

Annual dormancy patterns of weed seeds influence weed control

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Summary

Dormancy of buried weed seeds is not stable but fluctuates in an annual pattern. Tests of exhumed seeds at a range of temperatures have shown that relief of dormancy is characterized by a widening of the range of temperatures over which germination can occur, during induction of dormancy this range becomes narrower. Temperature in the field plays a dual role. On the one hand, germination depends on whether the actual temperature is within the germination-temperature range. On the other hand, annual fluctuations in temperature are the main driving force for the changes in dormancy. A model was developed that simulated the annual changes in dormancy. The value of descriptive models for the understanding of the behaviour of weed seeds in soil is discussed. Apart from the successful stimulation of *Striga* seed germination in soil by infusion of ethylene, other attempts to reduce seed banks by chemical methods have failed. Nitrate is the major naturally-occurring soil component that stimulates seed germination. It widens the annual period that seeds can germinate.

Introduction

Despite the total chemical warfare declared against them, weeds still thrive. While in some species this has been traced to development of tolerance or resistance to herbicides, in others survival is undoubtedly due to developmental strategies that provide protection of the original germplasm and, thereby, contributes to indefinite regeneration and reproduction. Developmental aspects of reproduction and dispersal physiology should be studied in depth. Such studies should provide essential information for the development of biological

or integrated weed control strategies. These might be the most promising way to limit the use of herbicides.

Seed dormancy is crucial to the survival of weeds and, as a consequence, causes serious problems to weed control strategies (13). Dormant seeds are often difficult to kill and, with the exception of soil sterilization methods, current weed control methods are not effective upon dormant weed seed (10).

However, it is often overlooked that dormancy of seeds under field conditions is not stable. In most species dormancy fluctuates in a seasonal pattern. This paper will discuss whether improved knowledge of such dormancy patterns may eventually lead to new and more effective methods of weed control. For instance, it may stimulate attempts to break dormancy of buried weed seeds by chemical and physical means.

Seed survival in soil

Most agricultural soils contain vast numbers of weed seeds. These seed banks provide a source of weed seedlings that extends the weed problem even when seed reinfestation is carefully prevented. Seed banks may range from 10,000 to 100,000 seeds m⁻² (26). Seed banks of some annual and perennial grasses and herbs are only transient. At the end of the growing season the banks are 'empty' due to massive germination or seed death. However, most major annual weeds form persistent seed banks, able to survive in soil for considerable periods of time. Extremely long periods of seed survival were reported by Odum (20), who examined the viable seed content of soil samples from beneath buildings of known antiquity. According to some of his records, 1600 years old weed seeds of *Chenopodium album* and *Spergula arvensis* were still viable.

The survival of crop seeds under commercial dry-storage conditions has been studied in much detail. However, little is known about the survival mechanisms of imbibed seeds, particularly in soils under field conditions. In

general; imbibed seeds may survive better than dry seeds, as damage to essential biochemical machinery can be repaired (36).

Germination followed by seedling emergence is the primary cause of diminishing seed banks. Therefore, cultivation of soils; which increases germination, reduces the seed bank. However, the seed banks also decrease in undisturbed soils. The activity of seed-destroying organisms may be one reason for the decrease, and seed death through metabolic exhaustion another. Imbibed seeds show a low but constant respiratory activity (M.P.M. Derkx, personal communication). Such respiration will inevitably deplete the reserves of low molecular weight metabolic substrates. The vast reserves of polymeric compounds (starch, lipids, proteins) often cannot be hydrolyzed before the start of germination.

A third cause of seed bank depletion may be **fatal germination**, i.e., when it is not followed by seedling emergence. This may occur when seeds germinate at the wrong time of the year or the wrong place in the soil. As a consequence, the seedlings may freeze, desiccate or even never reach the soil surface. Fatal germination indicates a lack of proper germination control, which may occur more frequently in aging seeds.

The relevance of the different causes for seed bank depletion in undisturbed soils are unknown. Better knowledge will help provide a better prediction and explanation of seed bank survival.

Annual dormancy patterns

Studies with both artificially buried and natural seed populations have shown that the emergence of many weed species occurs in a seasonal pattern, often at specific intervals.

For instance, emergence of many species is restricted to one or two months in spring, e.g., *Setaria lutescens*, *Abutilon theophrasti*, *Ambrosia trifida*, *A. artemisiifolia*, *Polygonum pensylvanicum* (34), and *Polygonum convolvulus* (12,27). Others germinate mainly in autumn and/or winter, e.g., *Aphanes arvensis* (30) and *Veronica hederifolia* (27,28). However, many of the latter may also emerge in spring.

For some species, the first large, spring flush emergence is followed by several smaller ones throughout summer, particularly when the soil is cultivated frequently, e.g., *Capsella bursa-pastoris* (23,27), *Senecio vulgaris* (23), *Spergula arvensis* (12), *Chenopodium album*, *Solanum nigrum* and *Amaranthus retroflexus* (21). Frequent cultivation of the soil increases the number of emerging seedlings for most species, but it does not greatly influence the periodicity of emergence (27,29).

As discussed, the exhaustion of available seeds only occurs with transient seed banks which reflect seasonal limitations of germination. In persistent seed banks, the seasonal emergence patterns reflect seasonal variations in dormancy (6,16). After shedding, seeds often possess primary dormancy (Figure 1). To break primary dormancy in either dry or imbibed seeds requires exposure to a certain temperature for a certain period. Only then will seeds become sensitive to factors that stimulate germination. However, germination will only occur when all factors occur, otherwise germination is inhibited. If inhibition is extended for too long, the seeds may enter secondary dormancy. Secondary dormancy can be broken through suitable variations in temperature. This cycle may be repeated for a number of years.

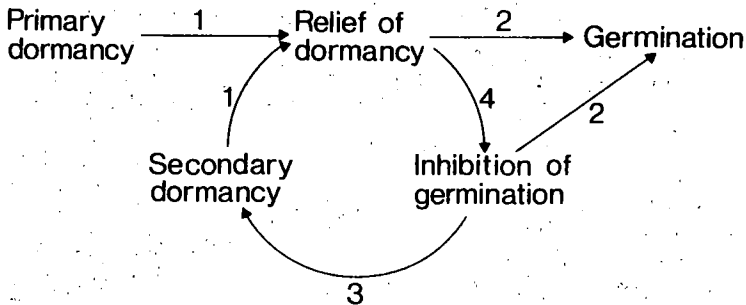


Figure 1 Dormancy in seeds. Dormancy changes caused by (1) factors breaking primary or secondary dormancy, (2) factors coinciding with conditions required for germination, (3) factors inducing dormancy, (4) factors different from conditions required for germination and/or inhibitory for germination (from (16)).

Dormancy patterns are studied by burying seeds in soil, usually in nylon sachets to aid retrieval. At regular intervals, portions of the seeds are exhumed and germination tested. These tests mostly test one condition only, but Baskin and Baskin (1,2,3,4,5) have shown that the test temperature strongly affects germination. Therefore, temperature can influence the results and predictions of the dormancy pattern. Also, non-optimal temperatures can falsely indicate seed dormancy. Therefore, germination tests of exhumed seeds should be performed over a range of temperatures. Such tests have shown that stimulation of germination is improved by widening the range of temperatures over which germination can proceed, conversely dormancy is induced when the range becomes narrower. In summer annuals it is the minimum temperature fluctuations which are more critical, whereas in winter annuals it is mainly the maximum temperature fluctuations.

In the field temperature plays a dual role. On the one hand, germination is dependent on temperature. On the other hand, it is the main driving force to induce dormancy. Therefore, temperature determines the width of the germination-temperature range.

Totterdell and Roberts (35) hypothesized that the loss of dormancy of *Rumex obtusifolius* and *R. crispus* at low temperatures results from two sub-processes: (i) **Relief** of primary dormancy and (ii) **induction** of secondary dormancy. They suggested that relief of primary dormancy only occurred at temperatures below a certain value. This critical temperature was estimated to be 15°C for the *Rumex* spp. It was hypothesized that this was independent of the lowest temperature, so long as it was below 15°C. In their opinion, induction of secondary dormancy occurred at all temperatures, with the rate of induction increasing with an increase in temperature. They also suggested that the effect of pretreatment temperature on the dormancy of *Rumex* spp. depended on these two sub-processes. This implies that, although relief of primary dormancy occurred equally at all temperatures below 15°C, temperatures just above zero gave the most effective net relief of dormancy, because induction of secondary dormancy was lowest at these low temperatures.

Although Totterdell and Roberts (35) used the term 'stratification' for the net result of the

two subprocesses, we prefer 'dormancy relief' or 'dormancy induction'. When, for example, germination increases due to pretreatment at a certain temperature, dormancy is said to be relieved, however the sub-processes defined by Totterdell and Roberts may occur simultaneously.

Development of a model

Recently we applied the theory of Totterdell and Roberts (35) to test whether changes in field temperature were indeed the driving force for dormancy patterns in buried seeds of *Polygonum persicaria*, *Chenopodium album*, *Spergula arvensis* and *Sisymbrium officinale* (8,9). It was assumed that the sub-processes of dormancy relief and induction were regulated by cold (C) and heat (H), respectively. C and H were calculated from soil temperature data measured at Wageningen over three successive years.

Because it is assumed that dormancy relief is independent of the actual temperature as long as it is below a critical temperature, the value of C was raised by an arbitrary value 1 for each period of 10 days that the mean soil temperature (at 10 cm) was below the critical temperature. Different critical temperatures were used for the calculation of C to determine which temperature was optimal for each species. H was calculated by totalling the mean soil temperature for each successive 10 day period. When the mean soil temperature was below 0°C over a 10 day period, which occurred only three times during the experiment, neither C nor H were increased. C and H were never reset to zero, because it would have been unreliable to predict when this occurred. Therefore, both factors increased throughout the experiment, C only when the field temperature was below the critical temperature, and H continuously. This implies that time was involved in both parameters.

A model was developed that simulated changes in dormancy during soil burial. It was based on the assumption that dormancy (D) is a function of C and H:

$$D = f(C, H) \quad [1]$$

It was shown that at a given time germination (G_t) can be described by a quadratic function of the germination temperature (T_g):

$$G_t = a.T_g^2 + b.T_g + c \quad [2]$$

where a, b and c are the coefficients of the quadratic function.

It was assumed that one or more of these coefficients are a function of dormancy, and/or of the factors that influence the germination results, such as the composition of the germination medium (M_p); in our study that was the presence or absence of KNO_3 . Experimental data suggested that temperature shortly before exhumation directly influenced germination, but not through C and H alone. Therefore, the mean pretreatment temperature (T_p) during a period (d_p) prior to exhumation (T_p, d_p) was considered as possibly influencing a, b and c. In summary:

$$a, b, c = f(C, H, M_p, T_p, d_p) \quad [3]$$

Although light is also an important environmental factor influencing germination it was omitted from the model because all our germination experiments were performed in light.

Equation [3] was substituted in [2]. With forward and backward stepwise regression the parameters were selected that maximized the fit of data from germination experiments with seeds that were exhumed at different times during three successive years. Germination

was tested at a range of constant temperatures. A model was developed with the parameter time (weeks of burial) instead of C and H but showed a much poorer fit.

The model was used to calculate the changes in the minimum and maximum temperatures (T_{gmin} and T_{gmax}) required for 50 % germination in water and nitrate for seeds exhumed at different times during three successive years. Data for *Spergula arvensis* are shown in Figure 2. The calculations were restricted to temperatures between 0°C and 30°C to maintain ecological relevance.

The calculated data clearly illustrate the opening and closing of the temperature window for germination. In *S. arvensis* both T_{gmin} and T_{gmax} changed from early spring onwards. During winter, 50 % germination in water did not occur at any temperature. Figure 2 also clearly shows that germination in the field was restricted to the period where field temperature and the germination-temperature range overlapped (cross hatched areas). The predicted period of germination nicely agreed with the actual period of germination in a field experiment (period between solid arrows).

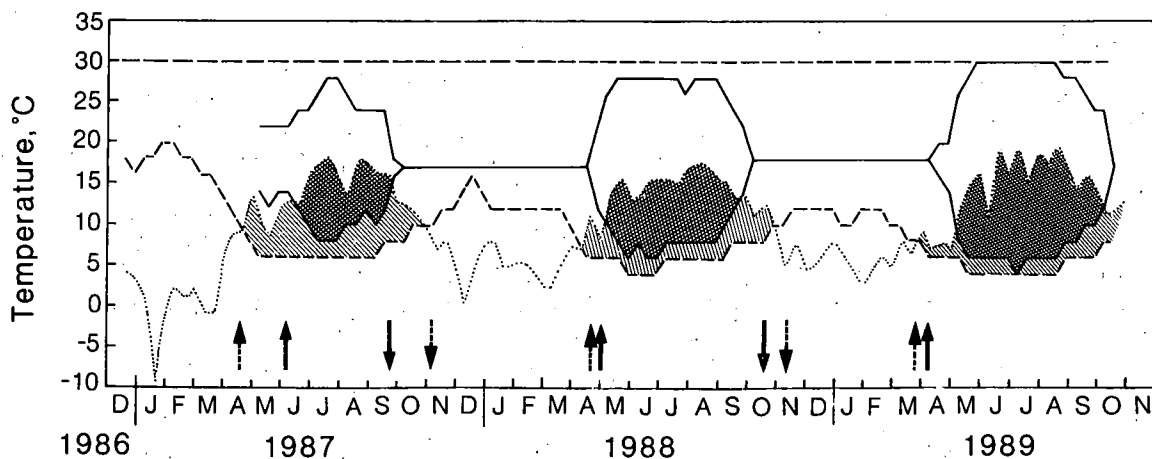


Figure 2 Seasonal changes in the range of temperatures over which at least 50% of *Spergula arvensis* seeds germinate after exhumation from soil. Seeds had been buried at 10cm depth in sandy loam. Solid and broken lines represent maximum and minimum temperature required for 50% germination in water and nitrate respectively (calculated with the model described in text). Arrows (solid for water, broken for nitrate) indicate the time germination in petri dishes placed outdoors at 1.50 m increased above (-) or decreased below 50 % (-). Double hatched and hatched areas indicate overlap of field temperature and germination temperature range in water and nitrate, respectively. The dotted line indicates air temperature at 1.50 m (from (9)).

The presence of nitrate in the germination medium strongly influenced T_{gmin} and T_{gmax} , thereby the period that germination was expected (hatched areas) and actually occurred in the field (period between broken arrows).

Similar calculations for *P. persicaria*, *C. album* and *S. officinale* (8) strengthened our general conclusion that the seasonal changes in field temperature regulate annual dormancy patterns. These are synonymous with the opening and closing of the germination-temperature range.

If there is a seasonal pattern in soil nitrate levels, it could be speculated that such a fluctuation would interfere with the seasonal pattern of weed emergence. The literature indicates that there is no consistent seasonal changes in nitrate level in different soil types (24,30). As nitrogen mineralization depends on temperature, higher production of both nitrate and ammonium can be expected during the summer growing season. Obviously, consumption also increases during this period (30). Other reports show high nitrate levels during winter and early spring, followed by a steady decline, due to utilization and possible nitrification inhibition by the root systems of established plants (19,24). Therefore, we can only conclude that soil nitrate is not a reliable mechanism by which seeds sense the time of the year. However, if increased nitrate levels coincide with correct temperatures, germination will be greatly stimulated (22). This may be particularly important in gaps where soil nitrate levels may increase due to decreased uptake by vegetation.

Practical applications of descriptive models

The above descriptive model is still far away from practical application in the field. The first limitation is that the light vs darkness factor was not included. Light sensing enables seeds to detect whether they are at or below the soil surface. Baskin and Baskin (1,2) showed that smaller fluctuations in the germination-temperature range are required in darkness compared to light for *Ambrosia artemisiifolia* and *Lamium amplexicande*. Another limitation of the present model is that the germination tests were performed under controlled temperature, light, moisture and nitrate availability conditions. To enable predictions of emergence in the field, exten-

sive knowledge of the behaviour of these physical parameters in the seed bed is of utmost importance.

Nevertheless, we believe that the development of descriptive models for dormancy and germination is essential for the understanding of weed seed behaviour in the field. Such information can be useful when attempting to reduce weed emergence, for example, by optimizing timing of soil tillage or sowing in periods of deep dormancy or by avoiding conditions that stimulate germination. Hartmann and Nezatal (14) succeeded in a massive reduction of weed emergence by performing the last cultivation before sowing on a moonless night.

However, it seems more realistic to try to maximize weed emergence and then destroy as many emerged seedlings as possible by mechanical or chemical control in an attempt to deplete the seed bank. Soil tillage at the optimum germination-temperature range would also be a good strategy. However, it would also be most appropriate if germination could be further stimulated by chemical means.

Chemical methods to reduce seed banks

Many chemicals stimulate seed germination when they are applied under standard laboratory tests (7,18). Hormones and nitrogenous compounds take a prominent position on the list of chemicals, but stimulative action is also reported for oxidants, sulfhydryl compounds, respiratory inhibitors, plant products like phenols and strigol and various alcohols.

There is only one reported example of a stimulant successfully enhancing germination in the field. Egle (10,11) induced germination of *Striga asiatica* by ethylene infusion into soil. Seeds of *S. asiatica* and other plant parasites normally require the presence of host roots, extracts or an exudate from these roots to germinate. However, ethylene stimulated germination independently from other factors. Stimulation of *Striga* seed germination in the absence of the host is lethal to the parasite, since attachment to the roots is essential for its survival. Tests indicated that the seed bank of *S. asiatica* was reduced up to 90% in the ethylene-treated field. Ethylene also stimulates the germination of many other weed seeds. However, successful field applications have not been reported.

The gaseous character of ethylene makes it an ideal compound to apply in the field by infusion. It is doubtful whether compounds applied as a solution will ever be useful to break dormancy or stimulate germination in the field. Apart from economic and technical problems, successful application is not likely because most compounds are chemically unstable or will be degraded in soil.

Nitrate is the major inorganic soil component that stimulates seed germination. Numerous wild species, both monocotyledons and dicotyledons, have been stimulated by nitrate (7,25). Since nitrate is central to the nitrogen cycle, most soil types contain nitrate, and often at levels within the range of concentrations that are effective in laboratory germination tests. Seeds may take up nitrate during development on the motherplant. For some species it has been shown that the nitrate content of seeds on the motherplant is directly related to soil nitrate levels (8,15,32,33). A positive relationship between endogenous nitrate content and germination in water has been found for *Chenopodium album* (32) and *Sisymbrium officinale* (8,17). In the latter species, the effectiveness of nitrate absolutely depends on the level of active phytochrome (Pfr) in the seeds. The interactive effect of light and nitrate on germination has been demonstrated in many weed species (37).

Direct application of nitrate to soil to stimulate germination is not a very obvious treatment. However, soil nitrate levels strongly influence the behaviour of weed seeds in soil and have to be taken into account when predicting weed emergence.

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