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Predicting changes in dormancy level in natural seed soil banks

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Abstract The possibility of accurately predicting timing and extent of seedling emergence from natural seed soil banks has long been an objective of both ecologist and agriculturalist. However, as dormancy is a common attribute of many wild seed populations, we should first be able to predict dormancy changes if we intend to predict seedling emergence in the field. In this paper, we discuss the most relevant environmental factors affecting seed dormancy of natural seed soil banks, and present a conceptual framework as an attempt to understand how these factors affect seed-bank dormancy level. Based on this conceptual framework we show approaches that can be used to establish quantitative functional relationship between environmental factors regulating dormancy and changes in the seed-bank dormancy status. Finally, we briefly explain how we can utilize population-based threshold models as a framework to characterize and quantify changes in seed sensitivity to environmental factors as a consequence of dormancy loss and/or induction.

Keywords Population-based threshold models · Seed soil banks · Seed dormancy · Soil temperature · Thermal-time

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Introduction

Dormancy can be defined as an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions (Benech-Arnold et al. 2000). This impediment or block to seed germination can be determined by both morphological and/or physiological properties of the seed (Nikolaeva 1967). On the basis of this fact Baskin and Baskin (1998, 2004), developed a classification system which includes five classes of seed dormancy: physiological, morphological, morpho-physiological, physical and a combinational of physical and physiological. In this paper we will refer mainly to physiological dormancy which is the most prevalent dormancy type in temperate seed banks and in most laboratory model species (Finch-Savage and Leubner-Metzger 2006). This type of dormancy is caused by a physiological inhibiting mechanism of the embryo that prevents radicle emergence, although other seed structures that cover the embryo can be involved as well (Baskin and Baskin 1998). From a physiological point of view there is enough evidence showing that the mechanism of seed dormancy is mainly regulated by the phytohormones abscisic acid and gibberellins (Hilhorst 1995, 2007; Finch-Savage and Leubner-Metzger 2006).

Dormancy can be also classified in primary and secondary dormancy. 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 seeds by unfavorable conditions for germination, or re-induced in once-dormant seeds after a sufficiently low dormancy had been attained. The release from primary dormancy followed by subsequent entrance into secondary dormancy (whenever conditions are given for this entrance) may lead to dormancy cycling under

field conditions. Evidence for dormancy cycling in natural seed soil banks has been obtained for many 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 seed-bank population. For example, in the case of a summer annual species (i.e., seed dispersal is at the end of the summer and seedling emergence is at the beginning of spring), seed-bank dormancy is alleviated during winter and re-induced during late-spring and early-summer; the emergence period is restricted to the time window when the population has reached its minimum dormancy (Fig. 1). In this way plants adjust their seasonal emergence window to guarantee their reproductive success, for example, in the case of summer annuals avoiding the risk of frost damage during winter.

Predicting seed-bank dormancy level is important because timing and extent of seedling emergence in the field is strictly related to the dormancy state of the seed-bank. Thus, for seeds that present dormancy, an accurate prediction of changes in seed dormancy level of buried seeds is essential if we aim to predict seedling emergence from natural soil seed banks. The possibility of predicting the dormancy state of the seed-bank, and consequently, timing and extent of seed emergence, has many practical applications. For example, in relation to increasing the efficacy of weed control methods, assessing both timing and extent of weed emergence through predictive models, is of capital importance (Ghersa et al. 1997; Batlla and Benech-Arnold 2007). In addition, predictive models can help us to design practices for managing native or introduced plant populations (Allen et al. 2007). Hence, processes as dormancy release and induction must be included in any attempt for producing predictive models of emergence from natural seed soil banks. To accomplish this goal, the following steps need to be followed: first, the effect of the different environmental factors on the dormancy level of buried seeds must be comprehensively understood; second, the effect of those factors on the dormancy level of the seed-bank population must be quantified; third, the developed quantitative relationships must be included in a consistent modeling framework.

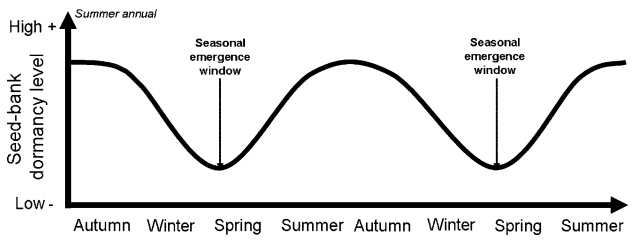

Fig. 1 Schematic representation of cyclic seasonal changes in natural seed soil bank dormancy level for summer annual species (Adapted from Batlla and Benech-Arnold 2007)

In the present paper we show examples of practical approaches to accomplish these three steps. It is not the aim of this paper to carry out a comprehensive review of dormancy modeling (for a recent review on this topic, see Allen et al. 2007) but to show how the "key" steps for developing predictive models of dormancy changes in natural seed soil banks can be achieved.

Environmental factors affecting dormancy in natural seed soil banks

Environmental factor affecting dormancy level of buried seed-banks can be divided in two classes: dormancy level regulating factors and dormancy terminating factors or germination initiating factors (Benech-Arnold et al. 2000). The dormancy level regulating factors are related to seasonal synchronicity of seed germination in the field (Finch-Savage and Leubner-Metzger 2006). These factors alter the depth of dormancy producing seasonal changes in the germinating behavior of the seed-bank by altering the sensitivity of seeds to environmental signals. There is enough evidence showing that soil temperature is one of the main factors governing seasonal changes in the seed-bank dormancy level in temperate environments, though there is evidence showing that there is an interaction between temperature and the hydration level of the seeds (Baskin and Baskin 1988, 1998; Benech-Arnold et al. 2000; Batlla et al. 2004; Allen et al. 2007). On the other hand, for most seed populations, dormancy must be terminated by specific environmental signals (i.e., dormancy terminating factors) which, from an ecological point of view, are factors that indicate in a more immediately way that conditions are suitable for germination (Finch-Savage and Leubner-Metzger 2006). Under field conditions the most important factors that terminate dormancy of buried seeds are light and alternating temperature. However, there are many other factors that can be acting as dormancy terminators under specific field conditions, as for example nitrate, ethylene, carbon dioxide, etc.

In the case of light, cancellation of dormancy by light is mediated by Pfr, the active form of phytochrome. During dormancy alleviation seeds sensitivity to light is progressively enhanced requiring lower amounts of Pfr to trigger dormancy termination. In the case of fluctuating temperatures, an enhanced sensitivity to the stimulus as related to dormancy alleviation, is evidenced through a low requirement in terms of both the composition of the cycles (i.e., lower thermal amplitude, lower maximum temperature

etc.) and the number of cycles of alternating temperatures required to terminate dormancy of a majority of the individuals in the population (Benech-Arnold et al. 2000).

An ecological interpretation of the requirement of light and alternating temperatures to complete exit from dormancy in many wild species has been related to the possibility of detecting canopy gaps, the light flash during tillage operations and depth of burial under field situations (Scopel et al. 1991; Casal and Sánchez 1998; Benech-Arnold et al. 2000).

Seed dormancy level and environmental conditions for seed germination

Dormancy is not an all-or-nothing seed property. On the contrary, seed dormancy status can vary over a continuous dormancy degree scale between some point where dormancy is maximal and some point where dormancy is minimum (Batlla et al. 2004). The degree or level of dormancy of a seed population establishes the width of the range of environmental conditions that allow germination. A low dormancy level is characterized by a wide range of environmental conditions permissive for seed germination, while seeds presenting a high dormancy level show a narrow range of environmental conditions permissive for seed germination. This relationship between seed dormancy level and the range of environmental conditions permissive for seed germination was first proposed by Vegis (1964). This author 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, while 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. More recent findings showed that not only the range of temperatures under which germination is possible changes in relation to seed dormancy level, but also the range of water potentials within which seed germination can proceed (Batlla et al. 2004). For example, for the summer annual *Polygonum aviculare* L. Batlla and Benech-Arnold (2003, 2004), demonstrated that during dormancy loss the range of temperatures and water potentials permissive for seed germination widened as a consequence of a decrease in the lower limit temperature for seed germination (T_l) and the base water potential (Ψ_b), respectively. On the other hand, dormancy induction was characterized through a narrowing of those ranges due to an increase in T_l and Ψ_b. Christensen et al. (1996) and Bauer et al. (1998) also found a progressive decrease in Ψ_b during dormancy loss in *Bromus tectorum*. Similar results were reported by Alvarado and Bradford (2005) during dormancy loss in true potato (*Solanum tuberosum*) seeds.

In those cases where dormancy requires to be terminated by light or fluctuating temperatures, changes in the degree of dormancy not only comprise changes in the temperature requirements for germination and in base water potential for germination, but also in sensitivity to the effect of dormancy-terminating factors (Benech-Arnold et al. 2000). Evidence for an increase or a decrease in sensitivity to dormancy terminating factors during dormancy loss and induction, respectively, has been shown for many wild species (Benech-Arnold et al. 1990; Hilhorst 1990; Hilhorst et al. 1996)

Conceptual model

Based on these considerations, it could be stated that the degree of dormancy of a seed population can be assessed through the width of the thermal and water potential range permissive for seed germination, and its sensitivity to the effect of dormancy terminating factors. In other words, the dormancy level of a population is high if it cannot germinate at any temperature or water potential (absolute dormancy), or if it can only germinate within a narrow range of temperatures and/or water potentials and displays low sensitivity to light or fluctuating temperatures; conversely, the degree of dormancy of a population is low if it can germinate in a wide range of temperatures and/or water potentials and presents high sensitivity to light or fluctuating temperatures. As stated before, the passage from a high dormancy state to a low dormancy one will be governed by soil temperature and modulated by the hydration state of the seeds; the latter determined by the soil water content (Fig. 2). Germination will take place when prevailing environmental conditions meet those required for seed germination, which in turn will depend on the dormancy state of the seed-bank.

This conceptual scheme can be proposed separately for both a summer and a winter annual species considering the differential effect of temperature on seed dormancy regulation and how the permissive thermal range changes with dormancy in each case (Fig. 3). In most summer annual species, which are those emerging in spring, exposure of moist seeds to low temperature produce dormancy release, a process named stratification, while high temperatures produce dormancy induction. In contrast, in winter species, which germinate in autumn, exposure of dry seeds to high temperatures produce dormancy release, a process commonly denominated dry after-ripening, while exposure to low temperature produce dormancy induction. This differential effect of soil temperature on seed dormancy level are responsible for the different seasonal dormancy pattern

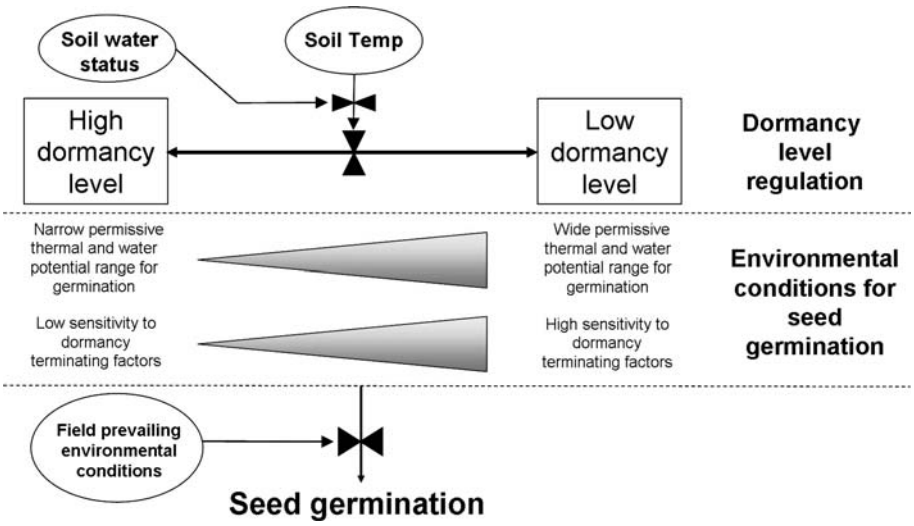

Fig. 2 Flowchart representing most relevant environmental factors regulating dormancy level and changes in the range of environmental conditions for seed germination in natural soil seed banks (Adapted from Benech-Arnold et al. 2000)

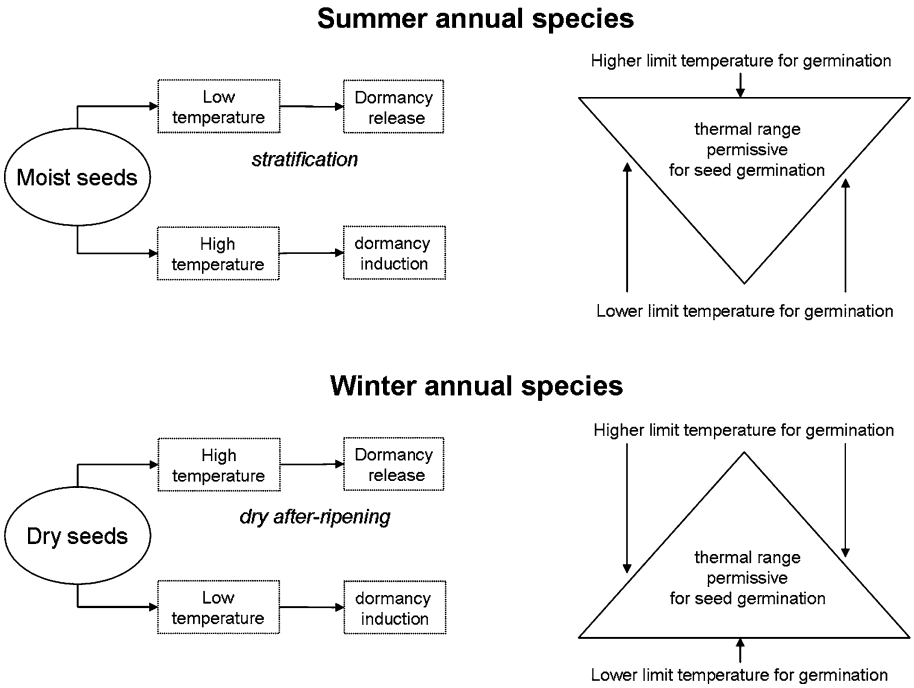

Fig. 3 Soil temperature effects on seed dormancy level and a schematic representation of changes in the range of temperatures permissive for seed germination in summer and winter annual species

and emergence timing observed of both type of species under field condition. Seeds of some summer annuals are dormant in autumn, lose dormancy in winter through the effect of low temperatures if they are imbibed (i.e., stratification), and recover it in summer through the effect of high temperatures (Fig. 1). Winter annuals lose their dormancy during spring and summer through the effect of high temperatures acting on dry seeds (i.e., dry after-ripening), and recover it in winter through the effect of cold temperatures (Baskin and Baskin 1998). Examples of summer and winter annuals species that can be part of natural soil seed banks are *P. aviculare* (Polygonaceae), *Sysimbrium officinal* (Brassicaceae), *Datura ferox* (Solanaceae) and *Solanum nigrum* (Solanaceae) in the case of the former, and *Arabidopsis thaliana* (Brassicaceae), *Avena fatua* (Poaceae), *Capsella bursa-pastoris* (Brassicaceae), *Sinapis arvensis* (Brassicaceae) and *B. tectorum* (Poaceae) in the case of the later.

In both cases, the high dormancy level of the seeds immediately after dispersal is evidenced 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 lower limit temperature for germination (T_l) and in winter annuals, through a progressive increase in the higher

limit temperature for germination (T_m; Fig. 3). Re-induction of dormancy results in a narrowing of the permissive thermal range through an increase in T_l in summer annuals and a decrease in T_m in winter annuals. In both cases, germination occurs in the field when soil temperature enters the permissive range (Fig. 3).

It is important to emphasize that, as seeds in a population present different dormancy levels, description of changes in the range of temperatures permissive for seed germination through changes in T_l or T_m, and/or in the range of water potentials permissive for seed germination through changes in Ψ_b, are usually characterized by the mean value of these parameters, namely $T_{l\ (50)}$, $T_{m\ (50)}$ and $\Psi_{b\ (50)}$, which describes the dormancy level of 50% of the seed population.

Temperature effects on seed dormancy level (establishing quantitative relationships)

To develop predictive models we should establish quantitative functional relationships between the rate of the biological process we want to predict and the environmental factors that regulate that process. As pointed out before, there is enough evidence supporting the fact that the main factor governing changes in seed-bank dormancy level under field conditions is soil temperature; indeed almost all attempts to model dormancy changes in natural seed soil banks used temperature as the key factor driving changes in seed dormancy status (Batlla and Benech-Arnold 2007). On the other hand, variations in the dormancy level of the seed-bank (the process we want to predict), are related to changes in seed requirements for germination, as for example, changes in the thermal and water potential range for seed germination, changes in seed sensitivity to light, changes in seed sensitivity to alternating temperatures, etc. Therefore, if we want to predict dormancy changes in seed soil banks we should establish quantitative relationships between soil temperature and changes in seed population requirements for germination.

A common approach successfully used by many researchers to establish quantitative relationship between temperature and the rate of a biological process has been the use of thermal time models (Trudgill et al. 2005). Thermal time models are basically threshold type models in which the effect of an input (in this case temperature) is equivalent to the difference between the level of the input and a threshold response level of the studied process to that input. This type of approach has been extensively used in biology to quantify the effect of temperature on many different processes, as germination (Garcia-Huidobro et al. 1982; Covell et al. 1986), plant development (Bonhomme 2000), insect development (Honek and Kocourek 1988), budburst (Cannell and Smith 1983), etc. In relation to dormancy, thermal-time based models has been successfully used to establish quantitative relationships between temperature and dormancy changes in dry and moist stored seeds (Pritchard et al. 1996; Bauer et al. 1998; Steadman et al. 2003; Batlla and Benech-Arnold 2007; Wang et al. 2009). For example, Batlla and Benech-Arnold (2003) characterised *P. aviculare* seed dormancy loss through changes in the range of temperatures permissive for germination as a consequence of changes in the value of the mean lower limit temperature permissive for seed germination ($T_{l\ (50)}$). In order to quantify the effects of stratification time and temperature on seed population dormancy status (assessed through changes in $T_{l\ (50)}$) the authors used a thermal time index calculated through the following equation (Fig. 4a):

$$S_{tt} = \text{Days} \times (T_c - T_s) \quad (1)$$

where S_{tt} is stratification thermal time units (°Cd), T_c is the dormancy release "ceiling" temperature (°C; the temperature at, or over, which dormancy release does not occur) and T_s is the daily mean storage temperature (°C). The optimal "ceiling" temperature for dormancy loss in *P. aviculare* seeds was 17°C (Batlla and Benech-Arnold 2003).

This thermal time approach is similar to that usually used to relate other biological processes to time and temperature. However, in contrast to common thermal time models in which degree days are accumulated over a base temperature for the process to occur, the stratification thermal time index accumulates degree days below a ceiling threshold. The same index was proven to be effective to predict changes in the response of *P. aviculare* seeds to other environmental factors in relation to the stratification temperature experienced by the seeds, as for example, changes in seed sensitivity to light (Batlla and Benech-Arnold 2005), changes in the range of permissive water potential for seed germination (Batlla and Benech-Arnold 2004) and changes in seed sensitivity to alternating temperature cycles (Batlla et al. 2003). This stratification thermal time model was successfully used to predict dormancy changes in seeds overwintered in the soil under real field conditions (Batlla and Benech-Arnold 2003, 2004).

In relation to the after-ripening process, Chantre et al. (2009) also used a thermal time approach to relate dormancy changes in *Lithospermun arvense*, a common weed in the south of Argentina, to temperature. In this model *L. arvense* variations in dormancy level were characterized by changes in the range of temperatures permissive for germination as a consequence of changes in the value of the mean maximum or ceiling temperature for seed germination ($T_{c\ (50)}$; Fig. 4b). Changes in this population parameter during dormancy loss were predicted through a

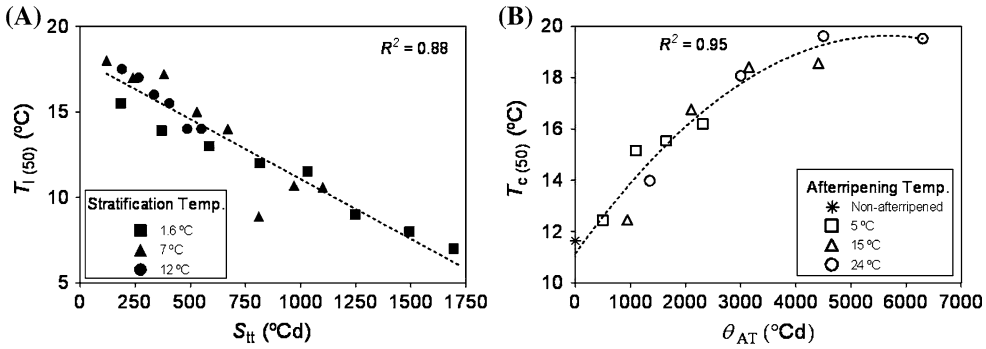

Fig. 4 Estimated values of the mean lower limit temperature ($T_{l\ (50)}$) for *P. aviculare* seeds stored moist at different temperatures plotted against stratification thermal time (S_{tt}) (**a**) and estimated values of the mean maximum or ceiling temperature ($T_{c\ (50)}$) for *L. arvense* seeds recently harvested and stored dry at different temperatures plotted against after-ripening thermal time (θ_{AT}) (**b**). *Fitted line* in **a** $y = 18.07 - x0.007$; *fitted line* in **b** $y = -2.66\ e^{-07}\ x^2 + 0.003x + 11.14$. Figure in **a** was adapted from Batlla and Benech-Arnold (2003), while figure in **b** was adapted from Chantre et al. (2009)

quadratic equation in relation to the accumulation of after-ripening thermal time units (°Cd) above a base temperature of −6°C for the after-ripening process to occur. Dormancy loss in *L. arvense* was also accompanied, as in most species, by a progressive increase in seed germination rate as a consequence of a decrease in the thermal time required for seed germination. Changes in the thermal time required for seed germination during after-ripening was also successfully predicted using the after-ripening thermal time index affected by the after-ripening temperatures (Chantre et al. 2009).

Although many models have been developed based on the effect of temperature on seed dormancy loss, less has been done in relation to the effect of temperature on seed dormancy induction. In a recent paper Batlla et al. (2009) quantified and modeled temperature effects in the range 2–25°C on the dormancy loss and induction rate in a *P. aviculare* seed population. Obtained results showed that dormancy induction and dormancy release can occur simultaneously, as first hypothesized by Totterdell and Roberts (1979), but with different rates depending on prevailing temperature (Fig. 5). As expected for summer annual species, dormancy release was the predominant process at low temperatures, while dormancy induction was predominant at high temperatures. However, the rate of dormancy induction at high temperature was two orders of magnitude higher than the rate of dormancy release at low temperatures. These results have important ecological and methodological implications. On one side, it highlights the importance of including the dormancy induction process in predictive models if we intend to predict seedling emergence under field conditions, as brief periods of relatively high temperatures in the field can shorten or even impede the seed soil bank emergence period in some species. On the other side, the high rate of dormancy induction observed for *P. aviculare* seeds stored at high temperatures

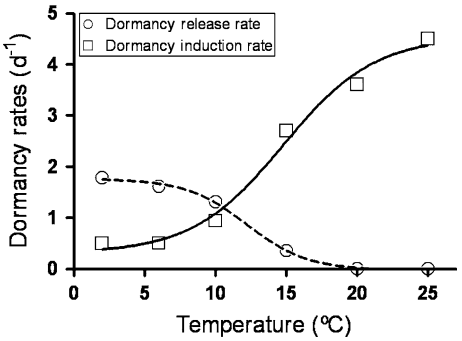

Fig. 5 Estimated values of dormancy release and induction rates in relation to storage temperature. *Lines* are fitted exponential equations; *Dashed line* $y = 1.758/\left(1 + 10^{((12.14-x)*-0.2092)}\right)$, R^2 0.99; *Full line* $y = 4.546/\left(1 + 10^{((14.79-x)*0.135)}\right)$, R^2 0.99 (Adapted from Batlla et al. 2009)

confirm that dormancy changes in some species can be acting in the same time scale as the germination process, and therefore can be affecting the results of germination assays usually performed to measure changes in the dormancy state of the seed-bank. Indeed, very often, particularly when working with wild species which are very reactive to temperature-dependent dormancy changes, the germination dynamics observed in the germination test can be the result of different competing forces. For example, if we incubate seeds at high temperatures, two processes might be taking place during the germination test; on one side germination, and on the other side dormancy induction, while when we incubate seeds at low temperatures we can have germination and dormancy release. The final observed germination dynamics would depend on the relative strength of each force, namely, the germination, dormancy induction and dormancy release rate at a certain germination test temperature. The possibility to correctly interpret the effect of temperature on the dormancy process from that on the germination process is of paramount

importance if we intend to establish functional relationships between temperature and dormancy changes in order to develop predictive models. Moreover, the mixed effect of germination and dormancy temperature-dependent processes during germination testing in wild species can lead to an incorrect interpretation of physiological and/or molecular obtained results.

Soil water status effects on seed dormancy level

As pointed out before, the other environmental factor that can be affecting the dormancy state of the seed-bank under field conditions is soil water content. However, the effect of soil water content on seed dormancy status under natural environments has been rarely studied, and most of the information regarding the effect of this factor comes from controlled experiments performed in a number of species, particularly those requiring dry after-ripening for dormancy loss (Leopold et al. 1988; Foley 1994; Steadman et al. 2003). Probably because there is less information available, there are just few models that take into account the effect of soil water status as affecting the dormancy state of seeds buried in the soil. One example of a predictive model which includes the effect of soil water status as affecting dormancy changes is that developed by Bair et al. (2006) for *B. tectorum* seeds. Bair and co-workers quantified through laboratory experiments the effect of solutions with different water potentials on the dormancy loss rate of *B. tectorum* seeds, relating this to the water potential that the seeds can experience in the soil (Fig. 6). Basically, they found four ranges of soil water potential affecting the dormancy loss rate. One in which seeds are too dry and after-ripening does not occur; an intermediate range within which the dormancy loss rate is affected by soil water status, in which the lower the water potential the lower the dormancy loss rate; a third range within which the dormancy loss rate just depends on prevailing soil temperature and is not affected by soil water status; and a fourth range within which seeds are too wet for after-ripening to occur. Based on obtained results they included the effect of soil water content as affecting the dormancy loss rate in a previously developed model driven just by soil temperature (Christensen et al. 1996; Bauer et al. 1998). Adding the effect of soil water potential as affecting the dormancy loss rate of seeds buried in the soil generally improved predictions of dormancy loss under dry soil conditions. Overall, experimental evidence indicates that there exist higher and lower threshold seed water contents above and below which after-ripening does not occur, and that within the permissive range, the after-ripening rate can be affected by the actual soil water potential perceived by the buried seed population. Including soil water content effects on seed dormancy loss can improve model predictions in environments in which the seed-bank is usually exposed to extremely dry or wet soil conditions during particular seasons of the year.

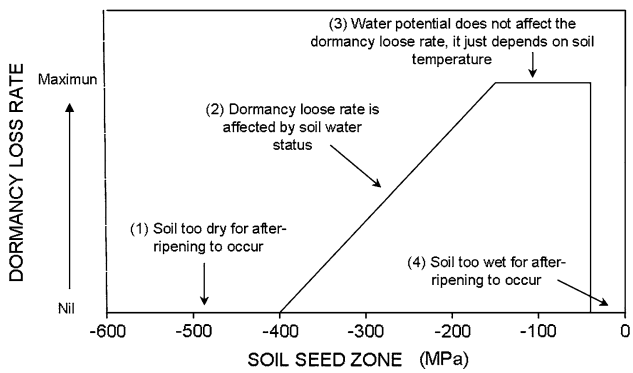

Fig. 6 Conceptual diagram showing how storage water potential influences after-ripening in seeds of *Bromus tectorum*. Threshold water potentials are approximate (Adapted from Allen et al. 2007, originally from Bair et al. 2006)

There is also evidence showing that seeds water status can affect the stratification process. In a recent paper Wang et al. (2009), quantified the effect of seed water content on the dormancy release for *Vitis vinicola* seeds stored at 5°C. They found almost nil seed dormancy loss for seeds presenting water content below 20%, and an increase in the dormancy loss rate between this value and 40% seed water content. Batlla et al. (2007) also found that the acquisition of an extreme sensitivity to light in *P. aviculare* seeds as a consequence of dormancy loss through stratification was affected by soil water content.

Although soil water status can be affecting the seed-bank dormancy level by establishing the seed hydration level, there is evidence indicating that soil moisture fluctuation to which superficially buried seeds are frequently exposed to in the field, can be also affecting the dormancy level of the seed-bank (Bouwmeester 1990; Allen et al. 1993; Batlla and Benech-Arnold 2006).

Population-based threshold models

Population-based threshold models have been proved to be an adequate modeling framework for developing dormancy predictive models (Bradford 1996, 1997, 2002; Finch-Savage and Leubner-Metzger 2006; Allen et al. 2007). The main feature that makes this type of models suitable for characterizing seed dormancy is that they explicitly recognize and incorporate the variation in dormancy level existing within the seed population. The possibility of characterizing and quantifying that variation is of paramount importance in predicting seed germination behavior of seed populations, especially in wild species in which the

variation in the response of seeds to environmental factors is larger than in domesticated species (Batlla and Benech-Arnold 2007). In most cases we can assume that dormancy levels within the population are normally distributed; hence, this distribution can be characterized by just two parameters the mean dormancy level of the population and its standard deviation. However, other types of distributions can be used as well. For example, if we intend to quantify the dormancy level of a seed population through their sensitivity to light in the low fluence response range (LFR), we can have the frequency distribution of the percentage Pfr (the active phytochrome mode for germination) required for germination within the seed population, with the most dormant fraction of the population requiring more Pfr for germination (the less sensitive fraction of the population), and the less dormant fraction requiring less Pfr for germination (the most sensitive fraction of the population; Fig. 7a). This type of approach allows us to quantitatively describe the response of individual seeds to a certain environmental factor in relation to their dormancy level. Assuming that the light environment establishes a Pfr of 40%, those seeds requiring less than this quantity would germinate; in the hypothetical case shown in Fig. 7a 50% of the population. However, if the Pfr established by the light environment is lower (for example 20%), only the fraction requiring less than this percentage of Pfr for germination will germinate (i.e., the more sensitive seeds in Fig. 7a).

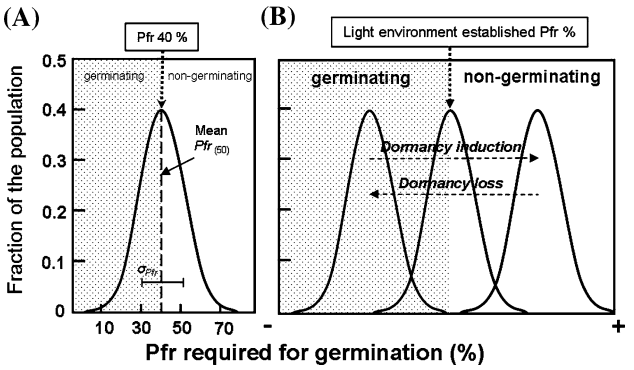

Fig. 7 **a** Hypothetical distribution of Pfr required for germination in the seed population. The *solid curve* represent the normal frequency threshold distribution of Pfr values among individual seeds, which is characterized by its mean ($Pfr_{(50)}$) and its corresponding standard deviation (σ_{Pfr}). The *dotted* and *non-dotted areas* indicate the fraction of germinating and non-germinating seed, respectively, in a hypothetical situation in which the Pfr value established by the light environment is 40% (indicated by a *dotted arrow* on the top of the figure) **b** Population-based representation of changes in seed population sensitivity to light through displacement of the threshold distribution of Pfr required for germination due to changes in seed dormancy level. Displacements of the threshold distribution during dormancy loss and/or induction are indicated by *dashed arrows*. The *dotted* and *non-dotted* areas indicate the fraction of germinating and non-germinating seed, respectively, for a hypothetical Pfr percentage established by the light environment (indicated by a *dotted arrow* on the top of the figure; Based on Allen et al. 2007). Examples **a** and **b** are based on the phytochrome system acting in the low fluence response action mode (LFR)

Using this modeling approach changes in the seed-bank dormancy level expressed as changes in seed responses to environmental factors can be described by shifting the threshold response distribution during dormancy release or induction (Allen et al. 2007). During dormancy release, both through after-ripening or stratification, seeds will become more sensitive to light, requiring less Pfr for germination, and this can be described by shifting the threshold response distribution to the left (Fig. 7b). Conversely, during dormancy induction, seeds will become less sensitive to light and will require more Pfr to germinate, and this can be described by shifting the distribution to the right. The same can be applied to changes in the response of seeds to any other environmental factor. For example, widening or narrowing the temperature range permissive for seed germination during dormancy loss and induction, respectively, can be described through shifting the distribution of the minimum temperature for seed germination (T_l) in summer annual species or the maximum temperature for germination (T_m) in winter annual species. Most studies showed that changes in mean population values, not altering the distribution of threshold around the mean, was enough to account for changes in the behavior of the seed population in relation to changes in their dormancy level from a modeling point of view (Finch-Savage and Leubner-Metzger 2006); however, changes in the standard deviation during dormancy release can be important in some situations for a correct prediction of the process (Batlla and Benech-Arnold 2003, 2007).

Population-based threshold models can be combined with previously explained thermal time approaches to develop a temperature driven dormancy model. Population-based thresholds models can be used to describe changes in seed responses to environmental factors in relation to the seed-bank dormancy level, while a thermal time index can be used to quantify the effect of temperature on the seed-bank dormancy level. For example, dormancy level regulation by temperature can be quantified by the accumulation of stratification or after-ripening thermal time units, and this can be related to changes in the parameters of the response distribution (the mean and/or the standard deviation) during dormancy release and/or induction (for examples, see Christensen et al. 1996; Batlla and Benech-Arnold 2004; Bradford 2005).

The utility of modeled species for physiological and molecular studies

Much of the molecular and genetic approaches to study the regulation of seed dormancy level by environmental factors

have been done using model species, such as *Arabidopsis thaliana*. In spite of the huge advances that have been produced through the use of these model organisms in the understanding of the molecular bases of dormancy expression, it must be acknowledged that most of *A. thaliana* accessions, excepting Cvi that presents a deeper dormancy, has a shallow dormancy (Cohn 1996) thus precluding the possibility of assessing the complexity of the environmental regulation of dormancy as it exists in other wild species. Modeling efforts in wild species that present a deeper dormancy and display a diversity of responses to many environmental factors (as examples presented in this paper for *P. aviculare* and *B. tectorum*), have yielded a deep understanding of how different environmental factors regulate dormancy in these species. Moreover, the relationships between those factors and the dormancy state of the seeds have been quantified. For example, in the case of *P. aviculare*, mature seeds present a very high dormancy level at maturity (full dormancy) that needs months of stratification to be relieved. During this slow dormancy release process seeds gradually acquire the capacity to germinate at lower temperatures and lower water potentials and increase their sensitivity to light and fluctuating temperatures. However, due to the strong response to dormancy terminating factors, dormancy level can be diminished through stratification but seeds would not germinate until exposed to light and/or fluctuating temperatures, clearly separating the dormancy release and the germination process. These features commented above make these species interesting candidates for physiological and molecular studies, and could probably allow a more clear way to link ecological observations of dormancy behavior in the wild to laboratory-based molecular work.

Indeed, one future challenge is the possibility of combining quantitative mathematical models which have been proved to be successful for characterizing dormancy changes in response to environmental stimuli in many species, with genetic and molecular work. As pointed out by Bradford (2005) and Finch-Savage and Leubner-Metzger (2006), one possible way may lie behind the use of population-based threshold models, particularly using base water potential (Ψ_b) as a measure of the dormancy status of the seed population. There are reasons to argue that the value of this parameter may have biological significance (Bradford 1995, 2002), as can relate to endogenous and/or exogenous physical constraints to embryo growth that can be blocking seed germination. Moreover, there is evidence showing that Ψ_b of different species seed populations changes as a consequence of dormancy release and induction processes elicited by different environmental factors, as for example stratification temperature (Batlla and Benech-Arnold 2004), after-ripening temperature (Bauer et al. 1998; Meyer et al. 2000) and alternating temperatures (Huarte and Benech-Arnold 2005), and in response to exogenous applications of the main plant hormones regulating dormancy, as abscisic acid and gibberellins, and the corresponding hormone synthesis inhibitors (Ni and Bradford 1992, 1993; Alvarado and Bradford 2005). This evidence suggest that dormancy changes in response to environmental stimuli and hormonal control can be related to a common scale based on changes in Ψ_b as a common index to measure seed dormancy status. Although the detailed biochemical and molecular mechanisms by which Ψ_b values are determined have yet to be identified, it could be speculated that known hormonal control mechanisms are behind this determination. Within this context the different components of abscisic acid and gibberellins synthesis and catabolism, as NCED and CYP707A2 in the case of the former hormone, and GA2ox2 and GA3ox1 in the case of the later, arise as obvious candidates to be investigated as responsible for changes in Ψ_b as a consequence of dormancy changes. The same applies to components of ABA and GA signaling networks. The combine action of these hormones (regulated by the environment at the level of synthesis and signaling) must be controlling the activity of enzymes committed to cell wall expansion that, ultimately, are responsible for changes in Ψ_b.

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