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Roberto L. Benech-Arnold[a,*], Rodolfo A. Sánchez[a], Frank Forcella[b], Betina C. Kruk[a], Claudio M. Ghersa[a]

[a]*IFEVA, Department of Ecology and Department of Crop Production, Faculty of Agronomy, University of Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina*
[b]*USDA-ARS, North Central Soil Conservation Research Laboratory, Morris, MN 56267, USA*

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[a]*IFEVA, Department of Ecology and Department of Crop Production, Faculty of Agronomy, University of Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina*

[b]*USDA-ARS, North Central Soil Conservation Research Laboratory, Morris, MN 56267, USA*

Abstract

Dormancy is a common attribute of many weed seed populations and this usually hampers the task of predicting timing and extent of emergence of weeds. Both the number of established plants and the timing of emergence of a weed are strongly related to the dynamics of dormancy release of the seed population. In this paper, we discuss the different factors that affect dormancy in weed seed banks in soil, aiming to set a conceptual basis that will facilitate the construction of predictive models. From the long list of factors that are known to control dormancy under field conditions, we distinguish those that modify the dormancy level of the population (i.e. soil temperature and soil hydric conditions) from those that terminate dormancy or in other words, remove the ultimate constraints for seed germination once the degree of dormancy is sufficiently low (i.e. light, fluctuating temperatures, nitrate concentration). We also discuss the effect of agricultural practices on dormancy of weed seed populations, making reference to studies that have evinced clearly the factor(s) involved in determining a particular pattern of response. Overall, we stress the importance of clarifying, both qualitatively and quantitatively, the interaction between soil thermal and hydric conditions in the modification of the degree of dormancy of seed populations. Similarly, it is essential that we understand the extent to which such changes in dormancy comprise changes in sensitivity to factors that terminate dormancy. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Dormancy; Seed banks; Weed seeds

1. Introduction

The result of the interference between a crop and a weed depends largely on the ability of each population to capture resources. Two attributes are instrumental for conferring to a population such an ability (Harper, 1977): (i) an earlier emergence timing in relation to that of its competitor; and (ii) a capacity to establish a large number of seedlings. These attributes are the reasons why assessment of both timing and extent of emergence are so important when studying and modelling crop–weed interactions.

Crops have been selected heavily for non-dormancy in seeds. Thus, their emergence timing can be described easily in relation to the factors that are known to modulate germination rate of non-dormant seeds; namely, temperature, water availability and the gaseous environment. This lack of dormancy also

* Corresponding author.
E-mail address: benech@mail.agro.uba.ar (R.L. Benech-Arnold)

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makes it easy to predict the number of established individuals (emergence success) of a crop population from its sowing density.

In contrast, dormancy is a common attribute of many weed seed populations; and this hampers the task of predicting timing and extent of emergence of weeds. Indeed, the number of established plants of a weed is strongly related to the proportion of the seed bank that has been released from dormancy. In addition, the timing of emergence of the weed in relation to crop emergence also depends largely on the dynamics of dormancy release of the weed population. Moreover, the crop itself and the tillage system may affect both the dynamics and the intensity of dormancy release, with important effects on both the extent and the timing of seedling emergence. All these considerations clearly show the importance of considering dormancy when assessing weed–crop interactions (Ghersa et al., 1997).

Dormancy release must not be confounded with seed germination: they are different processes and consequently, we should be able to predict them separately. They work on different time-scales and are affected by different environmental factors. In so far as they are influenced by the same environmental factors, optimal values for those factors may be quite different. For example, in some summer annual species, breakage of dormancy occurs at low temperatures while the optimum temperature for germination is found at a higher level.

In this paper, we discuss the different factors that affect dormancy in weed seed banks in soil. We propose a new classification of those factors with the aim of facilitating the conceptualisation of the system and setting the basis for the construction of predictive models.

2. Dormancy and factors affecting dormancy: definitions and classification

The definition of dormancy is a controversial subject. Hobson (1981) stated that there may be as many definitions of dormancy as there are investigators concerned with the subject. Our ignorance of the mechanisms involved is probably the main reason for the different views on dormancy. Vleeshouwers et al. (1995), Bouwmeester and Karssen (1992) emphasised that a sound concept of dormancy should clearly distinguish between internal and external factors that interact in seed germination. We agree with that view and accordingly, propose the following general definition of dormancy:

> "Dormancy is an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions."

This means that once the impedance has been removed, seed germination would proceed under a wide range of environmental conditions. The classification of primary and secondary dormancy is useful. Primary dormancy refers to the innate dormancy possessed by seeds when they are dispersed from the mother plant. Secondary dormancy refers to a dormant state that is induced in non-dormant seed by unfavourable conditions for germination, or re-induced in once-dormant seed after a sufficiently low dormancy had been attained. Thus, it is by no means a classification referring to mechanism or location, but one of timing of occurrence. The release from primary dormancy followed by subsequent entrance into secondary dormancy (whenever conditions are given for this entrance) may lead to dormancy cycling. Evidence for dormancy cycling has been obtained for seeds of many weed species, but it is not the only possibility. Indeed, the "transiency" or "persistency" of a seed bank, as defined by Thompson and Grime (1979), might be related, not only to the degree of dormancy with which a population is originally dispersed, but also to the existence of conditions that induce secondary dormancy, thus leading to dormancy cycling in the population. In adapted species, dormancy is either released or alleviated during the season preceding the period with favourable conditions for seedling development and plant growth. In adapted species presenting dormancy cycling, secondary dormancy is induced in a period preceding the season with environmental conditions unsuitable for plant survival. Vegis (1964) introduced the concept of degrees of relative dormancy from the observation that as dormancy is released, the temperature range permissive for germination widens until it is maximal; conversely, as dormancy is induced, the range of temperatures over which germination can proceed narrows, until germination is no longer possible

at any temperature, and full dormancy is reached. Clearly, Vegis' view relates the degree of dormancy of a seed population to the width of the thermal range permissive for germination. Karssen (1982) agreed with that view and emphasised that seasonal periodicity in the field-emergence of annuals is the combined result of seasonal periodicity in field temperature and seasonal periodicity in the widths of temperature ranges suited for germination. Germination in the field is therefore restricted to the period when the field temperature and the temperature range over which germination can proceed overlap.

The concept of base water potential (Ψ_b) for germination was originally proposed by Gummerson (1986) and both the concept and its use were expanded by Bradford (1990, 1995). The $\Psi_{b(g)}$ is the Ψ at which the germination rate (i.e. 1/time required for germination) of the fraction g of the population becomes 0 or in other words, the threshold or base Ψ that will just prevent the germination of g (Bradford, 1995). Bradford (1995) suggested that progressive loss of dormancy in a seed population may be related to a progressive decrease in mean water potential. Christensen et al. (1996) showed for the winter annual *Bromus tectorum* that dormancy release was accompanied by a progressive decrease in $\Psi_{b(50)}$. Those results reveal that, in addition to the above-mentioned changes in the thermal range permissive for germination, the dormancy status of a seed population could be assessed by monitoring changes in mean base water potential. Christensen Bauer et al. (1998), successfully used this approach for developing a simulation model to predict seed dormancy loss in the field for *B. tectorum*.

For most seed populations, once the degree of dormancy is sufficiently low, dormancy must be terminated by the effect of light, nitrate or fluctuating temperatures, to allow the germination process to proceed. In those cases, changes in the degree of dormancy not only comprise changes in the temperature requirements for germination (and eventually in base water potential for germination), but also in sensitivity to the effect of dormancy-terminating factors. Evidence for changes in sensitivity to the effect of these factors with changes in the degree of dormancy, was given by Derkx and Karssen (1993) for light, Hilhorst (1990) and Derkx and Karssen (1993) for nitrate, and Benech-Arnold et al. (1990a) for fluctuating temperatures. At least for the cases of response to light and nitrate, sensitivity was shown to increase when dormancy was alleviated and to decrease when dormancy was enforced.

Temperature has been identified as the main factor governing changes in the degree of dormancy in temperate environments, where water is not seasonally restricted. For example, for a summer annual like *Polygonum aviculare* presenting dormancy cycling, low winter temperatures alleviate dormancy while high summer temperatures reinforce it (Kruk and Benech-Arnold, 1998). However, there is evidence indicating that the effect of temperature on dormancy release may be modulated by soil moisture (Adámoli et al., 1973; de Miguel and Soriano, 1974; Reisman-Berman et al., 1991; Christensen et al., 1996; Christensen Bauer et al., 1998). Also, secondary dormancy can be induced by factors other than temperature as is discussed below.

Although real scenarios are far more complicated with interactions of many kinds, for the sake of simplicity, we define two different kinds of environmental factors that affect dormancy: (i) those that govern changes in the degree of dormancy of a seed population (i.e. temperature and its interactions with soil hydric conditions); and (ii) those that remove the ultimate constraints for seed germination once the degree of dormancy is sufficiently low (i.e. light, fluctuating temperatures, nitrate concentration).

The flow chart in Fig. 1 illustrates this view of the system and illustrates the conceptual framework derived from the above definitions on the different factors that affect dormancy in weed seed populations. It should be noticed that passage along the whole flow chart is by no means the only possibility for a seed population. On the contrary, the chart aims to illustrate the different "pathways" that a seed population could undergo. For example, a population might be dispersed with a low level of dormancy and might or might not require limited stimuli for dormancy termination. In that case, the population would not experience the left-hand side of the flow chart (unless induction of secondary dormancy takes place), and would or would not by-pass the "zone" of dormancy termination. In the following sections, we will discuss in more detail the effects of those factors within this conceptual framework.

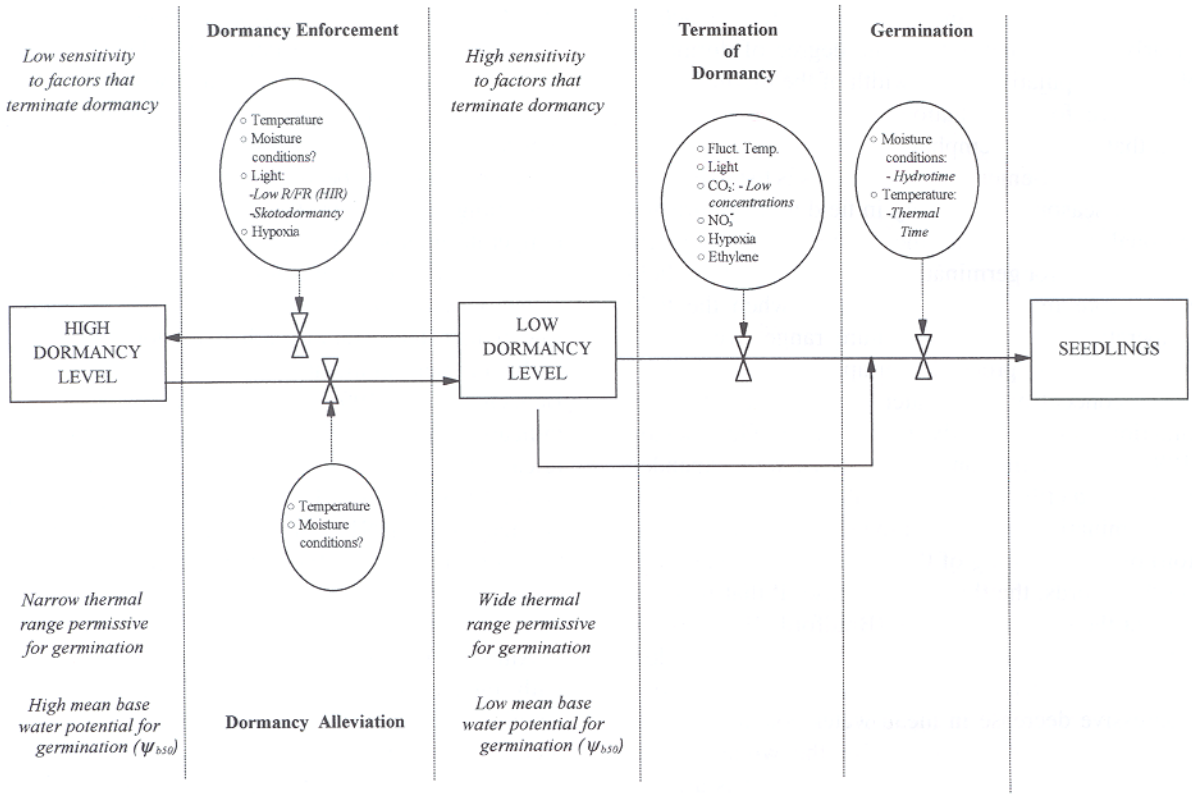

Fig. 1. Flow chart representing changes in dormancy level and termination of dormancy in seed populations and the factors that most likely affect each process.

3. Factors that govern changes in the degree of dormancy of seed populations

Changes in dormancy during burial of seeds have been reported for a number of species. In some studies, seeds were in primary dormancy at the moment of burial. In the course of one year, the seeds passed through a pattern of change in dormancy that started with alleviation of dormancy followed by a period of germinability under several test conditions and was concluded by a re-induction of dormancy (secondary dormancy). Seasonal fluctuations in dormancy were observed in both summer and winter annuals. Seeds of some summer annuals are dormant in autumn, lose dormancy in winter, and recover it in summer, whereas some winter annuals pass through these stages in spring, summer and winter, respectively. Following the ideas of Vegis (1964), Karssen (1982) proposed some useful schemes to explain the periodicity of seedling emergence for both a summer and a winter annual (Fig. 2). In both cases, the high dormancy level of the seeds immediately after dispersal is evinced by the fact that germination does not occur at any temperature. So long as the population is released from dormancy, the thermal range that permits germination expands. In summer annuals, this expansion occurs through a progressive decrease in the minimum temperature for germination and in winter annuals, through a progressive increase in the maximum temperature for germination (Fig. 2). Re-induction of dormancy results in a narrowing of the permissive thermal range through an increase in the minimum temperature for germination in summer annuals, and a decrease in the maximum temperature in winter annuals. In both cases, germination occurs in the field when soil temperature enters the permissive range (Fig. 2).

Examples of summer annuals presenting such a pattern of change are *Cyperus inflexus* (Baskin and

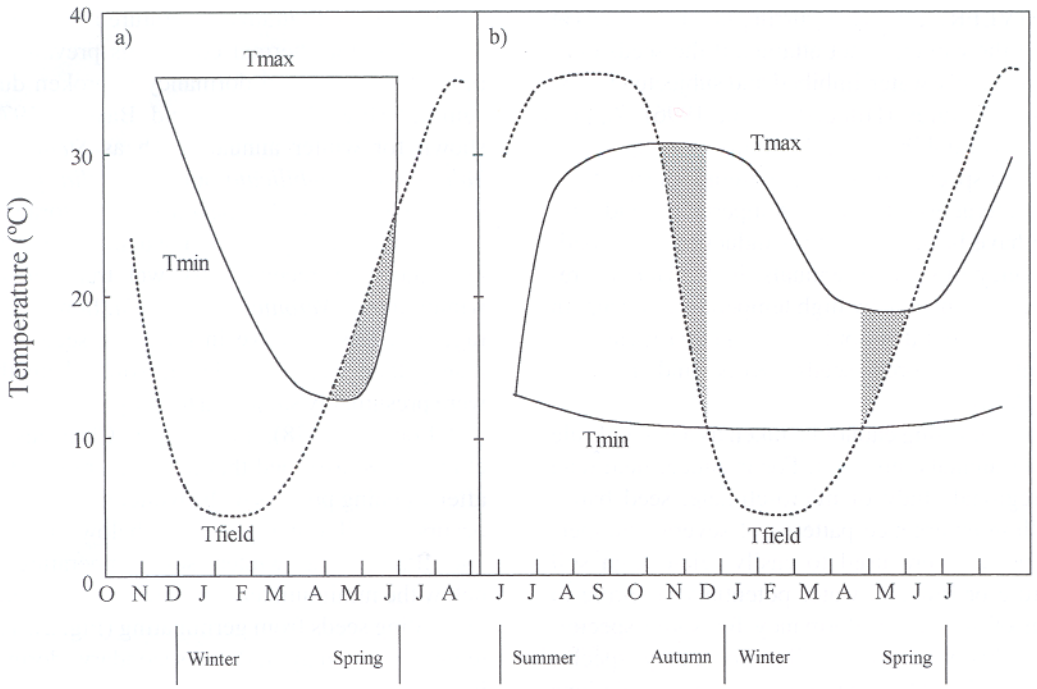

Fig. 2. Seasonal changes in the range of temperatures permitting germination and its relation with soil temperature dynamics. Maximum (T_{max}) and minimum (T_{min}) temperatures allowing germination are indicated by solid lines. Broken lines show mean daily maximum in the field. The shaded area represents the period when field germination takes place due to overlapping of required and actual temperature: (a) strict summer annual; (b) facultative winter species (from Probert, 1992, adapted from Karssen, 1982).

Baskin, 1978), *Barbarea vulgaris* (Taylorson, 1970), *Stellaria faberi* (Taylorson, 1972), *P. aviculare* (Courtney, 1968; Kruk and Benech-Arnold, 1998), *P. persicaria* (Karssen, 1980/81a,b; Bouwmeester and Karssen, 1992) and *Ambrosia artemisiifolia* (Taylorson, 1972; Willemsen, 1975; Baskin and Baskin, 1980). For all these species it has been suggested that dormancy release is promoted by low winter temperatures while re-induction of dormancy is triggered by high temperatures experienced at the beginning of the summer. The dormancy releasing effect of holding imbibed seeds at low temperatures has been recognised for centuries. Totterdell and Roberts (1979) hypothesised that the loss of dormancy during winter of the seeds of *Rumex obtusifolius* and *R. crispus* is in fact the result of two sub-processes: (i) relief of primary dormancy; and (ii) induction of secondary dormancy. It was argued that this relief of primary dormancy was independent of the actual temperature so long as it was below 15°C, and that induction of secondary dormancy occurred at all temperatures with the rate of induction increasing with the increase of temperature. Hence, although relief of primary dormancy occurred equally at all temperatures below 15°C, temperatures just above 0 caused the most effective net relief of dormancy because the rate of induction of secondary dormancy was lowest at those low temperatures. In contrast, as temperature increases throughout spring, induction of secondary dormancy would be the prevailing process.

Kruk and Benech-Arnold (1998), using a screening methodology proposed by Washitani (1987), have shown for *P. aviculare* that temperature was to a large extent responsible for dormancy cycling in this species. However, some interactions with soil moisture were detected; dormancy release occurred most rapidly when seeds were moist-chilled at 4°C, but relief of dormancy was also possible with seeds dry-stored at 4°C though at a much slower rate (Kruk and Benech-Arnold, 1998). Interactions of this kind also have been reported for the light-requiring species *Sisymbrium officinale*, where a very low fluence

response (VLFR), usually occurring in buried seeds at the end of the winter, is not attained if the seeds have been permanently water-imbibed and subjected to low winter temperatures (Hilhorst et al., 1996). Apparently, cycles of imbibition–dehydration are required in seeds of this species to acquire extreme sensitivity to Pfr. No interaction between temperature and soil moisture have been reported for induction of secondary dormancy in summer annuals. In *P. aviculare* re-induction of dormancy by high temperatures occurs in imbibed seeds, but it is not known whether it can also occur with dry-stored seeds (Kruk and Benech-Arnold, 1998).

Dormancy cycling cannot be taken as a general rule in summer annuals, however. For instance, field data from a regional study of micro-climate, seed banks and seedling emergence patterns of several summer-annual species were used to easily relate high soil temperature or low soil water potentials in spring to induction of secondary dormancy for some species. However, this was not possible for many species (Forcella et al., 1997). Moreover, even populations within the same species can either present a cyclic dormancy pattern or not, depending on the origin of the population. For example, no re-induction of dormancy was found in an Argentinean population of the light-requiring *Datura ferox* after one summer of burial and the extreme sensitivity to light attained at the end of the winter was maintained when the seeds were exhumed at the end of the summer (Botto et al., 1998a). Reisman-Berman et al. (1991) found, however, a cyclic dormancy pattern in a population of this species from Israel. This apparent inconsistency may indicate that a cyclic dormancy pattern could be inherent to ecotypes from environments with marked seasons.

The characteristic feature of winter annuals is that the active part of the life cycle occurs during the colder part of the year. Such annuals can be divided into strict and facultative winter species depending on whether their emergence period is strictly limited to autumn or not. In these species, dormancy prevails at the end of the spring season and has to be relieved during the summer period to allow germination in autumn (Karssen, 1982). A seasonal dormancy pattern dominated by a fluctuation of the maximum temperature for germination has been observed for some of these species. After seed dispersal during late spring/early summer, the maximum temperature for germination is well-below the thermal conditions prevailing at that time of the year and dormancy is broken during the summer (Fig. 2). Baskin and Baskin (1976) have shown for winter annuals such as *Stellaria media*, *Valerianella umbilicata* and *Phacelia purshii* that dormancy was only relieved during storage at high temperatures irrespective of whether the seeds were kept moist or received dry–wet treatments. In the winter annual *Veronica hederifolia*, however, dry storage was less effective in releasing seeds from dormancy than was burial in the soil, where the seeds were presumably subjected to dry–wet cycles (Roberts and Lockett, 1978). In contrast, Christensen Bauer et al. (1998) assumed that the temperature-dependent after-ripening process in the winter annual *B. tectorum* occurs at soil water potentials below approximately −4 MPa. During winter, soil temperature is often below the minimum temperature for germination, thus preventing seeds from germinating (Fig. 2). These low temperatures may induce secondary dormancy, as indicated by a sharp decrease in maximum temperature for germination (strict winter species) so that germination is restricted to autumn. In facultative winter species, the decrease in maximum temperature for germination as a result of exposure to low winter temperatures is less sharp thus enabling germination during spring (Fig. 2). Evidence indicating that low temperatures are responsible for induction of secondary dormancy in winter annuals has been provided by Baskin and Baskin (1975, 1977). However, dormancy cycling under field conditions was not detected in winter annuals such as *Anagallis arvensis* and *Carduus acanthoides* (Kruk and Benech-Arnold, 2000). Interestingly, low temperatures were shown to induce secondary dormancy in *A. arvensis* but only if the seeds were imbibed; the dryness of the winter in the area where the experiments were conducted might have been instrumental in impeding the development of secondary dormancy under field conditions (Kruk and Benech-Arnold, 2000).

Temperature cannot be regarded as the only factor that can induce secondary dormancy. In the field, the induction of secondary dormancy can proceed at temperatures that are within the range suitable for germination. In those cases it might result from inhibition of germination per se (i.e. germination-inhibitory water potentials or inhibition of germination

under leaf canopies) or from a situation in which factors that terminate dormancy are not met (i.e. loss of sensitivity to light in light-requiring seeds held in darkness; loss of sensitivity to fluctuating temperatures in seeds held at low thermal amplitudes). In any case, the process itself should involve the narrowing of the range of suitable conditions for germination, ultimately leading to a state of relative or total dormancy, to be regarded as induction of secondary dormancy (Karssen, 1982). For example, seeds of *Chenopodium bonus-henricus* held in solutions with low water potential lost their ability to germinate in darkness (Khan and Karssen, 1980). In addition, water stress has been shown to induce a secondary light requirement in seeds of other species (Khan, 1960; Hsiao and Vidaver, 1973; Berrie et al., 1974). Inhibition of germination caused by prolonged exposure to light with a high proportion of far-red light often results in the induction of a secondary light requirement (Górski, 1975; Górski et al., 1978; Fenner, 1980; Silvertown, 1980). In some cases this inhibition is mediated by the high irradiance response (HIR), particularly in seeds exposed to direct solar radiation (Górski and Górska, 1979; Lythgoe, 1997). In some seeds, inhibition of germination presumably mediated by HIR is not reversed after exposure to white light (Frankland and Taylorson, 1983).

Although oxygen concentration in soil air rarely falls below 19%, elevated soil humidity might dilute the oxygen concentration well to below this figure in the vicinity of a seed. Induction of secondary dormancy in hypoxia has been observed in seeds of *Xanthium pennsylvanicum* (Esashi et al., 1978), *Veronica hederaefolia* and *Veronica persica* (Lonchamp and Gora, 1979) and *Avena fatua* (Symons et al., 1986). In contrast, low oxygen concentrations have been shown to prevent induction of secondary dormancy at high temperatures in *S. officinale* (Karssen, 1980/81a) and *Rumex crispus* (Le Deunff, 1973). Also ethylene, a gas with a well-known role as a growth regulator, which is present at low concentrations in the soil, promotes germination at non-optimal temperatures in *X. pennsylvanicum* (Katoh and Esashi, 1975) and *Amaranthus retroflexus* (Schönbeck and Egley, 1981a,b), indicating that the establishment of secondary dormancy was prevented.

An example of induction of secondary dormancy resulting from a situation in which factors that terminate dormancy are not met, is the phenomenon of skotodormancy, which is described as loss of sensitivity to light during prolonged incubation in darkness. This type of dormancy has been reported for *Portulaca oleracea* (Duke et al., 1977) and for *Chenopodium album* (Karssen, 1970). Similarly, when the requirement of alternating temperatures to terminate dormancy in *Sorghum halepense* is not satisfied, a loss of sensitivity to fluctuating temperatures occurs in part of the population (Benech-Arnold et al., 1988).

4. Factors that terminate dormancy

4.1. Fluctuating temperatures

In several species, exit from dormancy is completed only after the seeds have been exposed to fluctuating temperatures. The ecological significance of this requirement has been related to the possibility of detecting canopy gaps as well as to depth of burial (Thompson and Grime, 1983; Benech-Arnold et al., 1988; Ghersa et al., 1992). It could also act as an effective mechanism for distributing germination over a longer period of time (Benech-Arnold et al., 1990a,b). Roberts and Totterdell (1981) identified nine characteristics of diurnal temperature cycles that could conceivably be responsible for stimulatory activity, viz.: the number of cycles, their amplitude, the upper temperature value, the lower temperature value, the period spent at the upper temperature, the period spent at the lower temperature, the rate of warming, the rate of cooling, and the timing of the cycle(s) with respect to the start of imbibition. Clearly, altering any one of these attributes without confounding it with a change in at least one other attribute is not possible. Nevertheless, evidence exists showing that not all of these characteristics have an active role. For example, the higher the upper temperature of the cycle for *Rumex* species, the shorter and more critical is the optimum temperature spent at it (Totterdell and Roberts, 1980). Thermal amplitude is of paramount importance; in *C. album*, the dormancy breakage response can increase from an amplitude of as little as 2.4°C up to about 15°C (Murdoch et al., 1989). However, the response to a given amplitude is greater the higher the mean temperature of the cycle (i.e. average of lower and upper temperature) up to an

optimum of about 25°C (Murdoch et al., 1989). In some cases, when diurnal cycles include some of the above-mentioned stimulatory characteristics, those factors tend to be additive in their effect. In *S. halepense*, 10 cycles with stimulatory characteristics release from dormancy twice the proportion of the population released with only five cycles (Benech-Arnold et al., 1990b). Finally, no evidence has yet been produced that indicates that the rate of warming or cooling has any effect. Interestingly, a recent paper has shown that seeds of *Echinochloa crus-galli* are able to perceive the dormancy-breaking effect of fluctuating temperatures even when incubated at water potentials that are not permissive for germination (Martínez-Ghersa et al., 1997). This indicates that the effect of alternating temperatures is uncoupled from germination. This response has also been observed for *Stipa tenuissima* (Moretto et al., 1996).

As stated before, changes in the degree of dormancy in seeds that require fluctuating temperatures to terminate dormancy are likely to comprise changes in sensitivity to such fluctuations. This has been shown clearly for *S. halepense* seeds (Benech-Arnold et al., 1990a,b), where an increase in sensitivity is expressed both as an increase in the proportion of the seed population capable of responding to fluctuating temperatures and as modification in seed responsiveness to any of the components of the temperature cycle. For example, in comparison to recently shed seeds, an *S. halepense* seed population that had after-ripened for a winter in the soil (this species is dispersed at the end of the summer) presented a greater proportion of seeds with sensitivity to fluctuating temperatures. The same seeds also required lower amplitudes, lower upper temperatures of the cycles, and a smaller number of cycles to be released from dormancy than recently shed seeds. In addition, thermal regimes with no additive effect when applied on a recently shed population became additive after the seeds had spent a winter in the soil.

4.2. Light

Termination of dormancy in seeds of many species can be markedly triggered by light (Bewley and Black, 1982). A large body of information about phytochrome stimuli of germination has accumulated since the seminal work of Borthwick et al. (1952). Depending on the dormancy state of the seeds, light treatment (i.e., spectral composition, irradiance, duration), and other environmental conditions, germination can be promoted, inhibited or be indifferent to light (Bewley and Black, 1982; Frankland and Taylorson, 1983; Casal and Sánchez, 1998).

4.2.1. Promotion of germination

Cancellation of dormancy by light is mediated by the phytochromes. These photoreceptors form a small family of chromoproteins. Five different phytochromes have been identified in *A. thaliana* (phytochromes A–E) and in tomato (phyA, phyB1, phyB2, phyD and phyF). A common chromophore, phytochromobillin, is covalently bonded to the specific apoprotein for each phytochrome, which is coded by the corresponding gene (Mathews and Sharrock, 1997). All phytochromes have two mutually photoconvertible forms: Pfr (considered the active form) with maximum absorption at 730 nm and Pr with maximum absorption at 660 nm. Phytochromes are synthesised as Pr and the proportion of the pigment population (P) in the active form (Pfr/P) in a particular tissue depends on the light environment. Exposure to light with a high red (R) to far-red (FR) ratio (R:FR) leads to larger Pfr/P although, due to the overlapping of the Pr and Pfr absorption spectra, transforming all Pr in Pfr or vice versa is not possible. After a saturating pulse of R, Pfr/P will be around 0.87, whereas after a saturating FR pulse it will be around 0.02 (Cone and Kendrick, 1986). There is an important difference between phyA and the rest of he phytochromes with respect of the stability of Pfr. PhyA has a Pfr half-life of 1–2 h, whereas the Pfr of the other phytochromes is more stable (Clough and Viestra, 1997). Pfr stability is an important issue for the perception of environmental signals. Seed germination requires Pfr function during a certain lapse (called the escape time). When Pfr is stable enough to remain longer than the escape time, just one light pulse is sufficient for germination, whereas if Pfr is reduced to ineffective levels before the end of escape time, more than one pulse or a longer exposure to light is necessary.

The relationship between Pfr levels and germination promotion can be described in terms of two action modes of phytochromes: the VLFR and the low-fluence response (LFR). VLFR requires seeds to have an extremely high sensitivity to light. Germination can

be induced by Pfr/*P* as low as 10^{-4} and is usually saturated by <0.03 Pfr/*P*. VLFRs can be elicited with very short exposures to sunlight (milliseconds) and are saturated with Pfr/*P* levels lower than those that can be achieved with FR filters; consequently, they do not show the classical R–FR reversibility. In contrast, LFRs require larger Pfr levels, the effects of R are reversed by FR, and response saturation may even require the maximum Pfr/*P* (i.e., ca. 87%).

Recent evidence reveals that each of the two germination-promoting action modes is: (a) mediated by different phytochromes; and (b) participates in the perception of different environmental situations. In *A. thaliana*, phyA is the only photoreceptor of VLFR (Botto et al., 1996; Shinomura et al., 1996), whereas LFR is mediated by phyB and other phytochrome(s) different from phyA (Shinomura et al., 1994; Botto et al., 1995). Similarly in *D. ferox*, LFR depends on a stable phytochrome pool of the phyB type (Casal et al., 1991) and VLFR depends on an unstable phytochrome resembling, in this aspect, phyA (Botto et al., 1998a).

Two environmental changes that promote germination and involve light signals are: (1) soil disturbance by agricultural operations; and (2) gap openings in dense canopies.

Soil disturbance by agricultural operations: It has long been known that soil disturbance in the presence of light provokes the germination of more seeds than the same procedure without light (Sauer and Struik, 1964; Wesson and Wareing, 1969). Seeds of several species can achieve a very large light sensitivity after some time in the soil so that an important faction of the population display VLFR of germination (Scopel et al., 1991; Derkx and Karssen, 1993). Such sensitivity allows exposures of the order of 100 ms to sunlight to induce germination. This explains the promotive effect (through VLFR) of the brief exposure to light of weed seeds during mould-board ploughing (Scopel et al., 1991). Often, daytime tillage induces the emergence of more weed seedlings than nighttime tillage (Hartmann and Nezadal, 1990; Jensen, 1992; Ascard, 1994; Scopel et al., 1994; Buhler, 1997; Gallagher and Cardina, 1998). However, the difference between daytime and nighttime tillage depends very much on the agricultural history of the field, the time of the year, the tillage tools, and the species involved (Botto et al., 1998b). Variation in the response can have different origins. Botanical composition of the soil seed bank, environmental factors that affect light sensitivity, and the type of soil perturbation are among the factors that may cause variability. In species presenting a cyclic dormancy pattern (i.e. *Sysimbrium officinale*), maximum light sensitivity is acquired when the level of dormancy is at its minimum, but this sensitivity is reduced progressively (i.e. higher Pfr levels are required to break dormancy) in so far the population enters secondary dormancy (Derkx and Karssen, 1993). In contrast, in *D. ferox*, whose seeds apparently did not show a cyclic dormancy pattern under the tested field conditions, the acquisition of extremely high sensitivity to Pfr allowed the seeds to germinate in the dark if they remained buried for an extended time (Botto et al., 1998a).

Gap openings in dense canopies: Gaps in closed canopies modify many environmental parameters, particularly light quality (Holmes and Smith, 1977; Deregibus et al., 1994). Reductions in canopy density lead to increases in the R:FR ratio and consequently, raise the Pfr level within the range of LFR, promoting germination through the action of phyB (and other phytochromes different from phyA). This has been found associated with death of large individuals in a forest (Vazquez-Yanes and Smith, 1982), grazing by large animals in pastures (Deregibus et al., 1994), or flooding events in herbaceous communities (Insausti et al., 1995). In a temperate grassland and in the understory of a tropical rain forest, high germination percentage of light-requiring seeds was observed only when R:FR ratio at seed level was larger than 0.5–0.6 and for at least several hours per day (Orozco-Segovia et al., 1993; Deregibus et al., 1994). These requirements may result from short escape times and a high threshold of Pfr/Pt for germination. Dark reversion of Pfr to Pr may also play a role in establishing the need for long periods of exposure to light with a high R:FR ratio. In this way, gap size can be detected and errors in perception derived from sun flecks or from the increase in the R:FR ratio observed under a canopy near the end of the photoperiod (related with the increase in diffuse light) can be avoided.

4.2.2. Inhibition of germination

Exposure of seeds to light may inhibit germination in various ways depending on the species and circumstances. The simplest cases involve inhibition by a single pulse of light. In *Bromus sterilis* (Hilton, 1982)

and some lines of *A. fatua* (Hou and Simpson, 1993), germination is inhibited by a single R pulse and this inhibition is abolished by a subsequent FR pulse. In these species, an LFR is operating just in the opposite direction to what is found in the vast majority of photoblastic seeds and Pfr inhibits, instead of promoting germination. On the other hand, a single FR pulse given to imbibed seeds has been shown to inhibit germination in several species, e.g., *Arabidopsis thaliana* (Shinomura et al., 1994). The FR treatment removes Pfr formed during seed ripening that persists in the dry seed and can induce germination after dark imbibition. In some species, just one FR pulse is not sufficient for inhibition and frequent repeated pulses over a period of several hours are required as in tomato (Mancinelli, 1994) and *Amaranthus caudatus* (Kendrick and Frankland, 1969). These observations have been interpreted in terms of Pfr formation from photoconversion intermediates; these intermediates are formed during ripening and remain in the dry seeds. When that process of Pfr formation operates, frequent FR pulses are required to keep Pfr levels below those stimulating germination (Bewley and Black, 1982).

Different findings support the idea that FR treatments can do something more than just establishing a low Pfr level. Continuous FR for several hours frequently inhibits germination in situations where a pulse of FR has little effect (Negbi et al., 1968) or even when it has some promotive effect (Negbi and Koller, 1964). Taking into account the irradiance-dependence of this inhibition, the effect was suggested to be similar to the high-energy reaction or HIR described in seedling photomorphogenesis (Frankland and Taylorson, 1983). Hartmann (1966) proposed that HIR inhibition of germination in the FR region of the spectrum was mediated by the phytochrome system but which member of the phytochrome family mediates these responses is unknown (Casal and Sánchez, 1998). The HIR of germination has maximum activity at 710–720 nm (Hartmann, 1966; Hendricks et al., 1968; Mohr, 1972) and the inhibitory effect of continuous FR can be observed, even in R-promoted seeds, after the escape time is over (Frankland and Taylorson, 1983).

After inhibition by prolonged irradiation, germination in some cases, can be re-induced by increasing the Pfr/*P*, while in others the seeds can become photodormant and lose the capacity to respond to a high Pfr level (Frankland and Taylorson, 1983).

The blue region of the spectrum also can be inhibitory of germination in many species when the seeds are exposed continuously for several hours (Gwynn and Scheibe, 1972; Malcoste et al., 1972). This effect of blue light involves an unidentified photoreceptor. Although blue light is absorbed by the phytochromes and in the appropriate scenario, can modify the proportion of the phytochrome pool that is in the Pfr form, the specific inhibitory action can be separated from its influence through phytochromes. Both HIR and the inhibition of germination by blue light are irradiance dependent and strongly influenced by exposure time.

Górski and Górska (1979) reported on the irradiance-dependent inhibition of germination in *Lactuca sativa* by sunlight. The irradiance required to attain a certain level of inhibition decreased when sunlight was filtered to reduce the R:FR ratio.

Prolonged exposure to canopy light (i.e. during all the natural photoperiod) inhibits germination of many species (Górski, 1975; King, 1975; Górski et al., 1978; Fenner, 1980; Silvertown, 1980). This inhibition might be in some cases, the result of just the low Pfr level established under a canopy (i.e. prevention of induction of germination through an LFR). However, there is an information that establishing a low Pfr level is not always sufficient for the inhibition of germination under vegetation cover. Germination of ryegrass seeds is not inhibited by a daily exposure of 1 or 3 h to canopy light estimated to be sufficient for phytochrome to reach photoequilibrium, but is strongly inhibited by a full natural photoperiod of canopy light (Lythgoe, 1997). Similarly, *Silene gallica* seeds that would not germinate in darkness were fully induced to germinate by light for 1 h under a sparse canopy, but germination was almost nil when the seeds were exposed to that same canopy light during the natural photoperiod (Batlla et al., 2000). Germination of the ryegrass seeds is restored when the canopy light is supplemented with red light provided by light-emitting diodes (LEDs). Apparently, in those cases, the proportion of seeds germinating is the result of the balance between the promotive LFR, depending of the Pfr level, and the inhibitory HIR action. When HIR is weak (short exposures times) or when Pfr levels are high, germination can reach higher values. The same interpretation can be applied to the results of Górski

and Górska (1979) mentioned above. Clearly, HIR action in the natural environment and its adaptive significance requires more experimental work.

4.3. Nitrate

A fairly recent review on the role of nitrate in terminating dormancy of seeds can be found in Karssen and Hilhorst (1992). Consequently, we will refer to it only briefly in this paper.

Nitrate is a requirement for dormancy termination in a number of species. Because nitrate concentration in the soil fluctuates seasonally (i.e. the higher the temperature, the higher the mineralisation rate of soil organic matter and consequently, the higher the actual nitrate concentration), the possibility that the requirement for nitrates could be an environmental signal determining the seasonal emergence of some weeds has been considered. No correlation was found between the period of emergence of weeds requiring nitrates to completely exit from dormancy, however, and soil nitrate concentration at different times of the year (Karssen and Hilhorst, 1992). Rather, this requirement has been proposed as a gap-detection mechanism, since mineralisation rates in open gaps are higher than in the soil under a vegetation cover (Pons, 1989).

Although the mechanisms by which nitrates stimulate exit from dormancy are largely unknown, they may act somewhere at membrane level (Karssen and Hilhorst, 1992). The interaction between nitrate and light has been detected in the termination of dormancy of some species. Germination of *S. officinale*, e.g., depends absolutely on the simultaneous presence of light and nitrate (Hilhorst and Karssen, 1988), while in the case of *A. thaliana*, germination depends only on light, but nitrate might modify light-induced germination to some extent (Derkx and Karssen, 1994).

Analysis of the response to nitrate has been carried out in a similar fashion to that for light, with the nitrate dose as the limiting factor under saturating light conditions (Hilhorst, 1990; Derkx and Karssen, 1993). The experiments were done with seeds exhumed from the soil at different dates throughout the year. In the summer annual, *S. officinale*, an increase in sensitivity to nitrates was observed during winter (dormancy release) followed by an apparently nitrate-independent germination during spring (Hilhorst, 1990). During the summer period, the pattern was reversed.

4.4. The gaseous environment

In addition to fluctuations in atmospheric conditions, which are the main driving force in soil aeration, factors that influence the composition of the gaseous phase in the soil include the soil porosity, the diffusion and solubility coefficients of gases, as well as oxygen uptake and CO_2 and ethylene release by living organisms (Corbineau and Côme, 1995). This means that although the concentration of those gases in the soil is rather stable, under some circumstances important variations might be expected. For example, oxygen concentration in soil air may fall below 1% by volume in flooded soils or even lower in those maintained at field capacity for a long time (Gambrell et al., 1991). Also, when a crust is formed at the soil surface, oxygen concentration can reach values lower than 10% (Richard and Guerif, 1988a,b). Oxygen is one of the requirements for the germination of non-dormant seeds together with water and temperature, and the role of low oxygen concentrations in modifying the degree of dormancy of seeds was described in the previous section. In some species, however, a low oxygen concentration or even anoxia, may have a dormancy-terminating effect (Bewley and Black, 1982; Corbineau and Côme, 1988).

The level of CO_2 in soil air does not usually exceed 0.5–1% (Karssen, 1980/81a,b). In those concentrations, carbon dioxide has been found to have a dormancy-breaking effect in seeds of *Trifolium subterraneum* and *Trigonella ornithopoides* (Ballard, 1958, 1967). CO_2 concentration in soil air can increase up to 5–8% in flooded soils after decomposition of organic matter (Jeffrey, 1987), however, and can inhibit germination of some species (Ballard, 1967).

Ethylene is another common component of the soil atmosphere. Partial pressure of this gas ranges between 0.05 and 1.2 MPa (Corbineau and Côme, 1995). At these concentrations it terminates dormancy of some species (Esashi and Leopold, 1969; Taylorson, 1979), but inhibits germination of others (Olatoye and Hall, 1973; Suzuki and Taylorson, 1981). Interactions between ethylene and other dormancy-terminating factors such as light and nitrate (see, e.g., Karssen and Hilhorst, 1992) or carbon dioxide (see,

e.g., Corbineau and Côme, 1988, 1995) have been reported.

5. Dormancy as affected by agricultural practices

5.1. Tillage

Tillage exposes seeds to a light flash before reburial, allows greater diffusion of oxygen into and carbon dioxide out of the soil, buries residue and promotes drying of the soil, thereby increasing the amplitude of temperature fluctuations and promoting nitrogen mineralisation (Mohler, 1993). All of these factors are known to terminate dormancy in several species as has been discussed in the previous sections. On the other hand, several studies have noted increased emergence following frequent, repeated tillage (Brenchley and Warington, 1933; Roberts and Dawkins, 1967; Roberts and Feast, 1972, 1973a,b). In some cases, the triggering factor has been identified. Increased weed seed germination after soil disturbance in the light vs. in darkness was documented by Wesson and Wareing (1969), who also proposed that cultivation during daylight serves to increase weed populations. Indeed, as commented in previous sections, Scopel et al. (1994) showed that daytime tillage increased seedling emergence of several winter annuals more than twofold the emergence observed in the nighttime tillage treatment. In addition, the induction of extreme sensitivity to Pfr in buried seeds of *D. ferox* and its relationship with their capacity to respond to soil cultivation was clearly demonstrated by Scopel et al. (1991).

Holm (1972), in an attempt to demonstrate the extent to which the effect of tillage on exit from dormancy was through renewal of the gas environment, showed that flushing the soil with air for a short period each day stimulated germination of seeds in the soil. Flushing with nitrogen was less effective than that with air.

No direct evidence exists, to the best of our knowledge, of the effect of tillage on dormancy through modification of temperature fluctuations or nitrate concentration. However, in an interesting work, De la Fuente et al. (1997) have shown that depletion of organic matter as a result of many years of continuous tillage, leads to a change in soil colour (less dark), which is accompanied by a concomitant modification of the soil thermal regime. Seeds of some species are prevented from germination as a consequence of dampened temperature amplitudes in light-coloured soils.

In addition, tillage modifies the position of the seeds in the soil profile (see Mohler, 1993). No-till cropping systems leave most seeds in the top 10 mm of the soil profile (Yenish et al., 1992), mould-board plowing tends to distribute seeds uniformly throughout the plow layer (Van Esso et al., 1986), while chisel plowing and other reduced tillage systems have intermediate effects. Different environments are experienced during after-ripening depending on the position in which the seeds are located, which might result in different degrees of dormancy in seeds located at different depths (Taylorson, 1972). Botto et al. (1998a) found that *D. ferox* seeds acquired extreme sensitivity to Pfr when they had been buried at 50 mm depth but not when they had after-ripened at 5 or 100 mm. Similarly, Ghersa et al. (1992) showed that the proportion of a *S. halepense* seed population with sensitivity to fluctuating temperatures after almost two years of burial, was different depending on the depth of burial. Moreover, the movement within the soil profiles as a result of a tillage operation, in itself, might produce changes in the degree of dormancy (Ghersa et al., 1992).

5.2. Fertilisation and chemical applications

In spite of the well-known dormancy-terminating effect of nitrates in seeds of several species, evidence for enhanced seed germination in the field by nitrates is inconsistent (Egley, 1986; Hurtt and Taylorson, 1986; Dyer, 1995; Egley, 1995). More likely, it has been suggested that one major influence of nitrate may be through fertilisation of the mother plant and the resulting increased nitrate level in developing seeds (Egley, 1995). Saini et al. (1985) concluded that a threshold nitrate level in *C. album* seeds was necessary for germination promotion by ethylene. Hilhorst and Karssen (1990) found a strong correlation between nitrate concentration in the seeds and their germination capacity. Nevertheless, fertility levels in terms of nitrate and nitrite concentration have been shown to stimulate dormancy release in seeds of some species (Fawcett and Slife, 1975). Although some species are known to be released from dormancy by ammonium,

no evidence has been provided so far showing that application of ammonium to the soil might indeed enhance germination of weeds.

The application of some hormonal herbicides have been shown to modify the dormancy level of the seeds produced by the surviving plants. Scursoni et al. (1999) have shown that seeds from *A. fatua* plants that had survived the application of diclofop-methyl in barley crops, had a lower dormancy level. Moreover, an anticipated emergence timing of *A. fatua* was detected in plots that had been treated with diclofop-methyl the previous year in relation to the emergence timing observed in plots that had not been treated with the herbicide (Scursoni et al., 1999).

5.3. Flooding

In agricultural systems where irrigation and flooding are common practices (e.g. rice), the environment in which weed seeds have to germinate is characterised by the existence of low oxygen concentrations. As stated previously, low oxygen concentration terminates dormancy in seeds of some species. This is the case with *Echinochloa turnerana* (Conover and Geiger, 1984) and *Leersia oryzoides* (Rosa and Corbineau, 1986), two well-known weeds of rice crops. Flooding can also cause the death of unadapted species, thus opening gaps in the vegetation and facilitating the establishment *Ambrosia tenuifolia*, a species that otherwise would not germinate because of the low R:FR ratio prevailing beneath the vegetation cover (Insausti et al., 1995); immersing the seeds of this species in water at low temperature for some weeks increases their sensitivity to light.

5.4. Crop residue and burning

In general, higher levels of residue increasingly reduce and delay emergence, most likely by decreasing soil thermal amplitude and preventing light penetration (Dyer, 1995). In addition, incorporated residues of several crops, especially wheat, exhibit allelopathic effects on weed seed germination (Steinsiek et al., 1982). Finally, it should be considered that decaying residues can immobilise large amount of N; this could result in a low nitrate content of the soil, which could prevent termination of dormancy in some species.

The effect of fire on dormancy of species from areas where wildfires are an integral part of the ecology is well documented (for reference, see Probert, 1992; Fenner, 1995). The stimulant effect of fire may result from the physical effect of dry heat on seed coat structure, the physiological effect of dry heat on seed embryos, and/or the dormancy-breaking effects of volatile compounds, such as ethylene and ammonia (van Staden et al., 1995). In addition, many other plant-derived smoke components have been found to have a dormancy-breaking effect (De Lange and Boucher, 1990); in particular, the role of nitric oxide has been identified clearly (Keeley and Fotheringham, 1997). To the best of our knowledge, no study has assessed the effect of residue burning on dormancy and germination of weeds in agroecosystems. However, an effect on termination of dormancy through any or several of the above-mentioned mechanisms might be expected.

6. Future directions and needs

We have attempted to analyse the existing information on the effects of several environmental factors on the dormancy status of weed species. Part of this information has already been used for the construction of the few existing models that consider dormancy in their structure. The amount of data that can be found in the literature is extremely large and for that reason we did not attempt an exhaustive review, but instead selected examples that would illustrate the complexity of the responses. The modelling of dormancy changes is considered in an accompanying paper (Forcella et al., 2000), but the wide range of interactions among factors that affect dormancy in the field, as described here, indicates that the development of such models will be an extremely difficult task. We believe, however, that the classification of factors that modify the degree of dormancy and factors that terminate dormancy permits some order and establishes some hierarchies for a modelling endeavour. Within that context therefore we foresee that much work is needed to clarify the suggested interactions between temperature and soil hydric conditions in the regulation of dormancy changes of seed populations. Also, solid functional relationships should be derived from such studies in order to use them in the construction of

predictive models. Similarly, comprehensive understanding is essential of the extent to which those changes in dormancy comprise changes in sensitivity to factors that terminate dormancy. For example, a detailed examination on the thermal and hydric conditions that reduce dormancy in a seed population, and lead to extreme sensitivity to light, would enable us to formulate models to predict the best timing for soil disturbance in order to maximise seedling emergence. Such models would be a step ahead towards the objective of improving weed management decisions, thus favouring crops in their race for resources against weed species.

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