing of burial since L.purpureum seeds were buried earlier in 1985 when seeds would normally have been losing dormancy whilst in 1984 seeds were entering dormancy when they were buried. On the other hand innate differences in the seed lots may have created these differences in dormancy level due to variation in maturation and drying conditions between years.

In an attempt to resolve these differences, seeds were collected earlier or later in the season and buried early or late. They were then exhumed on alternate months and their dormancy tested in a growth cabinet at the temperature which produced at least 50% germination to maximise variation (Chapter 5). The effect on dormancy of storage temperature and storage conditions was also examined by storing seeds in a Stevenson Screen and in a fridge at a constant 4°C.

For V.arvensis, early dispersed seeds were significantly less dormant than late dispersed seeds. Such variation has been observed for other species (Rorison 1973, Froud-Williams 1985) whilst the reverse was true for others (Froud-Williams 1985). Thus, somatic polymorphism occurs which may explain the discontinuous emergence observed in the field and the discrepancy betweeen Roberts' data and these results which was discussed in Chapter 4. However, these results do not explain the discrepancy between 1984 and 1985 seed dormancy, since 1985 seeds were collected later so were expected to be more dormant than 1984 seeds. The differences probably lie in the maturity of the seeds since 1985 seeds were collected during wet and cool conditions, many pods remaining closed until dried in the laboratory. The seeds may therefore have been less ripe than 1984 seeds such that dormancy was less developed.

Earlier dispersal requires earlier emergence such that the least dormant seeds are likely to be those derived from early-emerging plants. Thus, the earlier the soil is cultivated, the higher will be the proportion of less dormant seeds. This has implications for the amount of autumn emergence from fresh seeds and the input to the permanent seedbank. If autumn emergence of fresh seeds is high, fewer seeds will become part of the permanent seedbank. The extent to which this could affect the build-up of the seedbank requires further investigation.

The time of dispersal had no effect on L.purpureum seed dormancy. Only two weeks separated early and late seeds, whereas seeds can be dispersed throughout the year and this may have an effect on dormancy. Baskin and Baskin (1984) found autumn-dispersed seeds were able to germinate in spring.

Burial time also affected dormancy of V.arvensis. again, earlier burial leading to lower dormancy. This implies that seeds germinating in the first autumn of burial are those which were dispersed and buried earlier. Thus, delayed harvest will allow a higher proportion of dormant seeds to enter the seedbank. Dormancy of L.purpureum was unaffected by the time of burial after one month, suggesting that the season of burial is more important than the length of time buried.

Temperature during burial is thought to play an important role in the seasonal cycle of dormancy observed in buried seeds (Chapter 1). Screen-stored seeds were exposed to ambient temperatures similar to those in the soil but with greater fluctuations about the mean; an

approximation to field temperatures without actual burial. V.arvensis seeds stored in the screen followed a seasonal cycle similar to buried seeds but changes were more abrupt and may reflect the greater temperature alternation experienced in the screen. However, interactions of nitrate, gases and temperature alternations in the soil may also be important in the control of dormancy. Seeds stored in the refrigerator showed no cycle, contradicting the findings of H A Roberts (pers. comm.), so no endogenous control was present. Seeds gradually lost dormancy as they aged, this loss being slower than that observed in the screen. Thus, temperature is involved in the control of the dormancy cycle but a soil environment is necessary to produce the cycle observed in the field. Unburied seeds were always light-inhibited confirming the results of the gardens experiment discussed in Chapter 4, whereby most emergence ocurred from seeds mixed with soil. Therefore, soil temperature cannot be the only factor involved in this loss of light inhibition during burial since seeds stored in the screen were also light inhibited. Also, in one instance, buried seeds were light inhibited.

It was first thought that the mucus coating surrounding V.arvensis seeds may interfere with light penetration or prevent gas exchange. The effect of burial could be to remove this coat since seeds generally become darker and lose the mucus during burial. However, seeds stored in the screen lost this mucus layer yet they were still light-inhibited. Thus, a physiological effect must be involved rather than a physical effect on the seed coat. Such light-inhibition would prevent germination of seeds on the soil surface and thus allow them to enter the seedbank during cultivation. Any seedlings which emerged before cultivation would be destroyed so this represents an adaptation to

maximise survival.

For L.purpureum, dormancy of seeds stored in the screen was lost more slowly than that of buried seeds initially, but after a few months the seeds became infected with a fungus and so results were unreliable. In the soil seeds were protected from infection possibly by anaerobic conditions or other microorganisms. No seasonal cycle was apparent but these results may not represent the behaviour of uninfected seeds. V.arvensis seeds were not affected by this fungus except at the micropyle and did not decay in the screen. Possibly, the mucus layer and smooth seedcoat of V.arvensis resisted penetration of hyphae whilst the pitted seedcoat of L.purpureum allowed the entry of fungal hyphae.

L.purpureum seeds stored in the refrigerator lost dormancy gradually, similar to buried seeds so ambient temperatures were not the only cause of ageing in the soil. In the dark, peak germination was reached in February, similar to buried seeds implying some endogeneous control. Soil temperatures were therefore important for control of the seasonal cycle of dormancy though seeds did lose dormancy when stored at a constant 4°C, so alternating temperatures are not required for loss of dormancy. This implies that differences in soil temperatures between years may affect the dormancy status of the seed and thus may lead to differences in autumn emergence.

These experiments were conducted on single populations of seeds taken from one particular field each year (though the populations were different in each year). Variation in dormancy due to the time of dispersal or burial and differences between years have been discussed. Variability in dormancy may also occur between populations as discussed

in Chapter 1. This may involve phenotypic or genotypic effects. It was considered important to determine whether such variation existed in L.purpureum and V.arvensis since this would cast doubt on the general applicability of these results.

In Chapter 6, wild seeds were collected from plants obtained from several fields and their germination requirements examined in a growth cabinet. Seeds from these plants were then grown to maturity in a uniform environment to remove phenotypic differences (eg. Probert et al. 1985a,b, 1986). Seeds were collected from these transplants and their germination was examined. Dormancy of wild seeds varied between fields and between plants for L.purpureum but significant variation between fields disappered in transplant seeds. Conversely, in V.arvensis wild seeds there was no significant variation between fields, this being masked by variation between plants. Transplant seeds showed significant variation betwen fields and between plants. V.arvensis therefore exists as genetically distinct populations in terms of dormancy. Drabble (1929) and Pettet (1961) noted the presence of different morphological races of V.arvensis and it is possible that these differences in dormancy reflect the different races. Such variation provides a large potential for adaptation and may explain the high resistance to herbicides found in V.arvensis and also the increase in the average size of plants recently. Such genetic and phenotypic variation in dormancy, combined with a persistent seedbank means that dormancy levels of seeds in the seedbank will be variable. This variation is probably perpetuated by a persistent seedbank.

L.purpureum does not have a persistent seedbank in these fields but variability in dormancy between plants may allow the development of

resistance to herbicides, though this is less likely than for V.arvensis.

The existence of variability in dormancy between fields implies that dormancy of one seed population - even if derived from many plants - may not be representative of dormancy for the species as a whole. Since variation existed even within the study area, regional variation is likely to be far greater. This may partly explain differences found by Roberts (pers.comm.) and by Baskin and Baskin (1984) in the behaviour of V.arvensis and L.purpureum seeds discussed in Chapter 4. Such regional variation in dormancy has been found for several species (Chapter 1). The proportion emerging from the seedbank may therefore vary between populations and, combined with environmental effects on emergence, this explains variation in the proportion emerging described in Chapter 2. However, the relationship observed between the seedbank and emergence, in Chapter 2, for both species does provide an estimate of emergence expected from the seedbank being derived from data from several fields.

Population dynamics model

'The long term success of any weed control programme depends to a large extent on an understanding of the mechanisms that regulate the size of the weed population in the crop environment' (Mortimer et al 1978). The aim of this thesis was to produce a comprehensive view of the life cycle of V.arvensis and L.purpureum for the purposes of control. The data obtained in Chapter 2 can be incorporated into the Leslie Matrix model discussed by Mortimer et al (1978) and the effects of controlling the seed input can be simulated.

The Leslie Matrix is described in Figure 7.3. Multiplication of Matrix A and t^n at time t gives rise to the population structure at time t + 1. Progressive multiplication of the two matrices predicts changes in the population over a period of time. Age groups are described in Figure 7.3 and data is taken from Figure 2.40 for V.arvensis and Figure 2.41 for L.purpureum. Appendix 13 and 14 contains the Leslie Matrices for both species assuming 5, 40, 50, 60 and 100% seed input for V.arvensis and 5, 10, 20, 40, 50, 60 and 100% seed input for L.purpureum. Figures 7.4 and 7.5 show the critical seed input at which the population will start to increase or decrease.

Seed input to the seedbank was not calculated, though Thurston (1964) found 5% of Avena fatua seeds entered the seedbank.

Figure 7.3

A matrix model of the life cycle of an annual weed

(after Mortimer et al. 1978)

Transition Matrix

$$\begin{pmatrix} P_s & 0 & b^1 & b^2 \\ G_s & 0 & 0 & 0 \\ 0 & P^0 & 0 & 0 \\ 0 & 0 & P^1 & 0 \end{pmatrix} = A$$

Column vector of age classes

$$\begin{matrix} t^{=0} \\ t^{=1} \\ t^{=2} \\ t^{=3} \end{matrix} = t^{=}$$

P_s = proportion of seeds surviving from time t to t+1 (subtracting emergence and in situ germination)

G_s = proportion of seeds germinating from time t to t+1

P^0 = proportion of seedlings surviving to become young adults from time t to t+1

P^1 = proportion of seedlings surviving to become mature adults from time t to t+1

b^1 = number of seeds per plant produced by young adults from time t to t+1

b^2 = number of seeds per plant produced by mature adults from time t to t+1

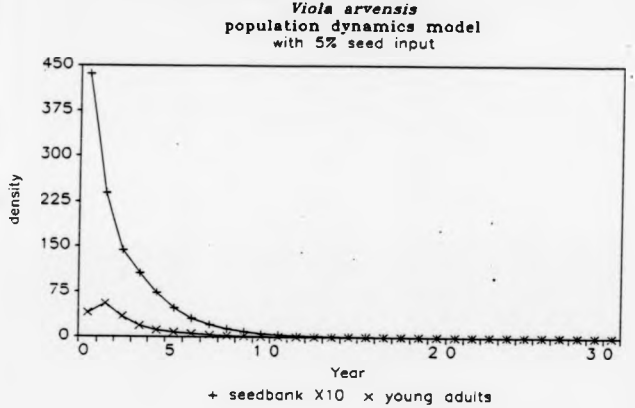
$t^{=0}$ = number of seeds at time t

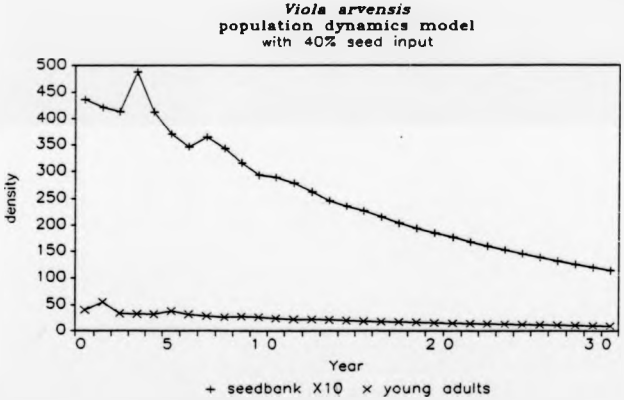
$t^{=1}$ = number of seedlings at time t

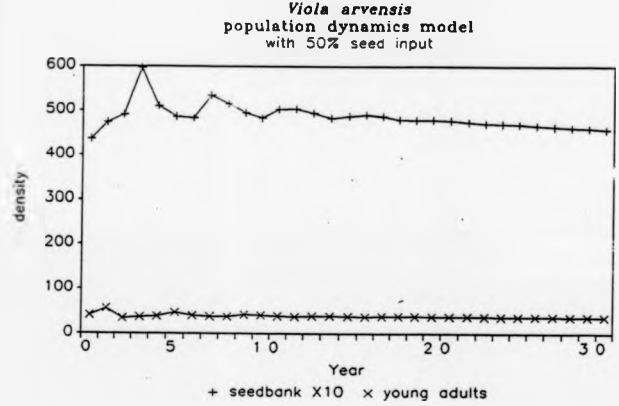
$t^{=2}$ = number of young adults at time t

$t^{=3}$ = number of mature adults at time t

Figure 7.4. Simulated changes in the seedbank and the adult population of Viola arvensis using a Leslie Matrix model and varying the seed input.






Viola arvensis
population dynamics model
with 50% seed input
600
500
400
300
200
100
0
density
0
5
10
20
30
Year
+ seedbank X10 × young adults

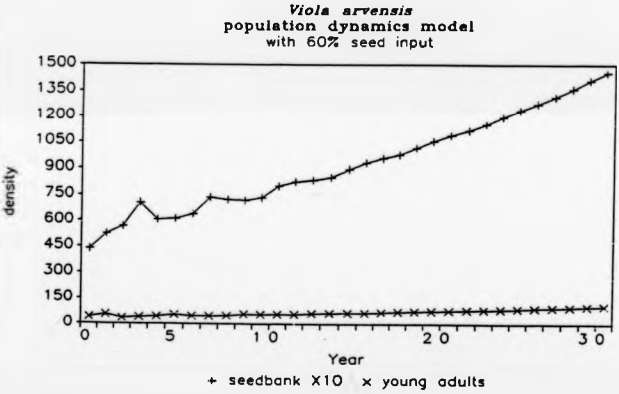
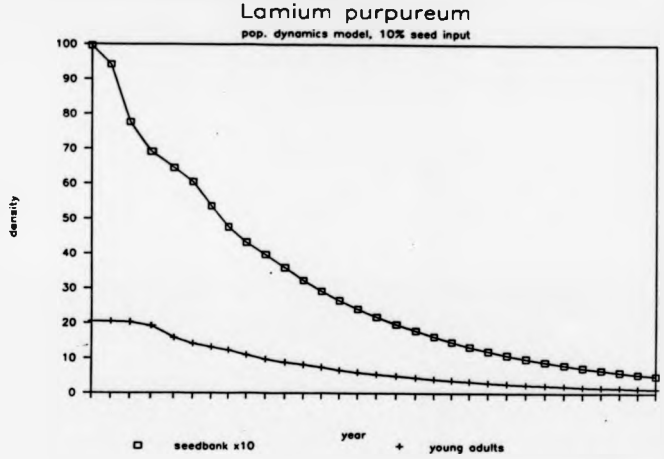
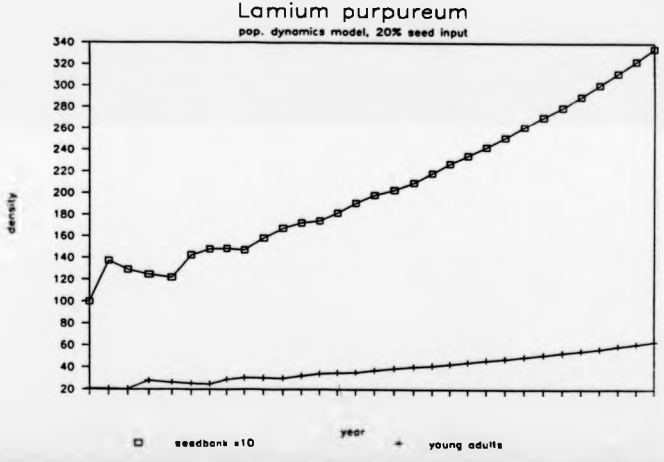
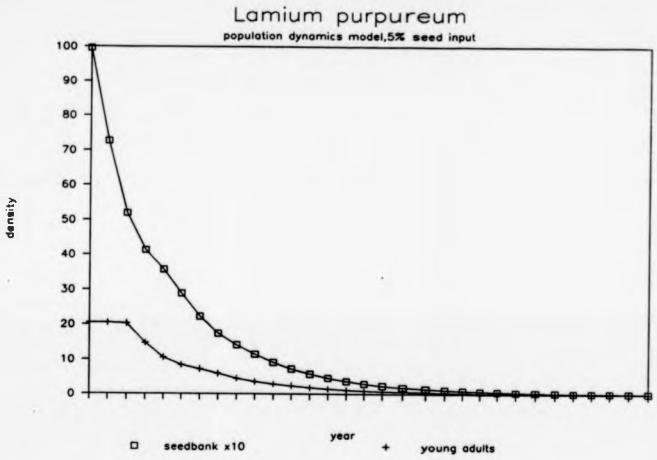

Viola arvensis
population dynamics model
with 60% seed input
1500
1350
1200
1050
900
750
600
450
300
150
0
density
0
5
10
20
30
Year
+ seedbank X10 × young adults

Figure 7.5. Simulated changes in the seedbank and the adult population of Lamium purpureum using a Leslie Matrix Model and varying the seed input.






Lamium purpureum
population dynamics model,5% seed input
density
100
90
80
70
60
50
40
30
20
10
0
year
seedbank x10
young adults

Assuming a 5% seed input for V.arvensis. the seedbank is seen to decrease rapidly to 0 after twelve years and, after a slight increase in the second year, the young adult population follows this trend. Such a trend continues up to 50% seed input but between 50% and 60% input, the population starts to increase. It is therefore important to ensure that less than 50% of the seeds are allowed to enter the seedbank each year if populations are to decrease.

In the short term, within the first five to ten years, there is little change in the young adult population except that with only 5% input a gradual decline occurs. In every case, a slight increase occurs in the second year and since it is the adult population which will affect grain yield, the value of this increase may be an important consideration.

Figure 7.4 shows the effects of controlling seed input on L. purpureum populations. Populations are smaller but the critical input at which the population starts to increase is between 10% and 20%, less than for V.arvensis and the decline at 5% input is also slower. Both reflect the greater survival of L.purpureum populations in the field. Neither is there any increase in the young adult population before the general decline occurs.

Mortimer et al (1978) assumed density-dependent mortality for Poa annua and Avena fatua. However, since this only occurred in one year and at certain times for V.arvensis and not at all for L.purpureum. this was ignored for the purposes of simplicity. Density-dependent fecundity and the effects of other weed species on mortality and fecundity may also be important but these factors were not studied here.

The model above can be used to study the effects of different control measures on the populations of these two species. For example, the long term effect of a particular herbicide could be determined if its effect on survival of any of the population age groups was known, substituting the revised transition probability into the transition matrix.

The main concern of the farmer is the opportunity cost of any control measure, so the effects of populations on yields and on seed contamination of the grain must be determined. Doyle et al. (1986) described a mathematical model for Alopecurus myosuroides population dynamics and knowing the effects of the weeds on yields and the costs and effects of particular control measures, they were able to discuss the opportunity costs of different management practices. Profits from any control strategy could be determined from the following equation:

$$P(t) = WP(1-rM(t))\ Ymax - CSF(t) - CC(t) - CH(t)$$

Where P(t) are the profits at time t, WP is the wheat price (£ per tonne), rM(t) is the proportionate reduction in wheat yields per unit density of black-grass plants, Ymax is the expected yield of a weed-free wheat crop (tonnes per ha), CSF(t) is the cost of seed and fertilizer (£ per ha) CC is the cost of cultivation (£ per ha), CH is the cost of herbicide (£ per ha).

The effects of the weeds on seed cleaning costs must also be considered, especially for V.arvensis. If grain is sold to the EEC, only 1-2% trash is allowed in winter cereals and cleaning costs range from £1.20 to £3 per tonne depending on whether the farmer possesses his own

cleaner or not. This is condsidered a major cost if infestation is high.

The model presented does not consider the effects of crop rotation on the seedbank, or environmental factors causing variation in emergence, survival and reproduction. Long-term study under different conditions must accompany predictions, since crop type, different sowing dates and different soil types could influence results. The sandiness of the soil and the number of years sown to winter barley has been shown to influence the seedbank and must be considered when a particular field is under consideration.

Chancellor and Froud-Williams (1986) suggest that early-sown winter cereals established by reduced cultivation systems will predominate in the future. In such systems, the primary factors influencing weed populations are the degree of reduction in soil disturbance, the method of straw disposal, the season of drilling, the fertilizer regime, trends in herbicide usage and crops sown. A reduction in soil disturbance will produce less emergence such that species with persistent seedbanks, such as V.arvensis. will take longer to eradicate. However, fewer seeds will be ploughed into the seedbank and until V.arvensis seeds are buried they are inhibited from germinating at the soil surface. Addition of nitrate fertilizer before herbicides to these seeds could stimulate germination and thus help to reduce the seedbank size. Hilton (1985) suggested that for A.fatua, addition of nitrogenous fertilizer along with cultivation could considerably reduce the seedbank in the second autumn of burial. However, an increase in the nitrogen content of the soil may also lead to a higher reproductive capacity and thus seed output.

Research into chemicals for releasing buried seeds from dormancy is being carried out. Release from dormancy of Sinapsis alba (Donald and Hoerauf 1985) has been reported. McBride (1985) reported that methyl isothiocyanate (MIT) can kill dormant seeds. However, MIT is too expensive for use in field crops and little success has been achieved in this area so far.

Secondly, an increase in early-sown winter crops will allow the establishment of populations of both species and will prevent cleaning of the land before sowing. V.arvensis plants will also reproduce earlier in summer and seeds will be less dormant during the first autumn. This may lead to a gradual reduction in the seedbank. The use of shorter strawed varieties may lower competition with V.arvensis which is intolerant of shade, and allow a greater seed input. L.purpureum is unlikely to be affected since it is shade tolerant.

In the study area, V.arvensis is a major problem weed whilst L.purpureum populations are very low. The difference appears to lie in seed dormancy. V.arvensis seeds are generally more dormant in the first year of burial, with less in situ germination in the first two years of burial. Seeds were also resistant to fungal infection in the screen and are disseminated farther, allowing the spread of populations and more seeds are produced per plant. V.arvensis plants are also resistant to most herbicides, except at the one or two leaf stage, so established plants are difficult to eradicate. The primary aim of any control programme must be to reduce the seedbank size and prevent further input and the Leslie Matrix model provides a means whereby the effect of different control measures can be examined. The opportunity costs of control will determine any management practice adopted.

Appendices

Appendix 1

Data from permanent m^2 quadrats.

4) 1984 A = adult; F = flowering; C = cotyledon

Field	Quadrat	May					June					July				
		V.a.			L.p.		V.a.			L.p.		V.a.			L.p.	
		A	F	C	A	F	A	F	C	A	F	A	F	C	A	F
Canal	1	125	9				60	125					133			
	2	79	5				24	45	1				11			
	3	50	13				30	57	1				32			
	4	378	20				229	106				22	60			
	5	3	1				5	5				2	9			
Canal 2	1	15					9	12	1				11			
	2	99					70	41	2				56			
	3	135	2				52	51					67			
	4	59					44	44				3	57			
	5	27	1				20	14				6	32			
Mills 1	1	21					29	15				11	9			
	2	1	-													
	3															
	4															
	5	2														
Mills 2	1	18					15		2			4	12			
	2	7	1				14	2	1			12	17			
	3	4					11	2				8	6			
	4	7					24	1	1			24	13			
	5	6					28	4	6			12	11			
Mills 3	1								1			3				
	2		1				1					10	4			
	3						2					1				
	4											3	2			
	5	3					7	1				8	3			
Mills 4	1	399	61				296	27	9			151	174			
	2	213	70				287		35			84	35			
	3	36	6				74	7	3			62	31			
	4	10	1				20		1			14	8			
	5	11					26					15	6			
Millfield	1	12			17		19	2		2	10	7	3			2
	2	9			2		8	1			1	2	1			
	3	1			1		2			1		1			1	
	4	2					2	1				1	3			
	5	18					19		4			7				
Jervis 4	1						2					1	1			
	2															
	3	22			2		16	1	1				2			
	4	27					28					7				
	5	4					2					2	1			
Jervis 5	1						1									
	2	33	2		1		15	12				13				
	3	9					7	7				8				
	4	77	7				33	26				1				
	5	48					45	7								
Crows	1	6			22		16	1	11		11	10	8			
	2	3			14		5	1	2		2	3	1			
	3				1											
	4	1									2					
	5	34		3			34	7				10	20			
Horse	1	1						1	2				1			
	2	52					34	23	3				29			
	3	52					50	5	5			3	23			
	4	5			1		7	2			2	1	3	1		
	5	5					6		3				4			

Appendix 1

b) Data from permanent 4th quadrats 1984-85

Field	Quadrat	Oct		Nov		Dec		Jan		Feb		Mar		Apr		May		June		July	
		V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.	V.s.	L.p.
																A F	A F	A F	A F	A F	A F
Jervis	1	16		23		18		14		15		16		18		15		21		13	10
	2	8		10				10		9		12		16		19		23			
	3	29		42		33		28		25		40		31		31				17	16
	4	55		42		47		36		32		41		34		33		30			7
	5	10		8		11		14		27		12		14		13		19		8	14
Hill	1	44		57		39		40		30		37		35		14		25		5	3
	2	30		26		24		21		18		15		18		9		13		6	7
	3	123		102		64		27		26		25		21		4		16		3	9
	4	179		174		120		131		56		112		121		57		64	40	13	71
	5	19		21		10		10		13		14		22		19		18	3		
Bull	1	4		7	19	7	17	5	20	2	14	8	13	7	15	10	2	10	1	2	10
	2	425		920	6	737	4	700	6	424	3	825	4	532	2	350		271	19		29
	3	138		280	2	259		208		222		150		134		123		61	18		30
	4	169		340	5	258	5	292		268		236		172		137		114	26		29
	5	211		317	2	231	1	268	2	106		215		136		97		65	37		
Sandy	1	323		747		604		539		174		258		70		81		48		21	27
	2	139		518		433		397		98		231		67		102		122	3	32	99
	3	120		118		105		67		58		74		17		51		43		17	25
	4			66		53		36		32		44		26		43			32	3	43
	5			6		6		3		5		2		2		2	2		4		
Wood	1	168		113		116		74		106		17		12		11		4		4	
	2	46		32		20		24		60		17		12		67		71	17	4	49
	3	184		176		65		61		84		67		52		33		24	26	2	36
	4	265		204		139		102		64		67		58		33		24	8	2	5
	5	24		22	2	22		76		41		22		84		56		27	22	2	23
Canal	1			283		261		210		115		79		101		10		10		15	
	2			140		106		158		114		117		115		70		73		39	8
	3			212		193		184		56		135		184		94		77		29	2
	4			367		371		300		148		261		189		102		146		29	
	5	1		358		257		295		112		148		114		68		48		23	
Sheldon	1	296		214		318		318		150		207		206		127		105	5	5	
	2	275		203	4	217	5	217	5	108	3	129	3	102	4	140	1	112	82	1	106
	3	96		32		34		34		44		23		13		20	1	24	24		68
	4	52		36		33		33		29		28		30		14		24	8		15
	5	68		65		53		53		42		71		47		8		2	1		6
Hill	1	26		45		18		18		5		6		7		10	2	17	12		
	2	98		73		31		31		8		6		24		25		8	4	10	7
	3	72		77		58		58		6	1	6		8		4		2		2	2
	4	72		60		64		64		21		30		67	1	20		27		13	14
	5	90		48		61		61		16		23		51		44					
Bank	1			33	210	19	28	19	28	10	4	12	10	24	1	58		32	10	39	26
	2	5		20	9	9	2	9	2	5	1	38	4	1		11		1	10		
	3	80		32	95	66	14	66	14	7	1		1	7	3	35		3	26	1	6
	4	56		88	32	62	9	62	9	1		21				107			65		3
	5	8		241		164	1	164	1	50		27									13
Hills 1	1	96		72		39		39		36	2	29		64		70		67		28	
	2	161		124		75		75		68	7	59		91		91		68		22	
	3	251		186		164		164		58	1	67		136		135		58		17	6
	4	202		137		105		105		31	1	34		68		89		63		12	
	5	138		93		74		74		42	1	32		57		93		90		60	2
Hills 2	1	24		62		14		14		8	1	8		7		20		18		8	1
	2	51		69		42		42		28	4	20		55		20		50		24	1
	3	20		25		20		20		17	2	12		28		24		25		9	
	4			30		34		34		22	3	12		21		21		30		9	7
	5	20		17		10		10		10		6		18		6				9	6

Appendix 1

(i) Tests from marksmen's quadrats 1985-86

Field	Quadrat	Oct V.a.	Oct Ass.	Nov V.a.	Nov Ass	Dec	Jan	Feb	Mar	Apr V.a.	Apr Ass.	A	May F	June A	June F	July A	July F	C
Hill a	1	48	59	77		69	51	35	13	13	8	23		23	3			
	2	20	39	21		27	16	9	3	3	0	8		12		11	1	
	3	31	47	88		58	45	22	16	6	10	22		14		1	2	
	4	136	67	271		255	212	88	39	42	34	58		41		13	5	
	5	92	58	229		196	158	66	13	21	30	47						
	6			31	123	50	32	29	28	19	20	20		24		25	3	
	7			88	15	57	33	22	16	17	26	24		28		3	24	
	8			154	66	127	119	69	52	29	20	43		9		25	16	
	9			20	21	11	9	6	2	4	11	9		8		6	7	
	10			5	9	2	1			1	11	1						
Hill b	1	498	110	458		448	340	282	133	86	7	83	1	57	7	31	12	
	2	184	66	334		240	231	184	100	54	14	73	4	67	15	48	34	1
	3	30	42	30		26	16	13	2	4		22		5			1	
	4	22	59	58		64	55	31	16	28	20	37		21	2	3	2	
	5	41	58	175		135	145	41	62	39	1	37		30				
	6			7	3	6	6	1		2	5	6				1	1	
	7			32	33	25	34	11	18	13	17	14		28	1	21	9	
	8			40	6	39	17	15	10	14	23	19						
	9			57	5	61	50	44	20	26	14	41		48	2	34	1	
	10			32	7	16	33	9	11	13	9	23		30	13	16	24	
Jervis	1			17		25	48	23	2	6		53		78		48	9	
	2			44		47	43	25	1	24	1	46		46		30	16	
	3			20		26	30	14		5	1	21		28		18	7	
	4			23		16	21	9		9		17		23		23	14	
	5			54		33	12	7		12		41		70		37	2	
	6			12		17	19	15	1			11				24	8	
	7			6		5	9	1				15		42		24	8	
	8			19		11	10	3		4		12		28		6	1	
	9			2		2		7				3		8				
	10			6		3	5	7		1		3		2				
Tunstall	1			98	16	157	137	146	148	134	240	114		44	74			
	2			129	65	253	184	193	124	192	352	174		84	11	65	66	
	3			39	21	143	148	118	76	130	195	67		38	7	21	9	
	4			53	38	117	113	117	80	97	176	71		35	10	32	13	
	5			76	10	143	122	98	72	66	97	53		33	2	20	13	
	6			71	134	118	111	93	67	74	188	53		44	14	16	44	
	7			112	177	124	105	107	98	127	158	63		35	15	17	34	
	8			141	92	159	178	167	117	121	119	68		43	10	6	68	
	9			38	36	23	14	14	12	17	23	13		11	1	1	4	
	10			15	31	14	9	4	4	9	18	3		3	1	1	4	
Wood	1		6							1	8	1		8				
	2		1	136		157	122	69	70	210	24	493		127		34	34	
	3		4	2						48	7	2						
	4		1	1						488	3	40		86		5	4	
	5		5	8						74	8	63		53		3	8	
	6			63	15	44	7	4	4	28	8	63		25		3	2	
	7			23	41	11	2	1		54	11	47		15		3	1	
	8			5	4	1				14	11	20		29		5	3	
	9			38	26	14				121	230	102		22		3	3	
	10			11	55	3	5	4	4	21	42	43		10				
Sandy	1			71		276	275	194	12	91	178	178		134	9	72	72	
	2			93		222	148	153	10	91	178	153		115	6	72	22	
	3			96		131	155	130	45	121	14	233		171	2	185	10	
	4			15		29	17	17	3	4		17		17		4		
	5			11		11	20	4	3	21		40		28		12		
	6			240	4	298	319	217	30	118	1	252		228		298	7	
	7			125	1	112	97	90	10	96		85		88		61		
	8			109	5	162	137	73	9	58	5	115		102		58		
	9			116	4	148	110	77	9	58		137		101		23		
	10			351	60	525	468	378	265	448	156	369		152	40	21	121	

Appendix 1

d] Fields monitoring V.arvensis and L.purpureum

Field	Quadrat	Dec				Jan			Feb		Mar			Apr			May				June				July		
		V.a.	L.p.		Ass.	V.a.	L.p.		V.a	L.p	V.a.	L.p.	Ass.	V.a.	L.p.		V.a.		L.p.		V.a.		L.p.		V.a.		L.p
		A	A	F		A	A	F	A	A	A	A		A	A	F	A	F	A	F	A	F	A	F	A	F	F
Bank	1		11	9		10	12	13	11		11		80	7		12	2	1		11	1	7	10s	1		8	
	2	15	40	40		21	22	55	24		24	9	47	20	20	1	18		7	15	3	1	20		4		
	3	13	24	31		13	11	26	13		10	9	30	14	4	1	18		1	6	11	11	5s		4	18	
	4	24	18	23		16	24	21	19		9	3	22	2	1	1	15	6		1	13	4	1s		3(1)	14	
	5	11	6	24		26	19	10	9		11	3	30	12	2		17	6				9	1		4(1)	9	
	6	30	2	14		39	8	4	36		22	2	30	16	1	2	20	5		2	2	12		2	11	3	1s
	7	25	4	11		16	8	6	19		8	2	15	21	2		20	5	1	1	9	4		1	12	1	
	8	16	2	5		21	4	2	19		6		10	7	1		14	3		1	6	7		1	8	5	
	9	33	5	2		28	5	5	23		13	1	30	2	10		8	4		2	1	9		1	8	2	
	10	17	1	2		19	2		4			?	13				1				1				2	3	
Tunstall	1	208		5	227	213	6		205	5	153	3	246	114	3		37			1	13	13			11	15	
	2	187		9	201	232	5		192	7	172	6	241	152	9		131			8	19	44	7		37	4	
	3	274		16	222	349	21		287	17	278	17	217	235	18		52			26	30	91			52	69	1s
	4	226		41	284	210	38		161	34	138	35	302	83	24		75			18	13	61	2		35	39	
	5	225		41	202	201	56		157	43	174	48	350	138	49		99			16	13	28	4		25	16	
	6	169		37	115	194	42		189	33	161	39	197	128	33		96			15	19	53			20	52	
	7	206		21	102	194	27		193	27	184	21	165	169	22		?			?	28	20	?		7	41	
	8	342		8	95	309	9		298	10	298	9	201	278	4		212			5	25	107	1		56	76	
	9	220		2	172	219	4		180	2	208	2	248	172	1		135			2	15	91			55	51	
	10	207		3	130	178	3		101	2	169	2	234	117	2		41			2	3	29			20	3	

e) Oilseed rape fields.

Field	Quadrat	Nov			Dec	Jan		Feb		Mar			Apr			May		June		July	
		V.a.	L.p.	Ass.	V.a.	V.a.	L.p.	V.a.	L.p.	V.a.	L.p.	V.a.	L.p.	Ass.	V.a.			V.a.		V.a.	
															A	F		A	F	A	F
Canal	1	236		55	203	203		151		135		96		8	21	50		2	69	8	63
	2	204		98	226	266		191		149		153		15	22	76		4	94	1	97
	3	263		150	191	241		158		107		105		5	16	73			89		89
	4	222	1	180	155	197		132		116	1	135	1	3	3	72			75		75
	5	202		54	155	188		98		47		51		2		36			36		
Shebdon	1	61		145	61	54		50		31		20		25	16	6		10	12	1	21
	2	114		58	86	103		78		44		37		15	16	10		4	22		26
	3	54		34	30	39		21		5		1		7							
	4	57		25	46	47	1	25	1	16		9		19	7	3		2	8		1
	5	120		37	117	108		55		5		6		25	2			8			8
Eaches	1	50		25	24	36		25		13		8		2	17	2		2	13	5	10
	2	57		25	36	45		20		14		15		29	16	3		7	16	5	18
	3	51		8	21	39		17		9		8		1	16	4		3	12	1	14
	4	160		85	81	109		43		23		32		24	90	4		46	9	29	26
	5	70		18	43	41		23		19		22		3	16	6		5	14	5	14
Bank	1	35		8	24	17		12		4		7		3	8	1		1	3	3	2
	2	13		10	12	13		7		5		3		6	3	1		2	4	6	4
	3	25		6	15	23		10		6		20		3	31	2		15	4	20	4
	4	11		4	5	7		5		1		3		1	4			3	3	4	3
	5	9		5	6	5		1		2		1		4	3			4	5	5	9

Appendix 2

Weather data

		Ground frost (days)	Rf (mm)	snow (days)	Air temp range (°C)	Mean soil temp at 10cm (°C)	Sunshine (hrs)	Mean air temp (°C)
	May	9	50.0	0	8.6	12.5	168.8	9.6
	June	0	52.9	0	8.3	16.4	144.3	13.5
	July	0	24.7	0	10.1	19.2	226.2	15.9
1984	Oct	4	60.8	0	6.8	10.3	79.4	10.2
	Nov	5	135.0	0	4.8	6.9	40.7	7.0
	Dec	20	49.6	0	5.1	4.1	45.9	4.2
	Jan	30	43.9	17	5.2	0.5	30.6	0.2
	Feb	22	11.5	14	4.9	1.9	75.5	1.8
	Mar	25	43.7	2	5.7	3.8	90.1	3.8
	Apr	10	89.1	0	7.1	8.2	110.8	7.3
1985	May	2	79.4	0	7.5	11.8	159.6	10.2
	June	1	110.2	0	7.7	14.6	148.5	11.5
	July	0	54.3	0	7.3	17.6	157.0	15.2
	Oct	3	50.7	0	5.4	10.6	81.1	10.3
	Nov	20	83.7	8	5.2	3.6	60.3	3.2
	Dec	13	79.6	0	4.6	5.1	30.6	5.2
	Jan	23	95.0	11	4.8	1.3	56.3	2.4
	Feb	26	2.0	5	4.0	-0.5	75.2	-1.1
1986	Mar	22	65.3	1	5.5	3.3	101.8	4.7
	Apr		92.6	0	7.0	5.7	101.8	5.0
	May	6	62.5	0	7.3	10.9	158.9	10.2
	June	2	61.1	0	8.4	15.6	143.3	14.0
	July	0	72.5	0	7.4	17.1	129.6	14.5

Appendix 3

Variation between fields and quadrats of the seedbank of V.arvensis.

(Values are number of seeds per core).

Field		Quadrat	Replicate				
			1	2	3	4	5
1	Hill	1	0	0	0	3	0
		2	1	0	1	0	1
		3	0	0	0	2	4
		4	0	1	0	0	0
		5	0	0	0	0	0
2	Mills 1	1	8	5	22	4	6
		2	8	1	14	13	3
		3	15	9	11	9	6
		4	6	5	5	50	16
		5	7	10	12	6	5
3	2	1	2	0	3	3	1
		2	3	4	7	9	10
		3	2	10	6	5	4
		4	4	11	0	15	2
		5	1	1	1	1	10
4	Sandy	1	13	0	10	17	0
		2	17	4	5	6	3
		3	1	0	2	0	0
		4	0	5	0	10	4
		5	5	0	0	0	1
5	Bull	1	0	1	0	0	0
		2	0	1	2	4	1
		3	1	4	2	0	0
		4	3	1	2	11	0
		5	2	9	1	14	0
6	Eaches	1	0	0	0	0	0
		2	0	0	0	0	7
		3	2	7	2	0	0
		4	0	0	1	0	1
		5	1	0	1	5	0
7	Sheldon	1	2	2	4	2	1
		2	7	1	0	0	2
		3	1	0	0	0	0
		4	2	0	0	0	0
		5	0	0	0	0	1

	Field	Quadrat	Replicate				
			1	2	3	4	5
8	Wood	1	1	1	0	0	0
		2	20	3	1	0	4
		3	0	1	2	0	0
		4	0	0	0	2	0
		5	0	0	0	0	0
9	Canal	1	3	11	5	2	2
		2	4	6	2	5	2
		3	10	4	4	5	1
		4	7	5	11	9	9
		5	18	8	16	1	7
10	Bank	1	1	1	0	1	0
		2	1	0	0	0	0
		3	0	0	1	2	1
		4	2	3	0	0	0
		5	1	1	0	1	0
11	Jervis	1	0	0	0	0	3
		2	1	1	0	0	0
		3	0	0	0	1	0
		4	0	0	1	0	0
		5	2	0	0	0	0

Nested Anova for variation in the seedbank between replicate cores within fields for V.arvensis

Level	Sums of squares	D.F.	Mean square	F.ratio
Fields	2419.7	12	201.64	9.3655
Quadrats	939.9	43	21.857	1.2903 NS
		47.8	21.531	
Cores	3726.8	220	16.94	

$p < 0.001$

Appendix 4

Field crop history since 1978 and the mean seedbank per m^2

Field		1978	1979	1980	1981	1982	1983	1984	1985	Mean seedbank per m^2
Hough		Sp.B.	S.B.	Sp.B.	O.	O.	W.W.			104
Bullfield		S.B	Sp.B.	W.B.	S.B.	Sp.B.	W.B.	W.B.	S.B.	1248
Knighton		O.	O.	W.B.	S.B.	Sp.B.	W.B.			416
Sandy		W.B.	O.	O.	W.B.	S.B.	W.B.	W.B.*	W.W.	2704
Woodfield		W.B.	O.	O.	W.B.	W.B.	W.W.	W.B.*	W.W.	104
Western Meadow		O.	O.	O.	W.B.	W.B.	W.W.			156
Crows Nest		Sp.B.	peas	Sp.B.	Sp.B.	W.B.	W.B.			416
Horse Pasture		S.B.	Sp.B.	Sp.B.	Sp.B.	W.B.	W.B.			156
Simkin (Winter cereals for last 20 years)	1		Sp.Oats	W.W.*	W.B.*	OSR.*	W.W.*			260
	2		S.B.*	Sp.Oats	W.W.*	W.W.*	W.B.*			52
	3		Sp.Oats	W.W.*	W.B.*	OSR*	W.W.*			104
	4		W.B.*	Sp.B.*	Sp.Oats	W.W.*	W.W.*			52
Mills (1st winter cereals 1980)	1		Sp.B.'	Sp.B.*	S.B.*	Sp.B.'	W.B.*			3702
	2		Sp.B.'	Sp.B.*	S.B.*	Sp.B.'	W.B.*			2652
	3		O.*	Sp.B.*	S.B.*	Sp.B.'	W.B.*			2756
	4		O.*	Sp.B.*	S.B.*	Sp.B.'	W.B.*			4212
Warrington	1	O.	O.	O.	O.	W.W.	W.W.*			156
	2	O.	O.	O.	O.	O.	W.W.*			0
	3	O.	O.	O.	O.	O.	W.W*			0
Wain	1	O.	O.	W.W.	W.W.	W.W.*	W.B.*			0
	2	O.	O.	W.W.	W.B.	W.B.*	W.B.*			205
	3	O.	Sp.B.	O.	O.	O.	W.W.			2288
Edwards (1st winter cereals 1980)	5			Potatoes	W.W.	W.W.	OSR			0
	6			W.W.	W.B.	OSR	W.W.			0
	7			W.W.	W.W.	W.B.	OSR			0
Braith.	1	W.B.	S.B.	Sp.B.	W.W.	W.W.	W.W.*	W.B.		52
	2			S.B.	Sp.B.	W.W.	W.W.*	W.B.		52
Ramsden 1969	2			W.W./W.B.	W.W.	W.W.	peas /W.B.	W.W. /W.B.		4576
1st Winter cereals 1970	5			W.B.	peas	W.W.	W.B.	W.B.*		0
1985	6			W.W.	peas	W.W.	W.B.	W.B.*		0
	7			W.B.	peas	W.W.	W.B.	W.B.*		468

Appendix 4

Field crop history since 1978 and the mean seedbank per m^2

Field		1978	1979	1980	1981	1982	1983	1984	1985	Mean seedbank per m^2
Millfield		1st Winter			W.W.	potatoes	W.W.	W.B.	OSR	5326
Bank		cereals in			W.B.	W.B.	W.B.	W.B.	OSR	1591
Eachen		1965		W.B.	potatoes	W.W.	W.W.	W.B.	OSR	117
Tunstall		1952		"	W.W.	W.W.	W.W.	OSR	W.W.	4767
Mills (1st winter cereals 1980)	5					W.B.	W.B.	W.B.	S.B.	13100
	6					W.B.	S.B.	W.B.	S.B.	11309
Jervis	1	G.	G.	G.	G.	G.	G.	W.B.*	G.	0
	2	G.	G.	G.	G.	G.	G.	W.W.*	W.W.*	0
	3	G.	G.	G.	G.	W.W.	W.W.	W.B.*	W.B.*	0
	5	W.W.*	W.W.*	S.B.*	W.B.*	W.B.*	S.B.*	S.B.*	S.B.*	752
Hill		W.C.	W.C.	Sp.B.	Sp.B.	Sp.B.	W.C.*	W.C.*	W.C.*	1182

Key

G. Grass
OSR Oilseed Rape
S.B. Sugar Beet
Sp.B. Spring Barley
W.B. Winter Barley
W.C. Winter Cereals
W.W. Winter Wheat
* Herbicide application

Appendix 5

Total annual emergence per m^2 of *V. arvensis*.

Field	Quadrat	Total emergence	Mean total emergence per m^2
1984-85			
Jervis	1	36	
	2	25	
	3	56	
	4	67	
	5	40	44.8
Hill	1	76	
	2	39	
	3	135	
	4	266	
	5	22	107.6
Bullfield	1	17	
	2	1121	
	3	294	
	4	340	
	5	463	447.0
Sandy	1	842	
	2	705	
	3	170	
	4	110	
	5	10	367.4
Woodfield	1	202	
	2	142	
	3	204	
	4	268	
	5	141	191.4
Canal	1	305	
	2	192	
	3	350	
	4	538	
	5	432	363.4
Shebdon	1	468	
	2	344	
	3	165	
	4	100	
	5	97	234.8

Field	Quadrat	Total emergence per m^2	Mean total emergence per m^2
Millfield	1	69	
	2	142	
	3	80	
	4	131	
	5	164	117.2
Bank	1	85	
	2	40	
	3	145	
	4	143	
	5	387	160.0
Mills a	1	144	
	2	199	
	3	320	
	4	269	
	5	241	234.6
Mills b	1	43	
	2	132	
	3	78	
	4	129	
	5	61	88.6
1985–86			
Canal	1	236	
	2	266	
	3	313	
	4	283	
	5	239	267.4
Shebdon	1	63	
	2	131	
	3	63	
	4	59	
	5	127	88.6
Eaches	1	73	
	2	75	
	3	81	
	4	259	
	5	73	112.2
Bank a	1	41	
	2	21	
	3	65	
	4	19	
	5	23	33.8

Field	Quadrat	Total emergence per m^2	Mean total emergence per m^2
Bank b	1	16	
	2	24	
	3	25	
	4	47	
	5	41	
	6	48	
	7	45	
	8	27	
	9	43	
	10	24	34.0
Tunstall	1	213	
	2	232	
	3	418	
	4	226	
	5	225	
	6	194	
	7	206	
	8	342	
	9	220	
	10	223	249.9
Hill a	1	92	
	2	40	
	3	110	
	4	193	
	5	343	
	6	90	
	7	98	
	8	170	
	9	34	
	10	6	117.6
Hill b	1	498	
	2	308	
	3	60	
	4	84	
	5	206	
	6	14	
	7	61	
	8	109	
	9	102	
	10	77	151.9

Field	Quadrat	Total emergence per m^2	Mean total emergence per m^2
Woodfield	1	6	
	2	551	
	3	58	
	4	447	
	5	84	
	6	270	
	7	77	
	8	33	
	9	159	
	10	449	213.4
Sandy	1	446	
	2	360	
	3	403	
	4	66	
	5	57	
	6	532	
	7	200	
	8	269	
	9	280	
	10	716	332.9
Jervis	1	123	
	2	124	
	3	59	
	4	75	
	5	144	
	6	28	
	7	52	
	8	55	
	9	12	
	10	11	68.3
Tunstall	1	168	
	2	389	
	3	162	
	4	127	
	5	143	
	6	137	
	7	178	
	8	191	
	9	46	
	10	19	156.0

Millfield	1	69	
	2	142	
	3	80	
	4	131	
	5	164	117.2
Bank	1	85	
	2	40	
	3	145	
	4	143	
	5	387	160.0
Mills a	1	144	
	2	199	
	3	320	
	4	269	
	5	241	234.6
Mills b	1	43	
	2	132	
	3	78	
	4	129	
	5	61	88.6
1985-86			
Canal	1	236	
	2	266	
	3	313	
	4	283	
	5	239	267.4
Shebdon	1	63	
	2	131	
	3	63	
	4	59	
	5	127	88.6
Eaches	1	73	
	2	75	
	3	81	
	4	259	
	5	73	112.2
Bank a	1	41	
	2	21	
	3	65	
	4	19	
	5	23	33.8

Bank b	1	16	
	2	24	
	3	25	
	4	47	
	5	41	
	6	48	
	7	45	
	8	27	
	9	43	
	10	24	34.0
Tunstall	1	213	
	2	232	
	3	418	
	4	226	
	5	225	
	6	194	
	7	206	
	8	342	
	9	220	
	10	223	249.9
Hill a	1	92	
	2	40	
	3	110	
	4	193	
	5	343	
	6	90	
	7	98	
	8	170	
	9	34	
	10	6	117.6
Hill b	1	498	
	2	308	
	3	60	
	4	84	
	5	206	
	6	14	
	7	61	
	8	109	
	9	102	
	10	77	151.9

Woodfield	1	6	
	2	551	
	3	58	
	4	447	
	5	84	
	6	270	
	7	77	
	8	33	
	9	159	
	10	449	213.4
Sandy	1	446	
	2	360	
	3	403	
	4	66	
	5	57	
	6	532	
	7	200	
	8	269	
	9	280	
	10	716	332.9
Jervis	1	123	
	2	124	
	3	59	
	4	75	
	5	144	
	6	28	
	7	52	
	8	55	
	9	12	
	10	11	68.3
Tunstall	1	168	
	2	389	
	3	162	
	4	127	
	5	143	
	6	137	
	7	178	
	8	191	
	9	46	
	10	19	156.0

Appendix 6

A. Two-way ANOVA of the effect on nitrate on germination in the light and in darkness for L.purpureum (arcsine transformed proportions).

Table of mean values.

Darkness + water	16.65
Darkness + nitrate	33.5
Light + water	27.25
Light + nitrate	49.5
Darkness	25.075
Light	38.55
Water	21.95
Nitrate	41.675

Source	Sums of squares	D.F.	Mean square	F-ratio
Rows	363.1523	1	363.15	94.985***
Columns	778.1523	1	778.15	203.532***
Interaction	16.5273	1	16.52	4.323 NS
Subtotal	1157.832	3		
Within	15.293	4	3.8232	
Total	1173.125			

B) Two-way ANOVA of the effect of nitrate on germination in the light and in darkess for V.arvensis (arcsine transformed proportions).

Table of mean values.

Darkness + water	45.88
Darkness + nitrate	69.85
Light + water	22.45
Light + nitrate	55.88
Darkness	57.86
Light	39.16
Water	34.16
Nitrate	62.86

Source	Sums of squares	D.F	Mean Square	F-Ratio
Rows	1398.78	1	1398.78	97.927***
Columns	3294.78	1	3294.78	230.665**
Interaction	89.30	1	89.3	6.252
Subtotal	4782.8594	3		
Within	171.4063	12		
Total	4954.2656	15		

Appendix 7a

Emergence from three soil types of V.arvensis

(Arcsine transformed proportions)

The Seedbank consisted of 1000 seeds per replicate

Date	Soil type	Replicates						Mean	CL
		1	2	3	4	5	6		
27/9	Sand	10.6	18.6	16.5	21.0	15.5	17.0	16.7	3.9
	Clay	20	22.2	21.4	21.0	25.5	21.5	21.9	1.9
	Intermediate	11.4	13.6	6.8	14.7	3.6	15.3	10.9	4.7
21/10	Sand	5.1	6.8	3.6	6.5	7.5	5.7	5.9	1.4
	Clay	5.4	10.3	6.8	9.6	4.4	12.7	8.2	3.2
	Intermediate	7.3	7.5	5.1	8.5	5.7	7.0	6.9	1.2
2/12	Sand	0	2.6	0	2.6	0	0	1.8	1.8
	Clay	1.3	0	0	0	1.3	0	0.8	1.0
	Intermediate	0	0	0	2.6	0	1.3	1.1	1.8
9/4	Sand	6.5	8.7	5.1	6.8	6.3	5.1	6.4	1.3
	Clay	2.6	3.1	3.1	1.1	4.4	3.1	3.4	0.7
	Intermediate	1.8	3.1	2.6	3.6	1.8	3.1	2.7	0.7
6/5	Sand	5.1	6.0	5.6	5.6	5.3	3.5	5.2	0.9
	Clay	5.9	4.9	5.5	4.0	5.1	5.1	5.1	0.6
	Intermediate	2.3	4.9	4.2	4.0	4.0	5.1	4.1	1.0
3/6	Sand	2.3	1.9	1.9	1.3	0	0	1.2	1.0
	Clay	4.2	3.0	4.6	2.3	1.9	4.1	3.4	1.1
7	Sand	0	0	1.9	0	3.9	0	2.2	1.6
	Clay	2.8	3.6	4.5	2.0	0	0	1.0	1.6
	Intermediate	1.9	3.9	4.2	3.4	3.8	2.8	3.3	0.8
8	Sand	5.4	5.4	1.9	5.0	0	2.7	3.4	1.7
	Clay	3.4	4.1	2.0	4.1	2.1	0	2.6	1.3
	Intermediate	0	3.3	0	2.0	1.9	2.8	1.7	1.1

No emergence in January, February or March

Appendix 7b

Analysis of variance for emergence from three soil types of Viola arvensis.

September

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	20.8	11.4	18.6	22.2	13.6	18.6	98.4
row 2	6.8	16.5	21.4	14.7	21.0	21.0	101.4
row 3	15.5	25.5	3.6	17.0	21.5	15.3	98.4
tots	96.2	109.5	98.5				296.2

tots s	99.2	C.T.=	4874.1	
total	65.4	block1tot	131.3	
C	131.6	block2tot	164.9	

	SS	CSS	DF	MS	F
blocks	44431.7	62.7	1.0	62.7	4.0
cols	29434.9	31.7	4.0	7.9	0.5
rows	29257.5	2.1	4.0	0.5	0.0
tms	31430.4	365.3	2.0	182.6	11.7
error		93.5	6.0	15.6	
total	5429.4	555.3	17.0	XMS'	

October

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	5.4	7.3	5.1	10.3	7.5	6.8	42.4
row 2	5.1	3.6	6.8	8.5	6.5	9.4	40.1
row 3	7.5	4.4	5.7	5.7	12.7	7.0	43.0
tots	42.5	42.0	41.0				125.5

tots s	35.2	C.T.=	875.0	
total	41.1	block1tot	50.9	
C	49.2	block2tot	74.6	

	SS	CSS	DF	MS	F
blocks	8156.0	31.2	1.0	31.2	5.2
cols	5251.3	0.2	4.0	0.0	0.0
rows	5254.0	0.8	4.0	0.2	0.0
tms	5348.1	16.5	2.0	8.2	1.4
error		36.1	6.0	6.0	
total	959.8	84.8	17.0	XMS'	

December

	block 1 col1	col2	col3	block 2 col1	col2	col3	tot s
row 1	1.3	0.0	0.0	0.0	0.0	2.6	3.9
row 2	0.0	0.0	0.0	0.0	2.6	0.0	2.6
row 3	0.0	1.3	1.3	0.0	0.0	0.0	2.6
tots	1.3	3.9	3.9				9.1

tots s	5.2	C.T.=	4.6	
total	1.3	block1tot	3.9	
C	2.6	block2tot	5.2	

	SS	CSS	DF	MS	F
blocks	42.3	0.1	1.0	0.1	0.0
cols	32.1	0.0	4.0	0.2	0.1
rows	28.7	0.2	4.0	0.0	0.0
tms	35.5	1.3	2.0	0.7	0.3
error		11.6	6.0	1.9	
total	18.6	14.0	17.0	XMS'	

April

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	2.6	1.8	6.5	3.1	3.1	8.7	25.8
row 2	2.6	5.1	3.1	3.6	6.8	4.1	25.3
row 3	6.3	4.4	1.8	5.1	3.1	3.1	23.8
tots	23.3	24.3	27.3				74.9

tmts s	38.5	C.T.=	311.7	
totsI	16.0	block1tot	34.2	
C	20.4	block2tot	40.7	

	SS	CSS	DF	MS	F
blocks	2826.1	2.3	1.0	2.3	1.4
cols	1870.7	1.4	4.0	0.4	0.2
rows	1872.2	0.4	4.0	0.1	0.1
tms	2154.4	47.4	2.0	23.7	14.4
error		9.8	6.0	1.6	
total	373.1	61.4	17.0	EMS'	

May

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	5.9	2.3	5.1	4.9	4.9	6.0	29.1
row 2	4.2	5.1	5.5	4.0	5.6	4.0	28.4
row 3	5.3	5.1	4.0	3.5	5.1	5.1	28.1
tots	27.8	28.1	29.7				85.6

tmts s	30.6	C.T.=	407.1	
totsI	24.5	block1tot	42.5	
C	30.5	block2tot	43.1	

	SS	CSS	DF	MS	F
blocks	3663.9	0.0	1.0	0.0	0.0
cols	2444.5	0.3	4.0	0.1	0.1
rows	2443.0	0.1	4.0	0.0	0.0
tms	2466.9	4.1	2.0	2.0	1.2
error		10.2	6.0	1.7	
total	421.8	14.7	17.0	EMS'	

June

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
1	4.2	3.2	2.3	3.0	3.0	1.9	
row 2	4.3	1.9	4.6	3.8	1.3	2.3	1
row 3	0.0	1.9	6.2	0.0	4.1	3.0	15.
tots	15.3	15.4	20.3				51.

tmts s	7.4	C.T.=	144.5	
totsI	23.5	block1tot	28.6	
C	20.1	block2tot	22.4	

	SS	CSS	DF	MS	F
blocks	1319.7	2.1	1.0	2.1	1.0
cols	883.3	2.7	4.0	0.7	0.3
rows	872.0	0.8	4.0	0.2	0.1
tms	1011.0	24.0	2.0	12.0	5.5
error		13.1	6.0	2.2	
total	187.3	42.8	17.0	EMS'	

July

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	3.8	1.9	0.0	3.6	3.9	0.0	12.2
row 2	4.2	1.9	4.5	3.4	0.0	2.0	16.0
row 3	3.9	0.0	3.8	0.0	0.0	2.8	10.5
tots	17.9	7.7	13.1				38.7

tmts s	5.8	C.T.=	83.2
total	20.0	block1tot	23.0
C	13.9	block2tot	15.7

	SS	CSS	DF	MS	F
blocks	775.5	3.0	1.0	3.0	0.9
cols	551.3	8.7	4.0	2.2	0.7
rows	515.1	2.6	4.0	0.7	0.2
tms	600.1	16.8	2.0	8.4	2.5
error		19.9	6.0	3.3	
total	134.2	51.0	17.0	EMS'	

August

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	3.4	0.0	5.4	4.1	3.3	5.4	21.6
row 2	0.0	1.9	2.0	2.9	5.0	4.1	15.0
row 3	0.0	2.1	1.9	2.7	0.0	2.9	9.6
tots	12.2	12.3	21.7				46.2

tmts s	28.4	C.T.=	118.6
total	10.1	block1tot	16.7
C	15.7	block2tot	29.5

	SS	CSS	DF	MS	F
blocks	1149.1	9.1	1.0	9.1	3.4
cols	771.0	9.9	4.0	2.5	0.9
rows	783.7	12.0	4.0	3.0	1.1
tms	764.7	8.9	2.0	4.4	1.6
error		16.2	6.0	2.7	
total	174.7	56.1	17.0	EMS'	

Total

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	45.6	27.9	35.0	51.2	39.3	50.0	249.0
row 2	37.2	36.5	47.9	40.0	48.8	47.1	
row 3	38.5	44.7	37.4	34.8	46.5	39.	
tots	236.5	241.7	246.6				

tmts s	242.8	C.T.=	29346.8
total	201.0	block1tot	330.7
C	283.8	block2tot	396.1

	SS	CSS	DF	MS	F
blocks	266257.7	237.6	1.0	237.6	6.7
cols	176133.5	9.0	4.0	2.3	0.1
rows	176295.3	38.8	4.0	9.6	0.3
tms	179441.8	560.4	2.0	280.2	8.9
error		211.4	6.0	35.2	
total	30401.0	1054.5	17.0	EMS'	

Appendix 8a

Emergence from three soil types of L. purpureum

(Arcsine transformed proportions)

The Seedbank consisted of 1000 seeds per replicate

Date	Soil type	Replicates						Mean	CL
		1	2	3	4	5	6		
27/9	Sand	4.4	6.5	16.2	7.5	13.8	10.6	9.8	4.7
	Clay	0	1.8	2.6	0	0	0	0.7	0.7
	Intermediate	3.1	1.8	2.6	0	2.6	3.1	2.2	2.3
6/5	Sand	1.8	0	0	0	0	0	0.3	0.8
	Clay	0	0	0	0	0	0	0	0
	Intermediate	0	0	0	0	0	0	0	0
3/6	Sand	1.8	3.6	2.7	4.8	1.9	0	2.5	1.7
	Clay	0	0	0	1.8	0	0	0.3	0.8
	Intermediate	1.8	1.8	0	0	0	0	0.6	0.9
7	Sand	0	5.5	5.7	9.4	5.0	6.2	5.3	2.5
	Clay	0	0	0	2.6	0	0	0.4	0.9
	Intermediate	2.6	1.8	0	0	0	0	0.7	1.0
8	Sand	3.6	5.8	5.1	8.0	6.5	7.7	5.5	1.3
	Clay	0	0	1.8	3.1	1.8	1.8	1.5	1.0
	Intermediate	1.8	1.8	0	0	0	2.6	1.0	1.0

Appendix 8b

Analysis of variance for emergence from three soil types of Lamium purpureum.

October

	block 1			block 2			
	col1	col2	col3	col1	col2	col3	tots
row 1	4.4	3.1	8.0	6.5	1.8	1.8	17.6
row 2	3.6	2.6	16.2	0.0	0.0	7.5	28.9
row 3	0.0	13.8	2.6	0.0	10.6	3.1	30.1
tots	13.5	31.9	31.2				76.6

tmts	A	59.0	C.T.=	326.0
tmts	I	13.2	block1tot	45.3
	C	4.4	block2tot	31.3

	SS	CSS	DF	MS	F
blocks	3031.8	10.9	1.0	10.9	1.2
cols	3173.3	36.2	4.0	9.1	1.0
rows	3051.0	15.9	4.0	4.0	0.4
tms	3674.6	286.5	2.0	143.2	16.0
error		53.7	6.0	8.9	
total	729.1	403.1	17.0	RMS*	

May

	block 1			block 2			
	col1	col2	col3	col1	col2	col3	tots
row 1	1.8	0.0	0.0	0.0	0.0	0.0	1.8
row 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
row 3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
tots	1.8	0.0	0.0				1.8

tmts A	1.8	C.T.=	0.2	
total	0.0	block1tot	1.8	
C	0.0	block2tot	0.0	

	SS	CSS	DF	MS	F
blocks	3.2	0.2	1.0	0.2	0.6
cols	3.2	0.4	4.0	0.1	0.3
rows	3.2	0.4	4.0	0.1	0.3
tms	3.2	0.4	2.0	0.2	0.6
error		1.8	6.0	0.3	
total	3.2	3.1	17.0	RMS*	

June

	block 1			block 2			
	col1	col2	col3	col1	col2	col3	tots
row 1	1.8	1.8	0.0	3.6	1.8	0.0	9.0
row 2	0.0	0.0	2.7	0.0	1.8	4.8	9.3
row 3	0.0	1.9	0.0	0.0	0.0	0.0	1.9
tots	5.4	7.3	7.5				20.2

tmts A	14.8	C.T.=	22.7	
total	3.6	block1tot	8.2	
C	1.8	block2tot	12.8	

	SS	CSS	DF	MS	F
blocks	211.2	0.8	1.0	0.8	0.4
cols	138.7	0.4	4.0	0.1	0.0
rows	171.1	5.8	4.0	1.5	0.6
tms	235.2	16.5	2.0	8.3	3.7
error		13.6	6.0	2.3	
total	59.9	37.3	17.0	RMS*	

July

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	0.0	2.6	0.0	5.5	1.0	0.0	9.0
row 2	0.0	0.0	5.7	0.0	2.6	9.4	17.7
row 3	0.0	5.0	0.0	0.0	6.2	0.0	11.2
tots	5.5	10.2	15.1				38.0

tots s	31.8	C.T.=	83.6	
total	4.4	block1tot	13.3	
C	2.6	block2tot	39.5	

	SS	CSS	DF	MS	F
blocks	827.1	8.3	1.0	8.3	1.7
cols	589.5	14.6	4.0	3.7	0.7
rows	536.7	5.0	4.0	1.5	0.3
tms	1037.4	89.3	3.0	44.6	9.0
error		29.7	6.0	5.0	
total	231.3	147.7	17.0	EMS'	

August

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	3.6	1.8	0.0	5.8	1.8	0.0	13.0
row 2	0.0	1.8	5.1	0.0	3.1	8.0	18.0
row 3	1.8	6.5	0.0	1.8	3.7	2.6	16.4
tots	13.0	10.7	15.7				47.4

tots s	32.7	C.T.=	124.8	
total	6.2	block1tot	30.6	
C	8.5	block2tot	26.8	

	SS	CSS	DF	MS	F
blocks	1142.6	2.1	1.0	2.1	0.6
cols	763.2	2.7	4.0	0.7	0.2
rows	762.6	2.2	4.0	0.5	0.2
tms	1180.0	71.8	3.0	35.9	10.1
error		21.4	6.0	3.6	
total	225.1	100.3	17.0	EMS'	

Total

	block 1 col1	col2	col3	block 2 col1	col2	col3	tots
row 1	11.6	9.3	8.0	21.4	7.2	1.8	51.3
row 2	2.6	4.4	29.7	0.0	7.5	29.7	73.4
row 3	1.8	27.2	2.6	1.8	20.5	5.7	59.6
tots	39.2	76.1	68.5				184.8

tots s	140.1	C.T.=	1897.3	
total	27.4	block1tot	89.2	
C	17.3	block2tot	95.6	

	SS	CSS	DF	MS	F
blocks	17095.0	2.3	1.0	2.3	0.1
cols	12158.1	129.1	4.0	33.3	1.2
rows	11645.1	43.6	4.0	10.9	0.4
tms	20878.1	1549.1	3.0	774.5	28.1
error		165.2	6.0	27.5	
total	3786.5	1869.2	17.0	EMS'	

Appendix 9

Analysis of Variance for longevity of seeds from sand, clay and intermediate soils.

ANOVA

L.purpureum

Source	Sums of squares	D.F	Mean square
Grand total	764.1995	16	
Grand mean	47.7625	1	
Total	99.1914	2	49.5957
Error	910.4023	13	70.0309
Total	1009.5938		

F = 0.708 2,13 df P = 0.511

V.arvensis

Source	Sums of squares	D.F	Mean Square
Grand Total	1610.0	18	
Grand Mean	89.4444	1	
Treatments	11.125	2	5.5625
Error	83.375	15	5.5583
Total	94.5	17	

F = 1.001 2,15 DF P = 0.391

Appendix 10.

The effect of a 30 second exposure to a green safety lamp every alternate day on germination of *V. arvensis* and *L. purpureum* seeds at 17.9,6.4°C. Figures are arcsine proportions.

	Exposed	Unexposed
V. arvensis	59.3	46.1
	54.3	58.1
L. purpureum	17.5	22.7
	16.8	27.8

ANOVA

Table of mean values

56.8	52.1	54.45
17.15	25.25	21.20
36.975	38.675	

ANOVA Table 1

Source	Sums of Squares	Degrees of Freedom	Mean Square	F
Means	2298.832	3	766.2773	31.3591
Within	97.7422	4	24.4355	
Total	2396.5742	7		

P = 0.0031 3,4 DF

ANOVA Table 2

Source	Sums of Squares	Degrees of Freedom	Mean Square	F
Rows	2211.1328	1	2211.1328	90.4884
Columns	5.7891	1	5.7891	0.2369
Interaction	81.9102	1	81.9102	3.3521
Subtotal	2298.8320	3		
Within	97.7422	4	24.4355	
Total	2396.5742	7		

F = 90.4884 1,4 DF P < 0.001
F = 0.2369 1,4 DF P = 0.6519
F = 3.3521 1,4 DF P = 0.1411

ANOVA Table 3

Source	Sums of Squares	Degrees of Freedom	Mean Square	F
Rows	2211.1328	1	2211.1328	61.5392
Columns	5.7891	1	5.7891	0.1611
Residual	179.6523	5	35.9305	
Total	2396.5742	7		

F = 61.5392 1,5 DF P < 0.001
F = 0.1611 1,5 DF P = 0.7047

Appendix 11a

Arcsine germination at 22.0/9°C of L.purpureum to determining factors affecting dormancy of buried seed.

A. 24th October 1985

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	81.30	47.90	90.00	53.40	81.90	64.80	52.70	28.10	64.40	18.80
	77.30	32.80	90.00	58.50	80.70	62.00	34.10	24.40	52.10	26.60
	81.30	25.00	90.00	57.90			53.30	0.00	54.40	23.80
	69.80	53.40	81.10	72.80			45.00	30.60	49.50	26.90
	75.00	46.90	90.00	62.00			49.40	24.10	48.50	19.70
	77.90	46.40	81.70	58.20			40.60	22.20	54.30	22.70
Mean	77.10	42.00	87.10	60.50	81.30	63.40	45.90	21.60	53.90	23.10
Overall Mean	59.60		73.80		72.40		33.70		38.50	
Total	715.00		885.60		289.40		404.50		461.60	

B. 20th December 1985

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	72.20	12.00	67.00	15.30	73.70	11.80	52.20	24.10	48.40	14.80
	62.40	8.40	69.30	30.00	77.80	16.40	77.10	36.70	48.70	34.80
	77.70	8.40	75.20	8.40			62.40	40.90	56.10	38.70
	78.00	17.20	81.70	24.10			90.00	0.00	49.90	20.70
	73.20	23.00	75.20	17.20			40.90	33.20	60.70	30.00
	81.20	19.00	70.50	8.80			48.20	45.00	64.10	27.80
Mean	71.10	14.70	73.20	17.30	75.80	14.10	61.80	30.00	54.70	27.80
Overall Mean	44.40		45.20		44.90		45.90		41.20	
Total	532.70		542.70		179.70		550.70		494.70	

Appendix 11a (cont'd)

C. 12th February 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	72.20	8.50	64.60	0.00	67.80	22.20	65.20	54.70	51.30	34.80
	74.10	8.40	71.20	25.70	67.00	14.30	54.70	40.00	65.90	32.70
	68.70	11.90	57.70	38.50			30.00	30.00	51.80	47.60
	51.90	40.70	63.40	66.40						
	69.80	38.10	67.50							
	63.40	26.00								
Mean	66.70	22.30	64.90	32.70	67.40	18.30	50.00	41.90	56.30	38.40
Overall Mean	44.50		50.60		42.90		45.90		47.30	
Total	533.70		455.00		171.30		275.50		284.10	

D. 11th April 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	65.20	8.10	61.20	0.00	53.60	0.00	45.00	90.00	55.60	34.40
	50.20	0.00	45.70	9.20	49.10	8.90	45.00	30.00	57.50	31.00
	62.10	8.10	44.40	8.20			90.00	90.00	50.50	37.30
	55.80	8.40	62.70	0.00						
	51.70	15.50	54.70	0.00						
	54.30	9.50	67.40	8.10						
Mean	56.60	8.30	56.00	4.30	51.40	4.50	60.00	70.00	54.50	34.20
Overall Mean	32.50		30.20		28.00		65.00		44.40	
Total	389.20		361.60		111.60		390.00		266.30	

E. 6th June 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	90.00	28.10	76.70	20.20	90.00	26.90	61.90	50.80	68.40	35.70
	90.00	12.30	74.50	11.70	76.00	15.90	63.40	54.70	60.30	29.30
	90.00	9.10	76.60	17.50	67.50	24.60	69.30	54.70	74.50	38.10
	71.30	37.10	90.00	0.00	76.20	12.30				
	90.00	28.40	90.00	31.20	67.20	30.40				
	74.50	22.20	80.80	24.70	56.20	36.50				
Mean	84.30	22.90	81.40	17.60	72.20	24.40	64.90	53.40	67.70	34.40
Overall Mean	53.60		49.50		48.30		59.10		51.10	
Total	643.00		593.90		579.70		354.80		306.30	

Appendix 11b

Analysis of Variance for 'Factors affecting dormancy of buried seeds.'

L. purpureum

24th October 1985

Source	SS	DF	MS
Grand Total	2756.1968	52	
Grand Mean	53.0038	1	
Treatments	14207.125	4	3551.7813
Error	12852.125	47	273.4495
Total	27059.25	51	

F = 12.989 4,47 DF P < 0.001

20th December 1985

Source	SS	DF	MS
Grand Total	2300.4971	52	
Grand Mean	44.2403	1	
Treatments	155.5625	4	38.8906
Error	33578.9375	47	714.4453
Total	33734.5	51	

F = 0.054 4,47 DF P = 0.994

12th February 1986

Source	SS	DF	MS
Grand Total	1718.6985	37	
Grand Mean	46.4513	1	
Treatments	258.6875	4	64.6719
Error	16304.1250	32	509.5039
Total	16562.8125	36	

F = 0.127 4,32 DF P = 0.972

11th April 1986

Source	SS	DF	MS
Grand Total	1518.6985	40	
Grand Mean	37.9675	1	
Treatments	6140.957	4	1535.2393
Error	2282.9805	35	648.0850
Total	28823.9375	39	

F = 2.369 4,35 DF P = 0.071

6th June 1986

Source	SS	DF	MS
Grand Total	2477.6973	48	
Grand Mean	51.6187	1	
Treatments	572.8125	4	143.2
Error	35299.3125	43	820.91
Total	35872.1250	47	

F = 0.174 4,13 DF P = 0.95

5th August 1986

Source	SS	DF	MS
Grand Total	764.1995	16	
Grand Mean	47.7625	1	
Treatments	99.1914	2	49.5957
Error	910.4023	13	70.0309
Total	1009.5938	15	

F = 0.708 2,13 DF P = 0.511

Appendix 12a

Arcsine germination at 17.9/6.4°C of V.arvensis to determine factors affecting dormancy of buried seeds.

A. 22nd November 1985.

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	25.80	8.10	8.10	8.10	0.00	11.50	10.00	27.30	8.10	20.30
	31.20	16.40	5.70	16.40	5.70	5.70	8.10	30.00	0.00	14.20
			11.50	11.50	0.00	8.10	11.50	16.40	0.00	12.90
			10.00	15.30	0.00	10.00	16.40	30.00	0.00	16.40
			11.50	5.70	5.70	8.10	10.00	28.00	0.00	12.90
			10.00	27.30	0.00	12.90	17.50	39.80	8.10	8.10
Mean	28.50	12.30	9.50	14.10	1.90	9.40	12.30	28.60	2.70	14.10
Overall Mean	20.40		11.80		5.70		20.50		8.40	
Total	81.50		141.10		67.70		245.00		101.00	

B. 17th January 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	28.60	17.00	10.00	0.00	6.10	8.10	0.00	0.00	16.40	39.70
	33.40	21.50	11.50	24.40	14.20	8.10	0.00	5.70	21.20	46.70
			15.40	12.90	11.70	20.30	0.00	0.00	27.30	46.40
			21.50	11.50	10.10	10.20				
			13.00	16.40	0.00	12.90				
			10.00	8.10	5.80	12.90				
Mean	31.00	19.30	13.60	12.20	8.00	12.10			21.60	43.60
Overall Mean	25.10		12.90		10.00		1.00		32.60	
Total	100.50		154.80		120.40		5.7		195.70	

C. 13th March 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	40.10	10.00	17.30	10.00	5.70	10.00	0.00	10.20	49.20	19.00
	27.10	0.00	13.00	23.20	5.80	5.70	0.00	10.10	44.70	55.60
			11.60	17.80	0.00	0.00	0.00	0.00	12.90	19.60
			13.10	20.10	8.40	8.30				
			14.80	28.20	5.70	5.90				
			16.40	33.80	14.30	14.40				
Mean	33.60	5.00	14.40	22.20	6.70	7.40	0.00	6.80	15.60	51.10
Overall Mean	19.30		18.30		7.00		3.40		18.50	
Total	77.20		219.40		84.20		20.30		291.00	

D. 9th May 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	8.50	0.00	0.00	0.00	0.00	0.00	11.50	0.00	54.70	58.70
	10.00	0.00	0.00	0.00	0.00	0.00	10.00	10.90	47.60	67.20
			0.00	0.00	0.00	0.00	12.00	13.50	49.70	56.80
			0.00	0.00	0.00	0.00				
			0.00	0.00	0.00	0.00				
			0.00	0.00	0.00	0.00				
Mean	9.30	0.00	0.00	0.00	0.00	0.00	11.20	8.10	50.70	60.90
Overall Mean	18.50		0.00		0.00		57.90		334.70	
Total										

E. 3rd July 1986

Treatment	1 Early seed buried early		2 Early seed buried late		3 Late seed buried late		4 Early seed in screen		5 Early seed in fridge	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark
	11.60	0.00	0.00	0.00	5.70	0.00	0.00	11.50	49.30	50.80
	7.90	0.00	0.00	0.00	8.10	5.80	5.70	21.10	53.70	55.60
			0.00	0.00	0.00	0.00	17.20	16.40	50.80	65.60
			0.00	0.00	0.00	0.00	14.50	21.10	54.90	64.20
			0.00	0.00	11.50	0.00	10.00	20.30	55.30	58.30
			5.70	0.00	5.70	0.00	8.10	23.60	52.00	49.00
Mean	9.80	0.00	1.00	0.00	5.20	1.00	9.30	19.00	52.70	57.30
Overall Mean	4.90		0.50		3.10		14.10		55.00	
Total	19.50		5.70		36.80		169.50		659.50	

Appendix 12b

Analysis of Variance for Factors affecting dormancy of buried seeds.

V. arvensis

22nd November 1985

Source	SS	DF	MS
Grand Total	646.2993	52	
Grand Mean	12.4288	1	
Treatments	1697.6797	4	424.4199
Error	2985.5508	47	63.5224
Total	4683.2305	51	

F = 6.681 4,47 DF P < 0.001

17th January 1986

Source	SS	DF	MS
Grand Total	577.1	40	
Grand Mean	14.4	1	
Treatments	3792.4	4	948.1
Error	1714.2	35	49.0
Total	5506.6	39	

F = 19.358 4,35 DF P < 0.001

13th March 1986

Source	SS	DF	MS
Grand Total	636.2993	52	
Grand Mean	12.2365	1	
Treatments	1767.668	4	441.917
Error	2656.2148	47	56.5152
Total	4423.8828	51	

F = 7.819 4,47 DF P < 0.001

9th May 1986

Source	SS	DF	MS
Grand Total	411.0596	40	
Grand Mean	10.277	1	
Treatments	15086.2266	4	3771.5566
Error	450.9727	35	12.8849
Total	15537.199		

F = 292.71 4,35 DF P < 0.001

3rd July 1986

Source	SS	DF	MS
Grand Total	890.9988	52	
Grand Mean	17.1346	1	
Treatments	23582.8164	4	5895.7031
Error	1208.8672	47	25.7206
Total	24791.6836	51	

F = 229.221 4,47 DF P < 0.001

Appendix 13

Simulated population changes assuming different seed inputs for Viola arvensis, using a Leslie Matrix Model described in Mortimer (1979). Data for the initial matrices is taken from figure 2.40.

Leslie Matrix — 5.0 % seed input

				year:	0
0.49	0.00	0.00	18.27		4360.00
0.03	0.00	0.00	0.00		214.30
0.00	0.26	0.00	0.00		40.50
0.00	0.00	0.35	0.00		14.20

1	2	3	4	5	6	7
2395.8	1432.9	1058.4	736.1	480.2	306.8	203.1
130.8	71.9	43.0	31.8	22.1	14.4	9.2
55.7	34.0	18.7	11.2	8.3	5.7	3.7
14.2	19.5	11.9	6.5	3.9	2.9	2.0

8	9	10	11	12	13	14
136.2	90.7	59.7	39.4	26.1	17.3	11.5
6.1	4.1	2.7	1.8	1.2	0.8	0.5
2.4	1.6	1.1	0.7	0.5	0.3	0.2
1.3	0.8	0.6	0.4	0.2	0.2	0.1

15	16	17	18	19	20	21
7.6	5.0	3.3	2.2	1.5	1.0	0.6
0.3	0.2	0.2	0.1	0.1	0.0	0.0
0.1	0.1	0.1	0.0	0.0	0.0	0.0
0.1	0.0	0.0	0.0	0.0	0.0	0.0

22	23	24	25	26	27	28
0.4	0.3	0.2	0.1	0.1	0.1	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0

Leslie Matrix 40.0 % seed input

				year:	0
0.49	0.00	0.00	146.16		4360.00
0.03	0.00	0.00	0.00		214.30
0.00	0.26	0.00	0.00		40.50
0.00	0.00	0.35	0.00		14.20

1	2	3	4	5	6	7
4211.9	4135.6	4876.8	4129.3	3704.0	3465.1	3643.8
130.8	126.4	124.1	146.3	123.9	111.1	104.0
55.7	34.0	32.9	32.3	38.0	32.2	28.9
14.2	19.5	11.9	11.5	11.3	13.3	11.3

8	9	10	11	12	13	14
3433.1	3160.2	2931.1	2890.2	2786.1	2626.2	2456.4
109.3	103.0	94.8	87.9	86.7	83.6	78.8
27.0	28.4	26.8	24.6	22.9	22.5	21.7
10.1	9.5	9.9	9.4	8.6	8.0	7.9

15	16	17	18	19	20	21
2356.9	2266.6	2158.5	2037.8	1939.0	1854.5	1770.0
73.7	70.7	68.0	64.8	61.1	58.2	55.6
20.5	19.2	18.4	17.7	16.8	15.9	15.1
7.6	7.2	6.7	6.4	6.2	5.9	5.6

22	23	24	25	26	27	28
1680.4	1597.1	1522.5	1452.3	1382.1	1314.5	1251.6
53.1	50.4	47.9	45.7	43.6	41.5	39.4
14.5	13.8	13.1	12.5	11.9	11.3	10.8
5.3	5.1	4.8	4.6	4.4	4.2	4.0

Leslie Matrix 50.0 % seed input

				year:	0
0.49	0.00	0.00	182.70		4360.00
0.03	0.00	0.00	0.00		214.30
0.00	0.26	0.00	0.00		40.50
0.00	0.00	0.35	0.00		14.20

1	2	3	4	5	6	7
4730.7	4907.8	5967.7	5098.8	4858.0	4828.3	5342.4
130.8	141.9	147.2	179.0	153.0	145.7	144.8
55.7	34.0	36.9	38.3	46.5	39.8	37.9
14.2	19.5	11.9	12.9	13.4	16.3	13.9

8	9	10	11	12	13	14
5160.9	4951.9	4834.6	5033.6	5040.6	4939.7	4831.8
160.3	154.8	148.6	145.0	151.0	151.2	148.2
37.7	41.7	40.3	38.6	37.7	39.3	39.3
13.3	13.2	14.6	14.1	13.5	13.2	13.7

15	16	17	18	19	20	21
4878.2	4904.4	4867.0	4794.8	4782.6	4789.6	4774.4
145.0	146.3	147.1	146.0	143.8	143.5	143.7
38.5	37.7	38.1	38.3	38.0	37.4	37.3
13.8	13.5	13.2	13.3	13.4	13.3	13.1

22	23	24	25	26	27	28
4731.0	4703.6	4693.7	4681.3	4653.5	4626.2	4607.9
143.2	141.9	141.1	140.8	140.4	139.6	138.8
37.4	37.2	36.9	36.7	36.6	36.5	36.3
13.1	13.1	13.0	12.9	12.8	12.8	12.8

Leslie Matrix 60.0 % seed input

				year:	0
0.49	0.00	0.00	219.24		4360.00
0.03	0.00	0.00	0.00		214.30
0.00	0.26	0.00	0.00		40.50
0.00	0.00	0.35	0.00		14.20

1	2	3	4	5	6	7
5245.6	5680.0	7058.7	6068.3	6115.5	6356.2	7359.0
130.8	157.5	170.4	211.8	182.0	183.5	191.9
55.7	34.0	40.9	44.3	55.1	47.3	47.7
14.2	19.5	11.9	14.3	15.5	19.3	16.6

8	9	10	11	12	13	14
7237.9	7206.9	7359.7	8010.8	8257.4	8359.6	8501.2
220.8	217.1	216.2	220.8	240.3	247.7	250.8
49.9	57.4	56.5	56.2	57.4	62.5	64.4
16.7	17.5	20.1	19.8	19.7	20.1	21.9

15	16	17	18	19	20	21
8960.2	9332.7	9576.5	9780.6	10155.4	10562.0	10907.2
255.0	260.8	280.0	287.3	293.4	304.7	316.9
65.2	66.3	69.9	72.8	74.7	76.3	79.2
22.5	22.8	23.2	24.5	25.5	26.1	26.7

22	23	24	25	26	27	28
11198.5	11565.5	11988.7	12402.7	12779.9	13184.4	13635.9
327.2	336.0	347.0	359.7	372.1	383.4	395.5
82.4	85.1	87.3	90.2	93.5	96.7	99.7
27.7	28.8	29.8	30.6	31.6	32.7	33.9

Leslie Matrix 100.0 % seed input

				year:	0
0.49	0.00	0.00	365.40		4360.00
0.03	0.00	0.00	0.00		214.30
0.00	0.26	0.00	0.00		40.50
0.00	0.00	0.35	0.00		14.20

1	2	3	4	5	6	7
7325.1	8768.8	11422.5	9946.3	12180.8	14715.9	18605.2
130.8	219.8	263.1	342.7	298.4	365.4	441.5
55.7	34.0	57.1	68.4	89.1	77.6	95.0
14.2	19.5	11.9	20.0	23.9	31.2	27.2

8	9	10	11	12	13	14
19038.4	21479.6	25204.7	30909.8	34137.4	38154.2	43838.3
558.2	571.2	644.4	756.1	927.3	1024.1	1144.6
114.8	145.1	148.5	167.5	196.6	241.1	266.3
33.3	40.2	50.8	52.0	58.6	68.8	84.4

15	16	17	18	19	20	21
52314.6	59687.6	67307.3	76711.1	89774.4	103530.4	117871.8
1315.1	1569.4	1790.6	2019.2	2301.3	2693.2	3105.9
297.6	341.9	408.1	465.6	525.0	598.3	700.2
93.2	104.2	119.7	142.8	162.9	183.7	209.4

22	23	24	25	26	27	28
134279.8	155350.9	179397.8	205487.0	234638.3	269941.8	311228.3
3536.2	4028.4	4660.5	5381.9	6164.6	7039.1	8098.3
807.5	919.4	1047.4	1211.7	1399.3	1602.8	1830.2
245.1	282.6	321.8	366.6	424.1	489.8	561.0

29	30
357483.8	409228.6
9336.9	10724.5
2105.5	2427.6
640.6	736.9

Appendix 14

Simulated population changes assuming different seed inputs for *Lamium purpureum*, using a Leslie Matrix Model described in Mortimer (1979). Data for the initial matrices is taken from figure 2.41.

Leslie Matrix — **5.0 % seed input**

				year:	0
0.51	0.00	0.00	10.52		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5
1	2	3	4	5	6
726.6	519.2	412.8	356.7	288.7	223.7
29.9	21.8	15.6	12.4	10.7	8.7
20.5	20.3	14.8	10.6	8.4	7.3
13.9	13.9	13.8	10.0	7.2	5.7
7	8	9	10	11	12
174.8	141.6	114.6	91.4	72.3	57.7
6.7	5.2	4.2	3.4	2.7	2.2
5.9	4.6	3.6	2.9	2.3	1.9
4.9	4.0	3.1	2.4	2.0	1.6
13	14	15	16	17	18
46.3	37.0	29.5	23.5	18.8	15.0
1.7	1.4	1.1	0.9	0.7	0.6
1.5	1.2	0.9	0.8	0.6	0.5
1.3	1.0	0.8	0.6	0.5	0.4
19	20	21	22	23	24
12.0	9.6	7.7	6.1	4.9	3.9
0.5	0.4	0.3	0.2	0.2	0.1
0.4	0.3	0.2	0.2	0.2	0.1
0.3	0.3	0.2	0.2	0.1	0.1
25	26	27	28	29	30
3.1	2.5	2.0	1.6	1.3	1.0
0.1	0.1	0.1	0.1	0.0	0.0
0.1	0.1	0.1	0.1	0.0	0.0
0.1	0.1	0.1	0.0	0.0	0.0

Leslie Matrix

10.0 % seed input

				year:	
0.51	0.00	0.00	21.04		0
0.03	0.00	0.00	0.00		996.0
0.00	0.68	0.00	0.00		30.2
0.00	0.00	0.68	0.00		20.5
					20.5

1	2	3	4	5	6
942.3	776.2	691.2	644.4	604.8	536.2
29.9	28.3	23.3	20.7	19.3	18.1
20.5	20.3	19.2	15.8	14.1	13.1
13.9	13.9	13.8	13.0	10.7	9.6

7	8	9	10	11	12
476.2	431.8	397.5	360.0	323.2	291.5
16.1	14.3	13.0	11.9	10.8	9.7
12.3	10.9	9.7	8.8	8.1	7.3
8.9	8.4	7.4	6.6	6.0	5.5

13	14	15	16	17	18
265.2	240.8	217.6	196.4	178.0	161.4
8.7	8.0	7.2	6.5	5.9	5.3
6.6	5.9	5.4	4.9	4.4	4.0
5.0	4.5	4.0	3.7	3.3	3.0

19	20	21	22	23	24
146.1	132.1	119.6	108.3	98.1	88.8
4.8	4.4	4.0	3.6	3.2	2.9
3.6	3.3	3.0	2.7	2.4	2.2
2.7	2.5	2.2	2.0	1.8	1.7

25	26	27	28	29	30
80.3	72.7	65.8	59.6	54.0	48.8
2.7	2.4	2.2	2.0	1.8	1.6
2.0	1.8	1.6	1.5	1.3	1.2
1.5	1.4	1.2	1.1	1.0	0.9

Leslie Matrix 20.0 % seed input

				year:	0
0.51	0.00	0.00	42.08		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5

1	2	3	4	5	6
1373.6	1290.4	1247.9	1219.8	1425.2	1482.2
29.9	41.2	38.7	37.4	36.6	42.8
20.5	20.3	28.0	26.3	25.4	24.8
13.9	13.9	13.8	19.0	17.8	17.3

7	8	9	10	11	12
1486.6	1472.6	1585.0	1675.7	1724.9	1742.0
44.5	44.6	44.2	47.5	50.3	51.7
29.0	30.2	30.3	30.0	32.3	34.1
16.9	19.7	20.5	20.6	20.4	21.9

13	14	15	16	17	18
1816.1	1907.0	1982.2	2030.7	2098.8	2186.6
52.3	54.5	57.2	59.5	60.9	63.0
35.1	35.5	37.0	38.8	40.4	41.4
23.2	23.9	24.1	25.1	26.4	27.4

19	20	21	22	23	24
2275.4	2349.2	2426.7	2517.5	2615.8	2709.2
65.6	68.3	70.5	72.8	75.5	78.5
42.8	44.5	46.3	47.9	49.4	51.3
28.1	29.0	30.2	31.5	32.5	33.6

25	26	27	28	29	30
2802.2	2902.7	3011.5	3121.7	3232.3	3347.6
81.3	84.1	87.1	90.3	93.7	97.0
53.3	55.2	57.1	59.1	61.3	63.6
34.8	36.2	37.5	38.8	40.1	41.7

Leslie Matrix 40.0 % seed input

				year:	0
0.51	0.00	0.00	84.16		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5

1	2	3	4	5	6
2236.2	2318.7	2361.3	2370.7	3819.2	4658.3
29.9	67.1	69.6	70.8	71.1	114.6
20.5	20.3	45.6	47.2	48.1	48.3
13.9	13.9	13.8	30.9	32.1	32.7

7	8	9	10	11	12
5138.3	5395.5	7213.6	9123.0	10661.2	11749.8
139.7	154.1	161.9	216.4	273.7	319.8
77.8	94.9	104.7	109.9	146.9	185.8
32.8	52.8	64.4	71.1	74.6	99.8

13	14	15	16	17	18
14424.6	18019.3	21653.9	24785.7	29505.8	36111.5
352.5	432.7	540.6	649.6	743.6	885.2
217.2	239.3	293.8	367.1	441.1	504.9
126.2	147.5	162.5	199.5	249.2	299.5

19	20	21	22	23	24
43731.2	51285.5	60655.3	73151.3	88431.3	105063.5
1083.3	1311.9	1538.6	1819.7	2194.9	2652.9
601.0	735.6	890.8	1044.7	1235.5	1490.1
342.8	408.1	499.5	604.9	709.3	838.9

25	26	27	28	29	30
124502.5	149020.5	179384.8	214322.1	254872.6	304215.0
3151.9	3735.1	4470.6	5381.5	6429.7	7646.2
1801.3	2140.1	2536.1	3035.5	3654.1	4365.7
1011.8	1223.1	1453.2	1722.0	2061.1	2481.1

Leslie Matrix 50.0 % seed input

				year:	0
0.51	0.00	0.00	105.20		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5

1	2	3	4	5	6
2667.5	2832.8	2918.0	2946.1	5392.8	6888.3
29.9	80.0	85.0	87.5	88.4	161.8
20.5	20.3	54.3	57.7	59.4	60.0
13.9	13.9	13.8	36.9	39.2	40.4

7	8	9	10	11	12
7779.5	8277.6	12093.2	16226.6	19643.7	22121.6
206.6	233.4	248.3	362.8	486.8	589.3
109.9	140.3	158.5	168.6	246.3	330.5
40.7	74.6	95.3	107.6	114.5	167.3

13	14	15	16	17	18
28944.5	38459.0	48312.0	56972.0	71342.1	92558.1
663.6	868.3	1153.8	1449.4	1709.2	2140.3
400.1	450.6	589.6	783.4	984.1	1160.5
224.4	271.7	306.0	400.3	531.9	668.2

19	20	21	22	23	24
117778.4	143317.1	177327.7	225645.3	287129.0	355830.1
2776.7	3533.4	4299.5	5319.8	6769.4	8613.9
1453.2	1885.4	2398.1	2919.4	3612.2	4596.4
788.0	986.7	1280.2	1629.0	1982.3	2452.7

25	26	27	28	29	30
440560.7	554331.8	702158.0	877956.0	1091427.3	1366480.2
10674.9	13216.8	16630.0	21064.7	26338.7	32742.8
5848.8	7248.3	8974.2	11291.7	14303.0	17884.0
3121.0	3971.3	4921.6	6093.5	7667.1	9711.7

Leslie Matrix 60.0 % seed input

				year:	
					0
0.51	0.00	0.00	126.24		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5

1	2	3	4	5	6
3098.9	3346.9	3474.7	3521.6	7217.4	9546.4
29.9	93.0	100.4	104.2	105.6	216.5
20.5	20.3	63.1	68.2	70.8	71.7
13.9	13.9	13.8	42.9	46.3	48.1

7	8	9	10	11	12
10964.3	11773.5	18641.7	26231.7	32601.1	37281.6
286.4	328.9	353.2	559.3	787.0	978.0
147.0	194.5	223.3	239.8	379.7	534.3
48.7	99.8	132.0	151.6	162.8	257.8

13	14	15	16	17	18
51674.9	72311.3	94018.9	113327.3	148364.1	202370.2
1118.4	1550.2	2169.3	2820.6	3399.8	4450.9
664.1	759.4	1052.6	1473.0	1915.2	2308.5
362.8	450.9	515.6	714.7	1000.2	1300.4

19	20	21	22	23	24
267978.1	335348.5	431085.6	574496.3	762621.0	976761.3
6071.1	8039.3	10060.5	12932.6	17234.9	22878.6
3022.2	4122.3	5458.7	6831.0	8781.2	11702.5
1567.5	2052.1	2799.0	3706.5	4638.3	5962.4

25	26	27	28	29	30
1253777.5	1646289.8	2176124.4	2821830.3	3636762.8	4740170.9
29302.8	37613.3	49388.7	65283.7	84654.9	109102.9
15534.6	19896.6	25539.4	33534.9	44327.7	57480.7
7946.0	10548.0	13509.8	17341.3	22770.2	30098.5

Leslie Matrix 100.0 % seed input

				year:	0
0.51	0.00	0.00	210.40		996.0
0.03	0.00	0.00	0.00		30.2
0.00	0.68	0.00	0.00		20.5
0.00	0.00	0.68	0.00		20.5

1	2	3	4	5	6
4824.1	5403.5	5701.5	5823.3	17026.1	24458.9
29.9	144.7	162.1	171.0	174.7	510.8
20.5	20.3	98.3	110.1	116.1	118.6
13.9	13.9	13.8	66.7	74.7	78.9

7	8	9	10	11	12
29139.2	31894.7	65909.4	104989.1	138657.1	163947.7
733.8	874.2	956.8	1977.3	3149.7	4159.7
346.8	498.2	593.6	649.7	1342.6	2138.6
80.5	235.5	338.3	403.0	441.1	911.6

13	14	15	16	17	18
275907.5	447068.4	632850.9	801755.1	1214216.1	1923902.6
4918.4	8277.2	13412.1	18985.5	24052.7	36426.5
2824.4	3339.6	5620.2	9106.8	12891.2	16331.8
1452.1	1917.8	2267.6	3816.1	6183.5	8753.1

19	20	21	22	23	24
2828615.6	3784260.0	5474804.5	8407306.1	12544476.3	17447856.6
57717.1	84858.5	113527.8	164244.1	252219.2	376334.3
24733.6	39189.9	57618.9	77085.4	111521.8	171256.8
11089.3	16794.1	26609.9	39123.2	52341.0	75723.3

25	26	27	28	29	30
24882928.6	37230966.4	55605050.7	79300237.7	**********	**********
523435.7	746487.9	1116929.0	1668151.5	2378007.1	3392778.1
255531.0	355412.8	506865.3	758394.8	1132674.9	1615345.8
116283.4	173505.5	241325.3	344161.5	514950.1	769086.2

Appendix 15

Aegilops kotschyi	Boiss.
Aegilops ovata	L.
Aellenia antrarii	L.
Agrostemma githago	L.
Aira praecox	L.
Alopecurus myosuroides	Huds.
Alysicarpus monilifer	DC.
Amaranthus retroflexus	L.
Amaranthus patulus	L.
Ambrosia artemisiifolia	L.
Aphanes arvensis	L.
Arabidopsis thaliana	L.
Artemisia vulgaris	L.
Aster acuminatus	Michx.
Aster pilosus	Willd.
Atriplex patula	L.
Avena barbata	Pott, ex Link.
Avena fatua	L.
Avena ludoviciana	Durieu.
Avena sterilis spp. ludoviciana	L.
Bromus mollis	L.
Bromus sterilis	L.
Capsella bursa pastoris	L.
Cardamine hirsuta	L.
Cassia obtusifolia	L.
Chenopodium album	L.
Chenopodium amaranticolor	Coste & Reyn.
Chenopodium bonus-henricus	L.
Commelina benghalensis	L.
Convolvulus arvensis	L.
Crupina vulgaris	Cass.
Cyperus inflexus	Muhl.
Dactylis glomerata	L.
Digitalis purpurea	L.
Digitaria milanjiana	(Rendle) Stapf.
Echinochloa crus-galli	(L.) Beauv.
Euphorbia supina	L.
Floerkea proserpinacoides	Willd.
Galium aparine	L.
Heracleum sphondylium	L.
Hyptis suaveolens	Poit.
Ipomoea muricata	L.
Lactuca serriola	L.
Lamium amplexicaule	L.
Lolium multiflorum	Lam.
Lolium perenne	L.
Ludwigia octovalis = Jussiaea suffruticosa	(Jacq.) L.
Lupinus texensis	Hook
Matricaria inodora	L.
Medicago lupulina	L.
Myosotis arvensis	(L.)Hill
Ononis sicula	L.
Phacelia dubia	L.
Phacelia purshii	Buckl.
Phytolacca americana	L.
Pisum elatius	Bieb.Fl. Taur.Cauc.
Pisum sativum	L.

Plantago lanceolata	L.	Torilis japonica	(Houtt DC)
Plantago major	L.	Typha latifolia	L.
Poa trivialis	L.	Verbascum thapsus	L.
Polygonum aviculare	L.	Veronica arvensis	L.
Polygonum pennsylvanicum	L.	Veronica hederifolia	L. Sensu lato
Polygonum persicaria	L.	Vulpia fasciculata	(Forskal)Samp.
Potentilla norvegica	L.		
Ranunculus acris	L.		
Ranunculus bulbosus	L.		
Ranunculus repens	L.		
Rumex crispus	L.		
Rumex obtusifolius	L.		
Salsola valkensii	Asch. et Schw.		
Scabiosa columbaria	L.		
Sedum pulchellum	Michx.		
Senecio jacobaea	L.		
Senecio vulgaris	L.		
Setaria faberi	Herrm.		
Setaria lutescens	(Weigel) Hubb.		
Setaria viridis	(L.) Beauv.		
Silene anglica	L.		
Silene secundiflora	L.		
Sinapsis arvensis	L.		
Sorghum bicolor	Moench.		
Spergula arvensis	L.		
Stellaria media	L.		
Teesdalia nudicaulis	L.		
Thlaspi arvense	L.		
Thlaspi perfoliatum	L.		

References

Adkins, S.W. (1981). Studies on the mechanism of seed dormancy in Avena fatua. PhD. Thesis University of Reading.

Allen, S.E. Ed. (1974). Chemical analysis of ecological materials. Blackwell Scientific Press.

Austin, R.B. (1972) Effects of environment before harvesting on viability. In Roberts, E.H. (Ed.), (1972) Viability of Seeds, Vol. 5. Chapman and Hall, London. 114-149.

Avalos, A. and Vicente, C. (1985). Phytochrome enhances nitrate reductase activity in the lichen Evernia **prunastri.** Can. J. Bot., 63. (8), 1350-1354.

Baalen, J.V. (1982). Germination ecology and seed population dynamics of Digitalis purpurea. Oecol., 53, 61-67.

Barralis, G. and Chadoeuf, R. (1976). Evolution qualitative et quantitative d'un peuplement adventice sous l'effet de dix annees de traitment. Cr. Veme Colloque int. sur la Biologie et l'ecologie des Mauvaises Herbes, Dijon, 179-186.

Bartley, M.R. and Frankland, B. (1984). Phytochrome intermediates and action spectra for light perception by dry seeds. Pl. Physiol., 74, 601-604.

Barton, L.V. (1962). Germination of weed seeds. Weeds, 10, 174-182.

Baskin, J.M. and Baskin, C.C. (1971). Germination ecology of Phacelia dubia var. dubia in Tennessee glades. Amer. J. Bot., 58, (1), 98-104.

Baskin, J.M. and Baskin, C.C. (1972). Physiological ecology of germination of Viola rafinesquii. Amer. J. Bot., 59, (10), 981-988.

Baskin, J.M. and Baskin, C.C. (1973). Delayed germination in seeds of Phacelia dubia var dubia. Can. J. Bot., 51, (3), 2481-2486.

Baskin, J.M. and Baskin, C.C. (1976). High temperature requirement for after-ripening in seeds of winter annuals. New Phytol., 77, 619-624.

Baskin, J.M. and Baskin, C.C. (1976). Some aspects of the autoecology and population ecology of Phacelia purshii. Amer. Midl. Nat., 96, 431-442.

Baskin, J.M. and Baskin, C.C. (1977). Role of temperature in the germination ecology of three summer annual weeds. Oecol. 30, 377-382.

Baskin, J.M. and Baskin, C.C. (1978). Temperature requirements for after-ripening of seeds of a winter annual induced into secondary dormancy by low winter temperatures. Bull. Torr. Bot. Club, 105, (2), 104-107.

Baskin, J.M. and Baskin, C.C. (1979)a. Promotion of Stellaria media seeds by light from a green safe lamp. New Phytol., 82, 381-383.

Baskin, J.M. and Baskin, C.C. (1979)b. Timing of seed germination in the weedy summer annual Euphorbia supina. Bartonia, 46, 63-68.

Baskin, J.M. and Baskin, C.C. (1979)c. The germination strategy of oldfield aster (Aster pilosus). Am. J. Bot., 66, 1-5.

Baskin, J.M. and Baskin, C.C. (1979)d. Effect of relative humidity on after-ripening and viability in seeds of the winter annual Draba verna. Bot. Gaz., 140, 284-287.

Baskin, J.M. and Baskin, C.C. (1979)e. The ecological Life cycle of Thlaspi perfoliatum and a comparison with published studies of Thlaspi arvense. Weed Res., 19, 285-292.

Baskin, J.M. and Baskin, C.C. (1980). Ecophysiology of secondary dormancy in seeds of Ambrosia artemisiifolia. Ecol. 61, (3), 475-480.

Baskin, J.M. and Baskin, C.C. (1981). Seasonal changes in the germination responses of Lamium amplexicaule seeds. Weed Res. 21, 299-306.

Baskin, J.M. and Baskin, C.C. (1982). Effects of wetting and drying cycles on the germination of seeds of Cyperus inflexus. Ecol., 63, 248-252.

Baskin, J.M. and Baskin, C.C. (1983). Germination ecology of Veronica arvensis. J. Ecol., 71, 57-68.

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

Baskin, J.M. and Baskin, C.C. (1984). The ecological life cycle of Campanula americana in northcentral Kentucky. Bull. Torr. Bot. Club., 111, (3), 329-337.

Baskin, J.M. and Baskin, C.C. (1985)a. The annual dormancy cycle in buried weed seeds: A continuum. Bioscience, 35, (8), 492-498.

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

Bazzaz, F.A. (1970). Secondary dormancy in the seeds of the common ragweed, Ambrosia artemisiifolia. Bull. Torr. Bot. Club, 97, 302-305.

Benjamin, S.K. (1974). The effect of environment on the germination of Chenopodium album, Capsella bursa-pastoris & Poa annua. PhD. Thesis, University of Reading.

Berrie, A.M.M. and Drennan, D.S.H. (1971). The effect of hydration-dehydration on seed germination. New Phytol., 70, 135–142.

Beuret, E. (1984). Stocks graniers des sols et practiques culturales: La relation flore reelle-flore potentielle. Recherche Agronom en Suisse, 23, 1/2, 89–97.

Bewley, J.D. and Black, M. (1982). Light inhibition. Physiology and Biochemistry of seeds, 2. (Springer-Verlag).

Bibbey, R.D. (1947). Physiological studies of weed seed germination. Pl. Physiol., 23, 467–484.

Black, M. (1970). Light-controlled germination of seeds. S.E.B. Symp., XXIII. Dormancy and survival, 193–217.

Black, M. and Wareing, P.F. (1960). Photoperiodism in the light-inhibited seed of Nemophila insignis. J. Exp. Bot., 11, 28–39.

Blackshaw, R.E., Stobbe, E.H., Shaykewich, C.F. and Woodbury, W. (1981). Influence of soil temperature and soil moisture on Green Foxtail (Setaria viridis) establishment in wheat (Triticum aestivum). Weed Sci., 29, (2), 179–184.

Bliss, D. and Smith, H. (1985). Pene tration of light into soil and it s role in the control of seed germination. Pl. Cell Environ., 8, 475–483.

Bonnewell, V., Koukkari, W.L. and Pratt, D.C. (1983). Light, oxygen and temperature requirements for Typha latifolia seed germination. Can. J. Bot., 61, 1330–1336.

Borthwick, H.A. Hendricks, S.B., Toole, E.H., and Toole, V.K. (1954). Action of light on lettuce seed germination. Bot. Gaz., 115, 205–225.

Bostock, S.J. (1978). Seed germination strategies of five perennial weeds. Oecol. (Berl.) 36, 113–126

Brenchley, W.E. (1918). Buried weed seeds. J. Agric. Sci., Camb., 9, 1–31.

Brenchley, W.E. and Warington, K. (1930). The weed seed population of arable soil. 1. Numerical estimation of viable seeds and observations on their natural dormancy. J. Ecol., 18, 235–272.

Brenchley, W.E. and Warington, K. (1933). The weed seed population of arable soil. II. Influence of crop, soil and methods of cultivation upon the relative abundance of viable seeds. J. Ecol., 21, 103–127.

Brenchley, W.E. and Warington, K. (1936). The weed seed population of arable soil. III. The reestablishment of weed species after reduction by fallowing. J. Ecol., 24, 479–501.

Bridges, D.L. and Walker, R.H. (1985). The influence of weed management and cropping systems on sicklepod (Cassia obtusifolia) seed in the soil. Weed Sci., 33, 800–804.

Carretero, J.L. (1977). Estimacion del contenido de semillas de malas hierbas de un suelo agricola como prediccion de su flora adventicia. Anal. Inst. Bot. Cavanilles, 34, (1), 267–278.

Cavers, P.B. and Harper, J.L. (1968). Germination polymorphism in Rumex crispus and Rumex obtusifolius. J. Ecol., 54, 367–382.

Chadoeuf-Hannel, R. (1985). La dormance chez les semences de mauvaises herbes. Agronomie, 5, (8), 761–772.

Chadoeuf-Hannel, R. and Taylorson, R.B. (1985). Anaesthetic stimulation of Amaranthus albus seed germination: Interaction with phytochrome. Physiol. Planta., 65, 451–454.

Champness, S.S.H. and Morris, K. (1948). The population of buried viable seeds in relation to contrasting pasture and soil types. J. Ecol., 36, 149-173.

Chancellor, R.J. (1965). Emergence of weed seedlings in the field and the effects of different frequencies of cultivation. Rept. Brit. Weed Control Conf. 7th, 599-606.

Chancellor, R.J. (1979). The long-term effects of herbicides on weed populations. Ann. Appl. Biol., 91, 141-144.

Chancellor, R.J. (1982). Dormancy in weed seeds. Outlook on agriculture, 11, (2), 87-93.

Chancellor, R.J. (1985). Changes in the weed flora of an arable field cultivated for 20 years. J. Appl. Ecol., 22, 491-501.

Chancellor, R.J. and Froud-Williams, R.J. (1986). Weed problems of the next decade in Britain. Crop Protection, 5, (1), 66-72.

Chancellor, R.J. and Peters, N.C.B. (1972). Germination periodicity, plant survival and seed production in populations of Avena fatua L. growing in spring barley. Proc. 11th Brit. Crop Prot. Conf.- weeds 218-225.

Cheam, A.H. (1983). In Panetta, F.D. (1985) Population studies on Pennyroyal mint (Mentha pulegium)L. II. Seedbanks. Weed Res. 25, 311-315.

Chepil, W.S. (1946). Germination of weed seeds. 1. Longevity, periodicity of germination and viability of seeds in cultivated soil. Sci. Agric., 26, 347-357.

Cideciyan, M.A. and Malloch, A.J.C. (1982). Effects of seed size on the germination, growth and competitive ability of Rumex crispus and Rumex obtusifolius. J. Ecol., 70, 227-232.

Cohen, D. (1958). The mechanism of germination stimulation by alternating temperatures. Bull. Res. Counc. of Israel, Vol 6D, 111-117.

Cohen, D. (1966). Optimising reproduction in a randomly varying environment. J. Theor. Biol., 12, 110-129.

Come, D. and Thevenot, C. (1982). Environmental control of embryo dormancy and germination. In A.A. Khan (Ed.). The physiology and biochemistry of seed development, dormancy and germination. Elsevier Biomedical Press, Amsterdam, New York, Oxford, 271-298.

Cone, J.W. and Spruit, C.J.P. (1983). Imbibition conditions and seed dormancy of Arabidopsis thaliana. Physiol. Planta., 59, 416-420.

Cook, R.E. (1980). The biology of seeds in the soil. In O.T. Solbrig. Demography and evolution in plant populations. Bot. Monog., 15, 107-129.

Courtney, A.D. (1968). Seed dormancy and field emergence in Polygonum aviculare. J. Appl. Ecol., 5, (3), 675-684.

Cousens, R., Pollard, F. and Denner, R.A.P. (1985). Competition between Bromus sterilis and winter cereals. Aspects of Appl. Biol., 9, The biology & control of weeds in cereals, 67-74.

Cresswell, E.C. and Grime, J.P. (1981). Induction of a light-requirement during seed development and its ecological consequences. Nature, 291, (5816), 583-585.

Cumming, B.G. (1963). The dependence of germination on photoperiod, light quality and temperature in Chenopodium spp. Can. J. Bot., 41, 1211-1234.

Datta, S.C., Gutterman, Y. and Evanari, M. (1972). The influence of the origin of the mother plant on yield and germination of their caryopses in Aegilops ovata. Planta, 105, 155-164.

Donald, W.W. and Hoerauf, R.A. (1985). Enhanced germination and emergence of dormant wild mustard seed by 2 substituted phthalimides. Weed Sci., 33, 894-902.

Douglas, B.J., Thomas, A.G., Morrison, I.N. and Maw, M.G. (1985). The biology of Canadian weeds. 70. Setaria viridis (L.) Beauv. Can. J. Plant. Sci., 65, 669-690.

Doyle, C.J., Cousens, R. and Moss, S.R. (1986). A model of the economics of controlling Alopecurus myosuroides Huds. in winter wheat. Crop Protection, 5, (2), 143-150.

Drabble, E. (1929). Key to the British pansies. J. Bot. (London), LXVII, 69.

Duke, S.O., Egley, G.H. and Reger, B.J. (1977). Model for variable light sensitivity in imbibed dark-dormant seeds. Pl. Physiol., 59, 244-249.

Dzlewanawska, K. and Lewak, S. (1982). Hydrogen cyanide and cyanogenic compounds in seeds. V. Effects of cyanide and azide on germination of apple embryos in relation to their dormancy. Physiologie vegetale, 20, (2), 171-177.

Dvorak, J. and Krejcir (1980). Reserve of weed seed in topsoil under different crop rotations and herbicide application. Acta Universitatis Agriculturae Facultas Agronomica, 28, (2), 9-23.

Egley, G.H. and Chancellor, J.M. (1978). Germination and viability of weed seeds after 2.5 years in a 50 year buried seed study. Weed Sci., 26, (3 230-239.

Egley, G.H. and Duke, S.O. (1985). Physiology of weed seed dormancy and germination. In Duke, S.O. (1985). Weed Physiology Vol. 1. Reproduction & ecophysiology. C.R.C. Press, 28-64.

Ervio, L.R. (1981). The emergence of weeds in the field. Annales Agriculturae Fenniae, 20, (4), 292-303.

Ervio, L.R. (1982). Weed germination in cereals and sugar beet. Weeds and weed control. 23rd Swedish Weed Conf., 2, 330-337.

Esashi, Y., Oota, H., Saitoh, H. and Kodama, H. (1985). Light actions in the germination of cocklebur seeds. J. Exp. Bot., 36, (170), 1465-1477.

Evanari, M. (1957). Les problemes physiologiques de la germination. Bull. Soc. Fr. Physiol. Veg., 3, 105-124.

Evans, G. (1959). In Schafer, D.E. and Chilcote, D.O. (1969) Factors influencing persistence and depletion in buried seed populations. II. The effect of soil temperature and moisture. Crop Sci. 10, 342-345.

Evans, R.A. and Young, J.A. (1982). Microhabitat variation in relation to weed seed germination and seedling emergence. In Hatfield J.L. and Thomason, I.J. (Eds). Biometeorology in integrated pest management, 421-448.

Fawcett, R.S. and Slife, F.W. (1978). Effects of field applications of nitrate on weed seed germination. Weed Sci., 26, (6), 594-596.

Feltner, K.C. and Vesecky, J.F. (1968). Light quality and temperature effects on weed seed germination in two Kansas soils. Trans. Kansas Acad. Sci., 71, 7-12.

Fenner, M. (1980). The inhibition of germination of Bidens pilosa seeds by leaf canopy shade in some natural vegetation types. New Phytol., 84, 95-101.

Fothergill, P.G. (1944). The somatic cytology and taxonomy of our British species of the genus Viola. New Phytol., 43, 23-35.

Frankland, B. (1977). Phytochrome control of seed germination in relation to the light environment. In Smith, H. (1977). Light and plant development. Butterworths, London, 471-491.

Frankland, B. (1980). Phytochrome and seed germination. What's new in plant physiology? 11, (8), 29-32.

Frankland, B. (1981). Germination in shade. In Smith, H. (1981). Plants and the daylight spectrum, London Acedemic Press, 187-204.

Frankland, B. and Taylorson, R. (1983). Light control of seed germination. In Shropshire Jr, W. and Mohr, H. Photomorphogenesis. Encyclopedia of Pl. Physiol. 16A. Springer-Verlag, 428-456.

Freijsen, A.H.J., Troclestra, S.R. and van Katz, M.J. (1980). The effect of soil nitrate on germination of Cynoglossum officinale and its ecological significance. Oecol. Plant., 1, (15), 71-79.

Frey, K.J. and Horner, T. (1957). Heritability in standard units. Agron. J., 49, (2), 59-62.

Frost, C. (1982). Effects of herbicides alone and in mixtures on dicoyledonous weeds in wheat and barley. Ir. J. Agric. Res., 21, 211-226.

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

Froud-Williams, R.J. (1985). Dormancy & germination of arable grass weeds. Asp. Appl. Biol. 9, 9-19.

Froud-Williams, R.J. (1985). Biology of cleavers (Galium aparine). Asp. Appl. Biol., 9, 189-195

Froud-Williams, R.J., Chancellor, R.J. and Drennan, D.S.H. (1983). Influence of cultivation regime upon buried weed seeds in arable cropping systems. J. Appl. Ecol., 20, (1), 199-208.

Froud-Williams, R.J., Drennan, D.S.H. and Chancellor, R.J. (1984). The influence of burial and dry storage upon cyclic changes in dormancy, germination and response to light in seeds of various arable weeds. New Phytol., 96, 473-481.

Froud-Williams, R.J., Hilton, J.R., and Dixon, J. (1986). Evidence for an endogenous cycle of dormancy in drystored seeds of Poa trivialis. New Phytol., 102, 123-131.

Fryxell, P.A. (1957). Mode of reproduction of higher plants. Bot. Rev., 23, 135-233.

Garbutt, K. and Witcombe, J.R. (1986). The inheritance of seed dormancy in Sinapis arvensis. Heredity, 56, 25-31.

Gherse, C.M., Satorre, E.H., and Van Esso, M.L. (1985) Seasonal patterns of johnsongrass seed production in different agricultural systems. Isr. J. Bot., 34, (1), 24-31.

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

Gorski, T., Gorska, K. and Rybicki, J. (1978). Studies on the germination of seeds under leaf canopy. Flora., Bd., 167 S, 289-299.

Gray, D. and Thomas, T.H. (1982). Seed germination and seedling emergence as influenced by the position of development of the seed on, and the chemical application to the parent plant. In Khan, A.A. Ed.) The physiology and biochemistry of seed development, dormancy and germination. Elsevier Biomedical Press, Amsterdam, New York, Oxford, 81-110.

Grime, J.P. (1979). Plant Strategies and Vegetation Processes. Wiley and Sons, New York.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neil, A.M. and Shaw, S. (1981). A comparative study of germination characteristics in a local flora. J. Ecol., 69, 1017-1059.

Gross, K.L. (1985). Effects of irradiation and spectral quality on the germination of Verbascum thapsus and Oenothera biennis seeds. New Phytol., 101, 531-541.

Grubisic, Dragoljub, Mirjana Neskovic and Ra-Domir Konjevic. (1985). Changes in light sensitivity of Paulownia tomentosa and P. fortunei seeds. Plant Sci. (Shannon) 39, (1), 13-16.

Gutterman, Y. (1973). Differences in the progeny due to daylength and hormone treatment of the mother plant. In Heydecker, W. (Ed). Seed Ecology. Butterworths, London. 59-80.

Gutterman, Y. (1980/81). Review: Influences on seed germinability: Phenotypic maternal effects during seed maturation. Isr. J. Bot., 29, 105-117.

Gutterman, Y. (1982). Phenotypic maternal effects on seed germination. In Khan, A.A. (Ed.). The physiology and biochemistry of seed development, dormancy and germination. Elsevier Biomedical Press, Amsterdam, New York, Oxford, 67-79.

Gutterman, Y. (1985). Flowering, seed development and the influences during seed maturation on seed germination of annual weeds. In Duke, S.O. Weed Physiology Vol. 1. Reproduction and ecophysiology. CRC Press, 1-25.

Hacker, J.B., Andrew, M.H., McIvor, J.G. and Mott, J.J. (1984). Evolution in contrasting climates of dormancy characteristics of seeds of Digitaria milanjiana. J. Appl. Ecol., 21, (3), 961-969.

Hakansson, S (1979). The influence of different factors on the development & control of weeds. Proc. EWRS Symp.

Hakansson, S. (1982). Germination of weed seeds in arable soil at different temperatures and times of year. Rapport Institutionen for Vaxtodling Sveriges Lantbaiksuniversitet No. 100.

Hand, D.J., Craig, G., Takaki, M. and Kendrick, R.E. (1982). Interaction of light and temperature on seed germination of Rumex obtusifolius. Planta, 156, 457-460.

Hanf, M. (1985). The arable weeds of Europe. BASF UK Ltd.

Harper, J.L. (1959). The ecological significance of dormancy and its importance in weed control. Proc. 4th Int. Congr. Crop Bot., 1, 415-420

Harper, J.L. (1977). Population biology of plants. Academic Press London, 892p.

Harper, J.L. and McNaughton, I.H. (1960). The inheritance of dormancy in inter and intraspecific hybrids of Papaver. Heredity, 15, 315-320.

Harper, J.L., Williams, J.T. and Sagar, G.R. (1965). The behaviour of seeds in soil. 1. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol., 53, 273-286.

Hartmann, K.M. (1966). A general hypothesis to interprete "H.E. phenomena" of photomorphogenesis on the basis of phytochrome. Photochem. & Photobiol., 5, 349-366.

Hendricks, S.B. and Taylorson, R.B. (1978). Dependence of phytochrome action in seeds on membrane organisation. Plant Physiol. (Bethesda) 61, (1), 17-19.

Henson, I.E. (1970). The effects of light, nitrate and temperature on the germination of Chenopodium album. Weed Res., 10, 27-39.

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

Hilton, J.R. (1985). The influence of light and potassium nitrate on the dormancy and germination of Avena fatua seed. Seed Ecology Meeting, Plymouth, 1985.

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

Holzner, W. (1982). The Ideal Weed. In Holzner, W. and Numata, N. (Eds.) Biology and ecology of weeds. Junk Pubs. Netherlands, Kluwer-Acedemic.

Hsaio, A.I. and Simpson, G.M. (1971). Dormancy studies in seeds of Avena fatua. 7. The effects of light and variation in water regime on germination. Can. J. Bot., 49, 1347-1357.

Hsaio, A.I. and Vidaver, W. (1984). Effects of temperature and various R and FR irradiations on phytochrome and gibberellin A3-mediated control in partially hydrated lettuce seeds. J. Exp. Bot. 35, (161), 1771-1781.

Hubbard, K.R. (1985). Cereal prospects for 1995 and after: technical implications for cereal production. Aspects Appl. Biol., 9, The biology and control of weeds in cereals., 1-8.

Inouye, R.S. (1980). Density-dependent germination response by seeds of desert annuals. Oecol., 46, 235-258.

Jain, S.K. (1979). Adaptive strategies: polymorphism, plasticity and homeostasis. In Solbrig, O.T., Jain, S., Johnson, G.B. and Raven, P.H. Topics in plant population biology. Columbia University Press, N.Y., 160-187.

Jain, S.K. (1982). Variation and adaptive role of seed dormancy in some annual grassland species. Bot. Gaz., 143, (1), 101-106.

Jana, S., Acharya, S.N. and Naylor, J.M. (1979). Dormancy studies in seeds of A. fatua. 10. On the inheritance of germination behaviour. Can. J. Bot., 57, 1663-1667.

Jana, S & Naylor, J.M. (1980). Dormancy studies in seed of Avena fatua. Heritability for seed dormancy. Can. J. Bot. 58, (1), 91-93.

Janczak, D. (1982). Monoculture of winter rape and weed infestation of crops and soil. Acta Universitatis Agriculturae, XX, 1033, (3).

Janssen, J.G.M. (1973). Effects of light, temperature and seed age on the germination of the winter annuals Veronica arvensis L. and Myosotis ramosissima Rochel ex Schult. Oecol.(Berl.) 12, 141-146.

Jensen, H.A. (1969). Content of buried seeds in arable soils in Denmark and its relationship to the weed population. Dansk Botanisk Arkiv, 27, (2).

Jones, K.H. and Medd, R.W. (1984). Extraction method for separating seeds from soil. 7th Aust. Weeds Conf., Perth.

Jordan, L.S. and Jordan, L.J. (1981). Field bindweed (Convolvulus arvensis) seed germination. Proc. N.C. Weed Control Conf., 35, 151-152.

Karssen, C.M. (1980/81). Patterns of change in dormancy during burial of seeds in soil. Isr. J. Bot., 29, (1/4), 65-73.

Karssen, C.M. (1982). Seasonal patterns of dormancy in weed seeds. In Khan, A.A. (Ed.). (1982). The physiology and biochemistry of seed development, dormancy and germination. Elsevier Biomedical Press, Amsterdam, New York, Oxford, 243-270.

Kendricks, R.E. and Frankland, B. (1969). Photocontrol of germination in Amaranthus caudatus. Planta, 85, 326-339.

Kigel, J., Ofir, M. and Koller, D. (1977). Control of the germination responses of Amaranthus retroflexus seeds by their parental photothermal environment. J. Exp. Bot., 28, (106), 1125-1136.

King, T.T. (1975). Inhibition of seed germination under leaf canopies in Arenaria serpyllifolia, Veronica arvensis & Cerastium holosteoides. New Phytol., 75, 87-90.

Kolk, H. (1962). Viability and dormancy of dry-stored weed seeds. Vaxtodling. Plant husbandry-Uppsala 18.

Kolk, H. (1978). Weed seeds. Recent adv. in seed sci. and technol. pt. 4.

Kropac, Z. (1966). Estimation of weed seeds in arable soil. Pedobiologia, Bd., 65, 105-128.

Lambelet-Haueter, C. (1985). Comparisons entre flore reelle et flore potentielle en grandes cultures de la region genevoise. Candollea, 40, 99-107.

Leguizamon, E.S. and Roberts, H.A. (1982). Seed production by an arable weed community. Weed Res., 22, 35-39.

Linhart, Y.B. (1976). Density-dependent seed germination strategies in colonising vs noncolonising plant species. J. Ecol., 64, 375-380.

Longchamp, J.P. and Gora, M. (1979). Influences d'anoxies partielles sur la germination de semences de mauvaises herbes. Oecol. Plant., 14, (2), 121-128.

Longchamp, J.P. and Gora, M. (1980). Effet de l'enfouissement sur les exigences germinatives des mauvaises herbes. VIe Coll. Int. Ecol. Biol. Syst. Mauvaises Herbes, Montpellier, 113-122.

Lyne, M. (1985). The effects if inorganic nitrate solutions on dormant seeds. Ph.D. Thesis, University of Keele.

Mandoli, D.F., Waldron, L., Nemson, J.A. and Briggs, W.R. (1982). In Bliss, D. and Smith, H. (1985). Penetration of light into soil and it's role in the control of seed germination. Pl. Cell Environ., 8, 475-483.

Marks, M.K. and Price, S.D. (1982). Seed physiology and seasonal emergence of wild lettuce, Lactuca serriola. Oikos, 38, 342-349.

Mason, G. (1976). An investigation of the effect of temperature upon the germination and growth of native species using temperature-gradient techniques. Ph.D. Thesis, University of Sheffield.

Maurya, A.N. and Ambasht, R.S. (1973). Significance of seed dimorphism in Alysicarpus monilifer. J. Ecol., 61, 213-217.

McBride, J. (1985). Weed problems could be solved by 'seedicide' Ag. Res., 33, (9), 10.

McCullogh, J.M. and Shropshire Jr, W. (1970). Physiological predetermination of germination responses in Arabidopsis thaliana. Pl. Cell Physiol., 11, 139-148.

McKeon, G.M., Rose, C.W., Kalma, J.D. and Tarsell, B.W.R. (1985). Pasture seed dynamics in a dry monsoonal climate. 1. Germination and seedbed environment of Stylosanthes humilis and Digitaria ciliaris. Aust. J. Ecol., 10, 135-147.

Miller, S.D., Nalewaja, J.D. and Mulder, C.E.G. (1982). Morphological and physiological variation in wild oats. Agron. J., 74, (5).

Mohammed, H.A., Clark, S.A. and Ong, C.K. (1985). The influence of temperature during seed development on the germination characteristics of millet seeds. Pl. Cell Environ., 8, 361-362.

Morbach, I. and Mayr, A.M. (1974). Permeability of seed coats to water as related to drying conditions and metabolism of phenolics (Pisum spp). Pl. Physiol., 54, 817-820.

Morbach, I. and Mayr, A.M. (1975). Changes in catechol oxidase and permeability to water in seed coats of Pisum elatius during seed development and maturation. Pl. Physiol., 56, 93-96.

Morgan, S.F. and Berrie, A.M.M. (1970). Development of dormancy during seed maturation in Avena ludoviciana. Nature, 288, 1225.

Mortimer, A.M. (1976). Aspects of the seed population dynamics of Dactylis glomerata L., Holcus lanatus L., Plantago lanceolata L. and Poa annua L. Proc. 1976 Brit. Crop Prot. Conf. Weeds, 687-695.

Mortimer, A.M. (1979). The influence of cultural measures and herbicide practices on the fates of weed seeds. Proc. EWRS Symp. The influence of different factors on the development and control of weeds. 1979, 135-143.

Mortimer, A.M., Putwain, P.D. & McMahon, D.J. (1978). A theoretical approach to the prediction of weed population sizes. Proc. 1978 Brit. Crop Prot. Conf. - Weeds, 467-474.

Naylor, R.E.L. (1972). Aspects of the population dynamics of the weed Alopecurus myosuroides in winter cereal crops. J. Appl. Ecol., 9, 127-139.

Naylor, J.M. (1983). Studies on the genetic control of some physiological processes in seeds. Can. J. Bot., 61, 3561-3567.

Naylor, J.M. and Abdalla, A.F. (1982). Variation in germination behaviour. Seed Sci and Tech., 10, (1), 67-76.

Naylor, J.M. and Jana, S. (1976). Genetic adaptation for seed dormancy in Avena fatua. Can. J. Bot., 54, 306-312.

Newman, E.I. (1963). Factors controlling the germination date of winter annuals. J. Ecol., 51, 625-638.

Newman, E.I. (1967). Response of Aira praecox to weather conditions. 1. The response to drought in spring. J. Ecol., 55, 539-556.

Olatoye, S.T. and Hall, M.H. (1973). Interaction of ethylene and light on dormant weed seeds. In Heydecker, W. (Ed.) Seed Ecology. Butterworths, London, 233-249.

Orson, J. (1981). Timed herbicides save cash. Farmers Weekly Extra Cereals., June 12, 25-27.

Palmblad, I.G. (1968). Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecol., 49, 26-34.

Palmblad, I.G. (1969). Population variation in germination of weedy species. Ecol., 50, 746-748.

Paterson, J.G., Boyd, W.J.R. and Goodchild, N.A. (1976). Effect of temperature and depth of burial on the persistence of seed of Avena fatua in Western Australia. J. Appl. Ecol., 13, (3), 841-847.

Pavlychenko, T.K. and Harrington, J.B. (1934). Competitive efficiency of weeds and cereal crops. Can. J. Res., 10, 77-94.

Pavone, L.V. and Reader, R.J. (1982). The dynamics of seedbank size and seed state of Medicago lupulina. J. Ecol., 70, 537-547.

Pegtel, D.M. (1985). Germination in populations of Solanum dulcamara from contrasting habitats. New Phytol., 100, 671-679.

Pemadasa, M.A. and Amarasinghe, L. (1982). The ecology of montane grassland in Sri Lanka. III. Germination of 3 major grasses. J. Ecol., 70, (2), 483-490.

Pemadasa, M.A. and Lovell, P.H. (1975). Factors controlling germination of some dune annuals. J. Ecol., 63, 47-59.

Pettet, A. (1961). Variation within the British representatives of the Melanium subgenus of Viola. Ph.D. Thesis, University of Southampton.

Pettet, A. (1964). Studies on British Pansies. II. The status of some intermediates between Viola tricolor and Viola arvensis Murr. Watsonia, 6, (1), 51-69.

Pitelka, L.F., Thayer, M.E. and Hanson, S.B. (1983). Variation in achene weight in Aster acuminatus. Can. J. Bot., 61, 1415-1420.

Popay, A.I. and Roberts, E.H. (1970). Factors involved in the dormancy and germination of Capsella bursa-pastoris and Senecio vulgaris. J. Ecol., 58, 103-122.

Pressman, E., Negbi, M., Sachs, M. and Jacobsen, J.V. (1977). Varietal differences in light requirements for germination of celery (Apium graveolens L.). Thermal and solute stress. Aust. J. Plant Physiol. 4, 821-831.

Probert, R.J., Smith, R.D. and Birch, P. (1985a). Germination responses to light and alternating temperatures in European populations of Dactylis glomerata. I. Variability in relation to origin. New Phytol. 101, 305-316.

Probert, R.J., Smith, R.D. and Birch, P. (1985b). Germination responses to light and alternating temperatures in European populations of Dactylis glomerata. II. The genetic and environmental components of germination. New Phytol. 101, 317-322.

Probert, R.J., Smith, R.D. and Birch, P. (1986). Germination responses to light and alternating temperatures in European populations of Dactylis glomerata. New Phytol., 102, 133-142.

Pulcher, M. & Hurle, K. (1984). Unkrautflora und Unkrautsamenvorrat in Weizenmonokultur bei underschiedlicher Pflanzenschutz-intensitat. Z. Pflkrankh. Pflschutz, sonderh. X, 51-61.

Rai, U.N. and Agrawal, S.O. (1985). Seed polymorphism and germination behaviour of Ipomoea muricata growing in cultivated Indian tropic deserts. Acta Bot. Indica, 13, 1-5.

Rai, J.P.N. and Tripathi, R.S. (1985). Effect of established populations of two annual weeds on their newly emerged seedling cohorts. Proc. Indian Acad. Sci. (Plant Sci.), 95, (2), 79-86.

Ramakrishnan, P.S. (1965). Studies on edaphic ecotypes in Euphorbia thymifolia. 1. Seed germination. J. Ecol., 53, 157-158.

Roberts, E.H. (1972). Dormancy: A factor affecting seed survival in the soil. In Roberts, E.H. (Ed.) Viability of seeds, Chapman & Hall, London, 321-359.

Roberts, E.H. (1981). The interaction of environmental factors controlling loss of dormancy in seeds. Ann. Appl. Biol., 98, 552-555

Roberts, E.H. and Totterdell, S. (1981). Seed dormancy in Rumex species in response to environmental factors. Pl. Cell Environ., 4, 97-106.

Roberts, H.A. (1958). Studies on the weeds of vegetable crops. I. Initial effects of cropping on the weed seeds in the soil. J. Ecol., 46, 759-768.

Roberts, H.A. (1962). Studies on the weeds of vegetable crops. II. Effects of 6 years cropping on the weed seeds in the soil. J. Ecol., 50, 803-813.

Roberts, H.A. (1963). Studies on the weeds of vegetable crops. III. Effects of different primary cultivations on the weed seeds in the soil. J. Ecol., 51, 83-95.

Roberts, H.A. (1964). Emergence and longevity in cultivated soil of seeds of some annual weeds. Weed Res., 4, 296-307.

Roberts, H.A. (1979). Periodicity of seedling emergence and seed survival in some Umbelliferae. J. Appl. Ecol., 16, 175-201.

Roberts, H.A. (1981). Seed banks in soils. Adv. Appl. Biol., 6, 1-55.

Roberts, E.H. and Benjamin, S.K. (1979). The interaction of light, nitrate and alternating temperature on the germination of Chenopodium album, Capsella bursa pastoris and Poa annua before and after chilling. Seed Sci. Technol., 7, 379-392.

Roberts, H.A. and Boddrell, J.E. (1983). Seed survival and periodicity of seedling emergence in 10 species of annual weeds. Ann. Appl. Biol., 102, (3), 523-532.

Roberts, H.A. and Boddrell, J.E. (1984). Seed survival and seasonal emergence of seedlings of some ruderal plants. J. Appl. Ecol., 21, 617-628.

Roberts, H.A. and Boddrell, J.E. (1985). Seed survival and seasonal emergence in some species of Geranium, Ranunculus, and Rumex. Ann. Appl. Bol., 107, 231-238.

Roberts, H.A. and Chancellor, R.J. (1979). Periodicity of seedling emergence & achene survival in some species of Carduus, Cirsium and Onopordum. J. Appl. Ecol., 16, 641-647.

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

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

Roberts, H.A. and Feast, P.M. (1973). Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. J. Appl. Ecol., 10, (1), 133-143.

Roberts, H.A. and Hewson, R.T. (1971). Herbicide performance and soil surface conditions. Weed Res., 11, 69-73.

Roberts, H.A. and Lockett, P.M. (1975). Germination of buried and dry-stored seeds of Stellaria media. Weed Res., 15, 199-204.

Roberts, H.A. and Lockett, P.M. (1978). Seed dormancy and periodicity of seedling emergence in Veronica hederifolia. Weed Res., 18, 41-48.

Roberts, H.A. and Neilson, J.E. (1980). Seed survival and periodicity of seedling emergence in some species of Atriplex, Chenopodium, Polygonum and Rumex. Ann. Appl. Biol., 94, 111-120.

Roberts, H.A. and Neilson, J.E. (1981). Changes in the soil seedbank of four longterm crop/herbicide experiments. J. Appl. Ecol., 18, (2), 64-68.

Roberts, H.A. and Neilson, J.E. (1982). Seasonal changes in the temperature requirements for buried seeds of Aphanes arvensis L. New Phytol., 92, 159-166.

Roberts, H.A. and Potter, M.E. (1980). Emergence patterns of weed seedlings in relation to cultivation and rainfall. Weed Res., 20, 377-386.

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

Roberts, H.A. and Stokes, F.G. (1966). Studies on the weeds of vegetable crops. VI. Seed populations of soil under commercial cropping. J. Appl. Ecol., 3, (1), 181-190.

Rorison, I.H. (1973). Seed ecology present and future. In Heydecker, W. (Ed.) (1973). Seed Ecology. Butterworths, London. 497-519.

Rozijn, N.A.M.G. and van Andel, J. (1985). Analysis of the germination syndrome of dune annuals. Flora, 177, 175–185.

Russell, E.W. (1961). Soil conditions and plant growth. 9th Ed., Longmans, London.

Sagar, G.R. and Mortimer, A.M. (1976). The population dynamics of plants. In Coaker, T.H. (Ed.) Appl. Biol. Vol. 1, Acad. Press, 1–47

Salisbury, E.J. (1965). Germination experiments with seeds of a segregate of Plantago major and their bearing on germination studies. Ann. Bot., 29, 513–521.

Sarukhan, J. (1974). Studies on plant demography: Ranunculus repens L., R. bulbosus L. and R. acris L. II. Reproductive strategies & seed population dynamics. J. Ecol, 62, 151–177.

Sauer, J. and Struik, G. (1964). A possible ecological relationship between soil disturbance, light flash and seed germination. Ecol., 45, 884–886.

Sawhney, R. and Naylor, J.M. (1982). Dormancy studies in seeds of Avena fatua. 13. Influence of drought stress during seed development on duration of seed dormancy. Can. J. Bot., 60, (6), 1016–1020.

Sawhney, R. and Quick, W.A. (1985). The effect of temperature during parental vegetative growth on seed germination in Avena fatua. Ann. Bot., 55, 25–28.

Sawhney, R., Hsaio, A.I. and Quick, Q.A. (1984). Temperature control of germination and its possible role in the survival of a non-dormant population of Avena fatua. Physiol. Plant., 61, 331-336.

Schaal, B.A. (1980). Reproductive capacity and seed size in Lupinus texenais. Amer. J. Bot., 67, (5), 703-709.

Schafer, D.E. and Chilcote, D.O. (1969). Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and& moisture. Crop Sci., 10, 342-345.

Schimpf, D.J. and Palmblad, I.G. (1980). Germination response of weed seeds to soil nitrate and ammonium with and without simulated overwintering. Weed Sci., 28, (2), 190-193.

Sharma, M.P., McBeath, D.K. and van den Born. (1976). Studies on the biology of wild oats. I. Dormancy, germination and emergence. Can. J. Plant Sci., 56, 611-618.

Siegel, S.M. (1950). Effects of exposures of seeds to various physical agents. 1. Effects of brief exposures to heat and cold on germination and light-sensitivity. Bot. Gaz., 112, 57-70.

Siegel, S.M. and Rosen, L.A. (1962). Effects of reduced oxygen tension on germination and seedling growth. Physiol. Plant., 15, 437-446.

Silvertown, J. (1980). Leaf-canopy-induced seed dormancy in a grassland flora. New Phytol. 85, 109-118.

Silvertown, J.W. (1984). Phenotypic variety in seed germination behaviour: The ontogeny and evolution of somatic polymorphism in seeds. Am. Nat., 124, (1), 1-16.

Silvertown, J.W. (1982). Introduction to plant population ecology. London: Longman.

Smith, H. (1982). Light quality, photoperception and plant strategy. Ann. Rev. Pl. Physiol., 33, 481-518.

Smith, B.H. (1983). Demography of Floerkea proserpinacoides, a forest-floor annual. 1. Density-dependent growth and mortality. J. Ecol., 71, (2), 391-404.

Smith, B.H. and Russell E.W. (1969). Occurrence of ethylene and its significance in anaerobic soil. Nature, 222, 769-771.

Sparke, C.J. and Bostock, S.J. (1985). Intraspecific variation in seed characteristics of herbaceous plants. Final Report to N.E.R.C.

Staniforth, R.J. and Cavers, P.B. (1979). Field & laboratory germination of achenes of Polygonum lapathifolium, P. pennsylvanicum and P. persicaria. Can. J. Bot., 57, 877-885.

Steinbauer, G.P. and Grigsby, B. (1957). Interaction of temperature, light and moistening agent in the germination of weed seeds. J. of Weed Soc. of Am., V, (3).

Stoller, E.W. and Wax, L.M. (1974). Dormancy changes and fate of some annual weed seeds in the soil. Weed Sci. 22, 151-155.

Taylorson, R.B. (1969). Photocontrol of rough cinquefoil seed germination and its enhancement by temperature manipulation and KNO3. Weed Sci., 17, 144-147.

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

Taylorson, R.B. (1972). Phytochrome controlled changes in dormancy and germination of buried weed seeds. Weed Sci., 20, (5), 417-422.

Taylorson, R.B. (1982). Interaction of phytochrome and other factors in seed germination. In Khan, A.A. (Ed.) The physiology and biochemistry of seed development, dormancy and germination. Elsevier Biomedical Press, Amsterdam, New York, Oxford, 323-346.

Taylorson, R.B. and Hendricks, S.B. (1969). Action of phytochrome during prechilling of Amaranthus retroflexus seeds. Pl. Physiol., 44, 821-825.

Taylorson, R.B. and Hendricks, S.B. (1971). Changes in phytochrome expressed by germination of A. retoflexus seeds. Pl. Physiol., 47, 619-622.

Taylorson, R.B. and Hendricks, S.B. (1977). Dormancy in seeds. Ann. Rev. Pl. Physiol., 28, 331-354.

Templeton, A.R. and Levin, D.A. (1979). Evolutionary consequences of seed pools. Am. Nat., 114, (2), 232-249.

Thill, D.C., Zamora, D.L. and Kambitsch, D.L. (1985). Germination & viability of common crupina (Crupina vulgaris) achenes buried in the field. Weed Sci., 33, 344-348.

Thompson, P.A. (1970). Changes in germination responses of Silene secundiflora in relation to the climate of its habitat. Physiol. Planta., 23, 739-746.

Thompson, P.A. (1973). Geographical adaptation of seeds. In Heydecker, W. (Ed.) (1973). Seed Ecology. Butterworths, London. 31-58.

Thompson, K. and Grime, J.P. (1979). Seasonal variation in the seedbanks of herbaceous species in 10 contrasting habitats. J. Ecol., 67, 893-921.

Thompson, K. and Grime, J.P. (1983). A comparative study of germination responses to diurnally fluctuating temperatures. J. Appl. Ecol., 20, (1), 141-156.

Thompson, K., Grime, J.P. and Mason, G. (1977). Seed germination in response to diurnal fluctuations of temperature. Nature, 267, 147-149.

Thompson, K. and Whatley, J.C. (1984). A thermogradient bar apparatus for the study of the germination requirements of buried seeds in situ. New Phytol., 96, 459-471.

Thorne, J.H. (1982). Temperature and oxygen effects on C - photosynthate unloading and accumulation in developing soybeans. Pl. Physiol., 69, (1), 48-53.

Thornton, N.C. (1936). Carbon dioxide storage. IX. Germination of lettuce seeds at high temperatures in both light and darkness. Contrib. Boyce Thompson Inst., 8, 25.

Thurston, J.M. (1964). Germination of Alopecurus myosuroides Huds. (Black grass). Proceedings 1964 Brit. Weed Contr. Conf., 349-351.

Thurston, J.M. (1969). Weed studies in Broadbalk. Report of the Rothamsted Experimental Station 1968, 186-208.

Toole, E.H., Hendricks, S.B., Borthwick, H.A. and Toole, V.K. (1956). Physiology of seed germination. Ann. Rev. Pl. Physiol., 7, 299-324.

Toole, E.H., Toole, V.K., Hendricks, S.B. and Borthwick, H.A. (1957). Effect of temperature on germination of light-sensitive seeds. Proc. Int. Seed Testing Assoc., 22, 196-204.

Totterdell, S. and Roberts, E.H. (1980). Characteristics of alternating temperatures which stimulate loss of dormancy in seeds of Rumex obtusifolius and R. crispus. Pl. Cell. Environ., 3, 3-12.

Totterdell, S. and Roberts, E.H. (1981). Ontogenetic variation in response to temperature change in the control of seed dormancy of Rumex obtusifolius L. and R. crispus L. Pl. Cell Environ., 4, 75-80.

Upadhyaya, M.K. (1982). The physiological basis of seed dormancy in Avena fatua. 1. Action of the respiratory inhibitors sodium azide and salicylhydroxanic acid. Physiol. Plant., 54, (4), 419-424.

Valio, I.F.M., Kurszenzaft, S.L. and Rocha, R.F. (1972). Germination of achenes of Bidens pilosa L. I. Effect of light of different wavelengths. New Phytol. 71, 677-682.

VanAbrams, G.J. and Hand, M.C. (1976). Seed dormancy in Rosa as a function of climate. Am. J. Bot., 43, 7-12.

Van der Meijden, E. and Van der Waals-Kooi (1979). The population ecology of Senecio jacobaea in a sand dune system. 1. Reproductive strategy and the biennial habit. J. Ecol., 67, 131-153.

Van der Woude, W.J. and Toole, V.K. (1979). Prechilling enhancement of phytochrome-dependent lettuce seed germination: Indication of a membrane-associated mechanism. Pl. Physiol. suppl., 63, 15.

Van der Woude, W.J. and Toole, V.K. (1980). Studies on the mechanism of enhancement of phytochrome-dependent lettuce seed germination by prechilling. Pl. Physiol., 66, 220-224.

Vanlerburghe, K.A. and Van Assche, J.A. (1986). Dormancy phases in seeds of Verbascum thapsus. Oecol., 68, 479-480.

Vegis, A. (1964). Dormancy in higher plants. Ann. Rev. Pl. Physiol., 15, 185–224.

Vincent, E.M. (1974). The ecology of some weed species in relation to their germination behaviour. PhD. Thesis, University of Reading.

Vincent, E.M. and Cavers, P.B. (1978). The effects of wetting and drying on subsequent germination of Rumex crispus. Can. J. Bot., 56, (18), 2207–2217.

Vincent, E.M. and Roberts, E.H. (1977). The interaction of light, nitrate and alternating temperatures in promoting the germination of dormant seeds of common weed species. Seed Sci. Technol., 5, 659–670.

Walker, A. and Barnes, A. (1981). Simulation of herbicide persistence in soil: A revised computer model. Pestic. Sci., 12, 123–132.

Walker, S.R. and Evensen, J.P. (1985). Biology of Commelina benghalensis L. in south-eastern Queensland. 2. Seed dormancy, germination and emergence. Weed Res., 25, 245–250.

Walker, H. (1963). Uber die stickstoffanspruche (die Nitrophile) der Ruderalplanzen. Mitt. flor.-soz. ArbGemeinsch. N.F., 10, 56–69.

Wareing, P.F., van Staden, J. and Webb, D.P. (1973). Endogenous hormones in the control of seed dormancy. In Heydecker, W. (Ed.) (1973). Butterworths, London, 145–155.

Washitani, I. (1985). Field fate of Amaranthus patulus seeds subjected to leaf-canopy inhibition of germination. Oecol., 66, 338–342.

Watanabe, Y. and Hirokawa, F. (1975). Ecological studies on the germination and emergence of annual weeds. 3. Changes in emergence and viable seeds in cultivated and uncultivated soil. Weed Res., Japan, 19, 14-19.

Watkins, F.B. (1966). Effect of nitrogen fertilizer on the emergence of wild oat (Avena ludoviciana). Queenaland J. Agric. Sci., 27, 49-53.

Watkinson, A.R. and Harper, J.E. (1978). The demography of a sand dune annual: Vulpia fasciculata. J. Ecol., 66, 15-33.

Wesson, G. and Wareing, P.F. (1967). Light requirements of buried seeds. Nature, London, 213, 601.

Wesson, G. and Wareing, P.F. (1969). The role of light in the germination of naturally occurring populations of buried weed seeds. J. Exp. Bot., 20, (63), 402-413.

Wesson, G. and Wareing, P.F. (1969). The introduction of light sensitivity in weed seeds by burial. J. Exp. Bot., 20, (63), 414-425.

Willemsen, R.W. (1975). Effect of stratification temperature and germination temperature on germination and the induction of secondary dormancy in common ragweed seeds. Am. J. Bot., 62, 131-135.

Williams, E.D. (1983) Effects of temperature fluctuation, red and far-red light and nitrate on seed germination of 5 grasses. J. Appl. Ecol., 20, 923-935.

Williams, E.D. (1984). Changes during 3 years in the size and composition of the seedbank beneath a long-term pasture as influenced by defoliation and fertilizer regime. J. Appl. Ecol., 21, 603-615.

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

Wilson, B.J. and Cussons, G.W. (1975). A study of the population dynamics of Avena fatua L. as influenced by straw burning, seed shedding and cultivation. Weed Res., 15, 249-253.

Woolley, J.T. and Stoller, E.W. (1978). Light penetration and light-induced seed germination in soil. Pl. Physiol., 61, 597-600.

Wulff, R. (1973). Intrapopulation variation in the germination of seeds in Hyptis suaveolens. Ecol., 54, 646-649.

Wulff, R.D. and Alexander, H.M. (1985). Intraspecific variation in the response to carbon dioxide enrichment in seeds of Plantago lanceolata. Oecol., 66, 658-660.

Wulff, R. and Briceno, M. (1976). Light and temperature interaction in the control of germination of seeds in Ludwigia octovalis. Planta, 128, 195-199.

Wurzburger, J. and Koller, D. (1976). Differential effects of the parental photothermal environment on the development of dormancy in caryopses of Aegilops kotschyi. J. Exp. Bot., 27, (96), 43-48.

TITLE THE POPULATION DYNAMICS OF FIELD PANSY (VIOLA ARVENSIS) AND RED DEADNETTLE (LAMIUM PURPUREM) IN WINTER CEREAL AND OILSEED RAPE FIELDS.

AUTHOR JANE GILBERT

INSTITUTION and DATE UNIVERSITY OF KEELE. 1987.

DX

83992