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Germination traits explain soil seed persistence across species: the case of Mediterranean annual plants in cereal fields

Arne Saatkamp[1,3,*], Laurence Affre[1], Thierry Dutoit[2] and Peter Poschlod[3]

[1]*Institut Méditerranéen d'Écologie et de Paléoécologie IMEP IRD UMR CNRS 6116, Université d'Aix-Marseille III, FST Saint-Jérôme, case 462, F-13397 Marseille Cedex 20, France,* [2]*Institut Méditerranéen d'Écologie et de Paléoécologie IMEP IRD UMR CNRS 6116, IUT Université d'Avignon, Site Agroparc BP 61207, Domaine Saint-Paul France, F-84914 Avignon, France and* [3]*Institute of Botany, University of Regensburg, Germany*
** For correspondence. E-mail arnesaatkamp@gmx.de*

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• *Background and Aims* Seed persistence in the soil under field conditions is an important issue for the maintenance of local plant populations and the restoration of plant communities, increasingly so in the light of rapidly changing land use and climate change. Whereas processes important for dispersal in space are well known, knowledge of processes governing dispersal in time is still limited. Data for morphological seed traits such as size have given contradictory results for prediction of soil seed persistence or cover only a few species. There have been few experimental studies on the role of germination traits in determining soil seed persistence, while none has studied their predictive value consistently across species. Delayed germination, as well as light requirements for germination, have been suggested to contribute to the formation of persistent seed banks. Moreover, diurnally fluctuating temperatures can influence the timing of germination and are therefore linked to seed bank persistence.
• *Methods* The role of germination speed measured by T_{50} (days to germination of 50 % of all germinated seeds), light requirement and reaction to diurnally fluctuating temperatures in determining seed persistence in the soil was evaluated using an experimental comparative data set of 25 annual cereal weed species.
• *Key Results* It is shown that light requirements and slow germination are important features to maintain seeds ungerminated just after entering the soil, and hence influence survival of seeds in the soil. However, the detection of low diurnally fluctuating temperatures enhances soil seed bank persistence by limiting germination. Our data further suggest that the effect of diurnally fluctuating temperatures, as measured on seeds after dispersal and dry storage, is increasingly important to prevent fatal germination after longer burial periods.
• *Conclusions* These results underline the functional role of delayed germination and light for survival of seeds in the soil and hence their importance for shaping the first part of the seed decay curve. Our analyses highlight the detection of diurnally fluctuating temperatures as a third mechanism to achieve higher soil seed persistence after burial which interacts strongly with season. We therefore advocate focusing future research on mechanisms that favour soil seed persistence after longer burial times and moving from studies of morphological features to exploration of germination traits such as reaction to diurnally fluctuating temperatures.

Key words: Diurnally fluctuating temperatures, delayed germination, T_{50}, gap detection, light requirement, dormancy, *Asteraceae*, *Campanulaceae*, *Apiaceae*, *Papaveraceae*, soil seed bank.

INTRODUCTION

Dispersal of seeds in time, or the persistence of seeds in the soil, plays a key role in population dynamics and the establishment of plant communities and is an important factor for restoration of habitats and populations from the seed bank (van der Valk and Pederson, 1989; Kalisz and McPeek, 1992; Bekker *et al.*, 1998*b*; Stöcklin and Fischer, 1999; Bossuyt and Honnay, 2008). However, understanding of soil seed persistence is still limited, and important features such as different seed decay curves (Rees and Long, 1993) are still not well understood from a functional point of view. This contrasts with recent work on seed dispersal in space which revealed details of the role of plant traits and environment for the shape of spatially dispersed kernels and which provided detailed information on how spatial dispersal potential can be modelled (Tackenberg *et al.*, 2003; Poschlod *et al.*, 2005; Römermann *et al.*, 2005). It is now an important task to study how different functional processes shape soil seed decay curves and how different mechanisms succeed each other in order to disperse seeds through time.

Several evolutionary models propose which constraints are important for dispersal through time. First of all, 'bet-hedging' proposes that seed germination should be delayed and dispersed through time as a function of environmental hazards in order to maximize the fitness of the mother plant (Cohen, 1966; Ellner, 1986; Venable, 2007). Furthermore, models on competitive interactions suggest that long-lived seed banks enhance the local co-existence of otherwise competitively exclusive species through the storage effect (Warner and Chesson, 1985; Facelli *et al.*, 2005). The storage effect implicitly uses the 'regeneration niche' and stresses how germination cues, such as seasons and specific disturbances, can maximize fitness of seeds (Grubb, 1977; Donohue, 2005).

Germination cues illustrate how seeds detect establishment opportunities, e.g. favourable climatic conditions via specific temperatures, gaps via diurnally fluctuating temperatures (DFTs) and red/far red ratios (Grubb, 1977; Thompson and Grime, 1983; Baskin and Baskin, 1998; Fenner and Thompson, 2005). Therefore, the storage effect model can give insights into which processes and traits are related to soil seed persistence. Finally, germination should be delayed in order to avoid competition with the mother plant (Silvertown, 1999). This parent–offspring conflict states explicitly which trait should evolve (i.e. delayed germination) and how long it should act (until the death of the mother plant). There are both seed morphological traits and physiological germination traits that potentially contribute to soil seed persistence when temporally variable habitats favour species with persistent seed banks under bet-hedging or storage effect conditions (Warner and Chesson, 1985; Silvertown, 1999; Facelli *et al.*, 2005; Venable, 2007).

Mortality of seeds in the soil may occur for several reasons: (*a*) fungal attack or predation (Blaney and Kotanen, 2001; Schafer and Kotanen, 2003); (*b*) ageing (Priestley, 1986); and (*c*) fatal germination in soil layers which are too deep, or 'suicide germination' (Bond *et al.*, 1999; Benvenuti *et al.*, 2001; Traba *et al.*, 2004). Since these processes are different and vary in their importance according to environment, different traits evolved in order to maximize seed survival. Morphological plant traits have been suggested to be related to soil seed bank persistence, especially seed size, which may be negatively (Bekker *et al.*, 1998*a*) or positively (Moles and Westoby, 2006) related to persistence in the soil. Since this trait is in a trade-off with seed production and its predictive value depends on how soil seed persistence is measured (Saatkamp *et al.*, 2009), there is a need for alternative traits to predict soil seed persistence. Even if evidence is still limited, seed coat thickness gave promising results for the prediction of soil seed longevity in arable weeds (Gardarin *et al.*, 2010). Moreover, germination physiological traits can be used to predict longevity. They differ from morphological features because of their ability to schedule germination and in this way maximize the fitness of offspring and enhance soil seed bank persistence (Baskin and Baskin, 1998; Donohue, 2005). According to previous considerations (Thompson and Grime, 1983; Grime, 1989; Baskin and Baskin, 1998), germination traits that relate to soil seed persistence include three main aspects: delayed germination, light requirement for germination and reaction to DFTs.

First, delayed germination has been proposed as an important factor for the formation of a persistent soil seed bank, notably through a diversity of dormancy mechanisms and breaking cues (Baskin and Baskin, 1989). However, comparative analyses correlating data on soil seed persistence and categorical dormancy data across species from various sites revealed no strong relationships between these variables (Thompson *et al.*, 2003; Baskin and Baskin, 2006). This may again be explained by the methods used to determine soil seed persistence (Baskin and Baskin, 2006; Saatkamp *et al.*, 2009) but also by the effect of habitat conditions on soil seed bank persistence (Schafer and Kotanen, 2003). In addition, the use of dormancy data varies, since dormancy can be classified into different types and levels according to physiological, physical and morphological characters (Baskin and Baskin, 1998). In contrast to these comprehensive categorical data of dormancy mechanisms, delayed germination can be quantified by the germination rate or T_{50} (days to germination of 50 % of all germinated seeds) (Baskin and Baskin, 1998; Finch-Savage and Leubner-Metzger, 2006). T_{50} turned out to be a useful tool for interspecific comparisons on a quantitative basis (Kos and Poschlod, 2010) and has already been proposed (but never tested) to be related to soil seed persistence (Grime, 1989).

Secondly, a light requirement for germination can result in the persistence of buried seeds until disturbances occur (Grime *et al.*, 1981; Baskin and Baskin, 1989; Grime, 1989; Milberg *et al.*, 2000), since light only enters the soil slighly (Benvenuti, 1995).

Thirdly, DFTs, which are smaller in deep soil layers than at the soil surface (Miess, 1968), and which are more important in large gaps or sparse vegetation (Bullock, 2000), can enhance soil seed persistence over unfavourable periods for seedling establishment. Relatively better germination under DFTs permits the detection of disturbances from below the soil surface; a mechanism which is termed 'gap detection' (Thompson *et al.*, 1977; Grime *et al.*, 1981; Thompson and Grime, 1983). However, DFTs may also permit the detection of depth of burial (Thompson and Grime, 1983). The 'gap detection' role of DFTs has been well documented, whereas their suggested functional role in soil seed persistence has never been tested experimentally across species.

Comparative studies across many species have been particularly informative (Grime *et al.*, 1981; Milberg *et al.*, 2000; Thompson *et al.*, 2003), although, until now, the survival of seeds in the soil seed bank in experimental seed burial has been studied for only a few species simultaneously. Moreover, data on mortality of buried seeds have not yet been combined with experimental data on germination characteristics for a larger set of species. We therefore expected that burial experiments together with studies on germination characteristics should provide new insight into the control of germination below ground (Milberg and Andersson, 1998; Baskin and Baskin, 2006), extending previous observations from germination cueing (Merritt *et al.*, 2007) to the prediction of soil seed mortality. Soil seed persistence is related to traits that are known to be phylogenetically conserved (Shipley and Dion, 1992; Silvertown, 1999) and that potentially contribute a phylogenetically determined component. We therefore advocated studying soil seed persistence using phylogenetically explicit methods distinguishing phylogenetic effects from random effects at the species level (Housworth *et al.*, 2004).

Functional differences in formation of soil seed banks across species are most important for short-lived plants since they rely heavily on the soil seed bank for reproduction via seeds, buffering populations against reproductive failure and local extinction. Constraints on the evolution of a persistent soil seed bank are particularly strong for annual plants (Venable and Brown, 1993). Plants with a short-lived seed bank regress heavily under changing land use (Stöcklin and Fischer, 1999) and they may decline, for example with decreasing grazing intensity (Saatkamp *et al.*, 2010). Moreover, annuals of arable fields, where temporal variability of habitat quality is high, show a large range of different seed bank types (Thompson *et al.*,

1997; Baskin and Baskin, 2006). This makes annual plants of arable fields an interesting model system to study the relationships between germination physiological traits and soil seed persistence for comparative studies.

Here we report two comparative experiments, one on soil seed longevity and another on germination traits for 25 species in order to answer the following questions. (*a*) How is the germination speed (T_{50}) of a seed population related to its soil seed persistence? (*b*) What are the effects of a light requirement for germination and germination in darkness on soil seed persistence? (*c*) Is germination in response to DFTs related to soil seed persistence? (*d*) What do the interactions between these germination traits and time after burial or season tell us about seed decay in the soil?

MATERIALS AND METHODS

Study site and species

Annual plants from cereal fields in the Luberon area in South Eastern France were studied. The climate is Mediterranean type with highly variable rainfall, peaking in October and April (mean rainfall 1971–2000: 623 mm in 60 d). There is a marked summer drought and moderate frost during winter. The beginning of the humid season and cereal cultivation is October, which results in autumn being the main germination season, although germination also occurs in winter and in spring after disturbances (Filosa, 1997). Traditional agriculture in this area has maintained a high diversity of rare arable weeds extinct elsewhere in Europe (Filosa, 1997).

The selection of species focused on 25 annual plants from cereal fields (Table 1), including species pairs of rare and common species in the study region. Seed material was collected in the study region between June and September 2005 for the burial experiment and between June and September 2006 for the study of germination characteristics. Ripe seeds were taken from at least ten individuals of one single large population and mixed before use. Seed material was stored dry in paper bags in conditions similar to those in the field for a maximum of 3 months until use in the experiments. The data thus refer not to fresh, but to dry stored seeds, that have already undergone after-ripening for a maximum of 3 months. This is similar to what would happen to the seeds in the field between dispersal in summer and the first Mediterranean autumn rains (Finch-Savage and Leubner-Metzger, 2006; Karlsson and Milberg, 2007*b*).

Seed burial experiment and viability testing

To test seed viability under field conditions, a burial experiment, also described in detail in Saatkamp *et al.* (2009), was set up using the 25 annual cereal weed species. Seed samples were buried in 4×4 cm nylon mesh bags at 10 cm depth. Collected seed lots were mixed and sub-divided into 30 samples with a fixed number of seeds for each species. For each species, 25 seed samples were buried in a randomized block design, enabling five replicated samples to be retrieved for five different dates. Every 6 months, five seed samples per species were retrieved and tested for germinability and viability; these were also tested before starting the burial experiment in autumn 2005. There were three retrieval dates in spring and two in autumn, with the last being 2·5 years after burial. These dates were chosen to capture the two main germination periods in autumn and spring.

For the germinability and viability tests, controlled conditions in a growth chamber were first used to test germination

TABLE 1. *T_{50} and relative germination rates for fluctuating temperatures (ΔG_{DFT}) and light requirement (ΔG_{light}) of the 25 studied species; letters indicate closely related species pairs*

Species	Family	T_{50} 16/8 °C	ΔG_{DFT} %	ΔG_{light} %	Pair
Agrostemma githago	Caryophyllaceae	3·6	0	−3·1	A
Anagallis arvensis	Primulaceae	9·1	−100	100	B
Androsace maxima	Primulaceae	8·8	24	−48·3	B
Bifora radians	Apiaceae	16·7	35	−31·8	C
Bupleurum rotundifolium	Apiaceae	13·8	11	3·1	C
Carthamus lanatus	Asteraceae	5·5	0	0	
Camelina microcarpa	Brassicaceae	5·7	0	0	D
Centaurea cyanus	Asteraceae	5·0	25	3·2	E
Centaurea sostitialis	Asteraceae	2·7	43	95	E
Cnicus benedictus	Asteraceae	6·0	−80	0	
Conringia orientalis	Brassicaceae	10·5	100	33·3	
Consolida regalis	Ranunculaceae	14·6	25	52·4	
Legousia hybrida	Campanulaceae	8·5	−60	98·8	F
Legousia speculum-veneris	Campanulaceae	5·8	33	75·6	F
Neslia paniculata	Brassicaceae	13·0	−8	−89·5	D
Nigella damascena	Ranunculaceae	16·6	16	−81·6	
Papaver argemone	Papaveraceae	7·0	65	60	G
Papaver hybridum	Papaveraceae	21·0	0	0	
Papaver rhoeas	Papaveraceae	8·5	−7	49·4	
Ranunculus arvensis	Ranunculaceae	17·8	64	62·5	H
Ranunculus falcatus	Ranunculaceae	16·5	−75	93·5	H
Roemeria hybrida	Papaveraceae	5·3	33	92·7	G
Silene latifolia	Caryophyllaceae	4·8	1	−1·3	A
Turgenia latifolia	Apiaceae	17·0	−100	100	
Vaccaria hispanica	Caryophyllaceae	5·0	−4	−39·7	

percentages at each retrieval date. These controlled conditions were 4 weeks at DFTs of 22 °C for 14 h of light (cool white fluorescent tubes, ± 10 000 lux; ± 250 μmol m^{-2} s^{-2}) and 14 °C for 10 h in darkness. After these 4 weeks, 6 weeks of chilling at 4 °C were applied to the seed samples. Then, seeds were again exposed to 4 weeks of 22 °C for 14 h of light and 14 °C for 10 h of darkness. To test the percentage viability of the studied seed lot at the beginning of the experiment a viability test was run with five replicates in autumn 2005. These conditions were maintained for comparability all through the burial experiment. In all cases, all remaining ungerminated seeds have been tested by means of the tetrazolium test (International Seed Testing Association, 1996). Seeds were cut through the embryo prior to imbibition in a 1 % tetrazolium staining solution, stained at 24 °C for one night and seeds were classified as viable when the embryo was well stained and not damaged. In *Consolida regalis*, *Legousia hybrida* and *Legousia speculum-veneris*, entire seeds stained well without cutting, so entire seeds were classified. For *Papaver rhoeas*, *P. argemone*, *P. hybridum* and *Roemeria hybrida* no seeds stained in the first trials, and therefore seeds were classified as viable when embryos were stiff and white after removal of the seed coat. In some cases (e.g. *Adonis annua*) underdeveloped embryos complicated the use of the tetrazolium test; therefore the maximum number of viable seeds was taken from subsequent tests as the initial number of living seeds.

Seeds were considered as living when they either germinated under the above germination conditions (22 °C/14 °C) including the chilling phase (4 °C) or were classified as viable during the tetrazolium teast. The soil seed mortality data used in the analysis were the difference between the number of living seeds at one retrieval date (t_n) and number of living seeds at the previous retrieval date (t_{n-1}) divided by the number of living seeds at the previous retrieval date (t_{n-1}). This yields five subsequent and independent sets of mortalities per species, corresponding to five burial phases each of 6 months duration and spaced 6 months in time.

Germination testing conditions

A series of experiments were then set up to study the effects of DFTs and light on germination for each of the species after dispersal prior to burial in soil. Seeds were not stratified in the cold prior to these experiments because the Mediterranean species studied here were known to germinate directly in autumn after a dry summer period and were generally induced into secondary dormancy by cold temperatures (Bell *et al.*, 1995; Baskin and Baskin, 1998; Merritt *et al.*, 2007) which was confirmed by our own data (Fig. 1D).

For each experimental condition, eight replicates of 25 seeds were used for each of the 25 species. Previous work on germination at four different temperatures revealed a different optimum temperature for germination from that used for assessment of the viability of seeds. Therefore, in the study of germination traits, DFTs of 16 °C day (14 h) and 8 °C night (10 h) and a constant temperature of 12 °C were used. For these two temperature conditions, germination experiments were also conducted in complete darkness. After preparing samples, this experiment started with watering in complete darkness to avoid the influence of light on germination (Baskin and Baskin, 1998). Petri dishes were then closed with a stretch of Parafilm and samples were transferred into lightproof boxes in the growth chamber. After 10 d, water content in darkness was controlled and adjusted by touching the filter paper at its margins and adding water. After 4 weeks, at the end of the experiment, germinated seeds were counted. All germination traits were studied at once on dry stored seeds after dispersal that had not been buried previously, and all necessary germination assays were finished within 4 weeks.

Analysis of germination data

In order to extract relevant information from the germination experiments three indices were used. First, to capture the importance of germination speed we used T_{50}, i.e. the

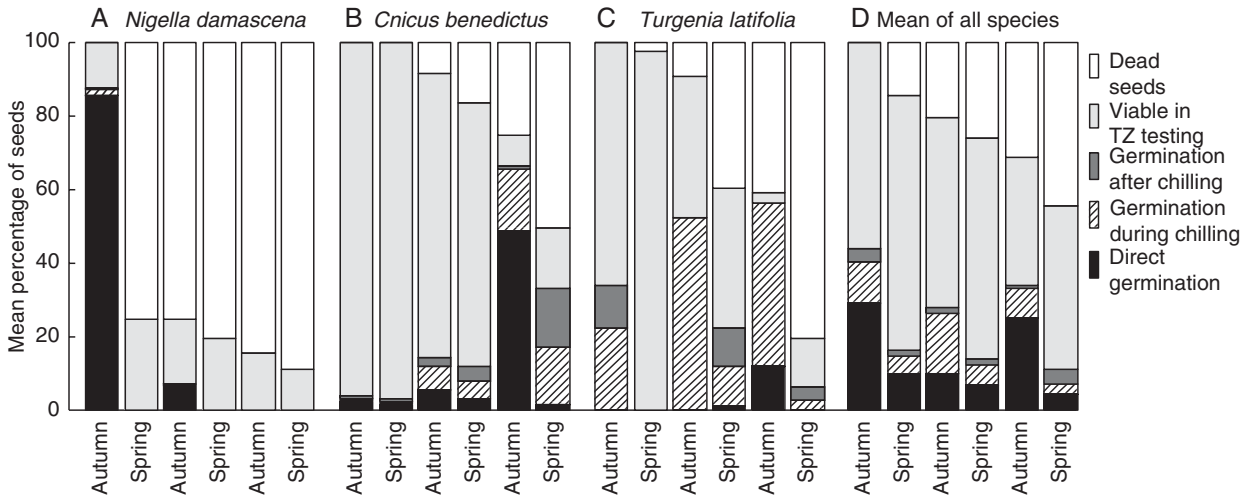

FIG. 1. Dormancy cycles and mortality in three contrasting species (A) *Nigella damascena*, (B) *Cnicus benedictus* and (C) *Turgenia latifolia*, and mean dormancy cycles of 25 species (D). The key indicates: seeds germinating directly after retrieval in 22 °/14 °C; germination in the chill phase (4 °C); germinated seeds after chilling in 4 °C; non-germinated but viable seeds [tetrazolium (TZ) test]; and dead seeds.

number of days to germination of 50 % of all germinated seeds (at 16 °C day and 8 °C night temperature) calculated according to Coolbear (1984):

$$T_{50} = t_i + (t_j - t_i) \times (N/2 - n_i)/(n_j - n_i)$$

This index uses the weighted mean between the two days t_i and t_j with cumulative seed counts (n_i and n_j) adjacent to half of the total sum of germinated seeds ($N/2$) so that $n_i < N/2 < n_j$. For each species, the mean values of eight replicates were used in the analyses. For the graphical representation of interactions, the species were divided into two groups according to the median value of 8·5 d, one of rapidly germinating species ($n = 12$) and one of slowly germinating species ($n = 13$).

Species were also classified according to their relative light germination (ΔG_{light}) modified from Milberg *et al.* (2000), extending the scale below zero, with negative values accounting for better germination in darkness:

$$\Delta G_{light} = [(G_{light} - G_{dark})/(G_{light} + G_{dark})] \times 100$$

ΔG_{light} was calculated as the ratio of the number of seeds germinating in light (G_{light}) minus the number of seeds germinating in darkness (G_{dark}) for all seeds germinating in the paired experiment ($G_{light} + G_{dark}$). germination percentage after 4 weeks was used in an experiment under DFTs of 16 °C for 14 h and 8 °C for 10 h. When ΔG_{light} is +100 %, seeds germinated only in light; when ΔG_{light} is −100 % seeds germinated in darkness and never in light. For the presentation of interactions, the species were classified into groups that germinated better in darkness than in light ($\Delta G_{light} > 0$, $n = 13$) and species that germinated better in light than in darkness ($\Delta G_{light} < 0$, $n = 8$); four indifferent species ($\Delta G_{light} = 0$, Table 1) were omitted from this graph.

Similarly, we calculated an index for the relative germination in DFTs compared with constant temperatures, ΔG_{DFT}, being positive when germination percentages are higher under DFTs than at constant temperatures and negative when germination was higher under constant temperatures relative to DFT (in darkness):

$$\Delta G_{DFT} = [(G_{fluct.} - G_{const.})/(G_{fluct.} + G_{const.})] \times 100$$

For ΔG_{DFT}, we used the difference between the number of germinated seeds in darkness at DFTs of 16 °C (14 h) and 8 °C (10 h), $G_{fluct.}$, and the number of germinated seeds under constant 12 °C, $G_{const.}$, relative to the sum of seeds germinated in these two experimental conditions ($G_{fluct.} + G_{cons.}$) in the germination experiment. We did not use values measured in light because we think that the most informative situation for DFTs vs. constant temperatures is when seeds are buried, since seeds exposed to light in cereal fields always encounter DFTs. Again two groups were identified for graphical representation, one of 14 species germinating better under DFTs ($\Delta G_{DFT} > 0$) and one of eight species that germinated better under constant temperatures ($\Delta G_{DFT} < 0$), omitting four indifferent species ($\Delta G_{DFT} = 0$, Table 1).

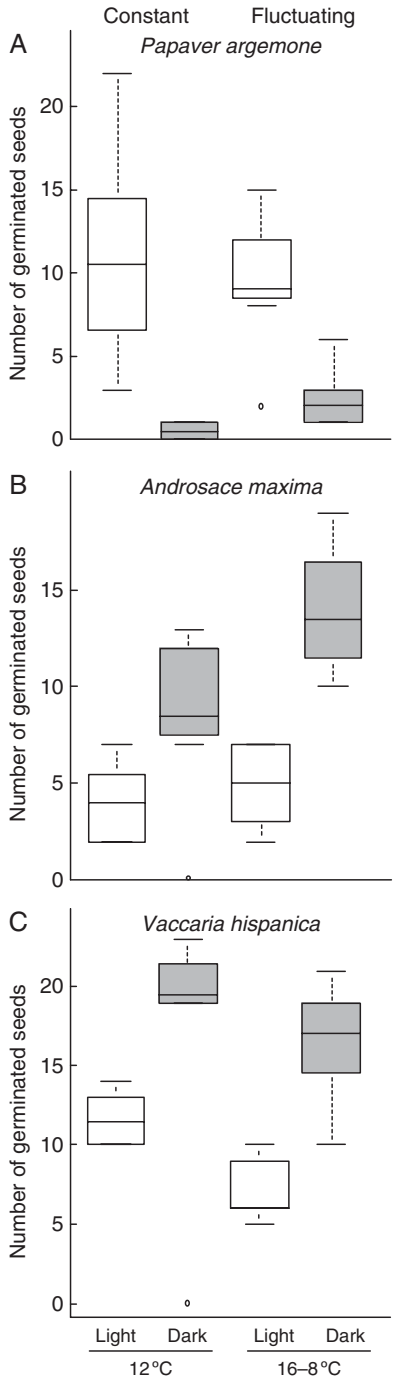

FIG. 2. Germination pattern in light and darkness, and in diurnally fluctuating vs. constant temperature of (A) *Papaver argemone*, (B) *Androsace maxima* and (C) *Vaccaria hispanica*.

Phylogeny and statistical analysis

Phylogeny was integrated into the analysis as a covariance matrix in generalized linear mixed models (GLMMs) using a phylogeny for all species compiled from recent molecular phylogenetic works of the studied species, using APGIII for supra-familiar relationships (Angiosperm Phylogeny Group, 2009). We had no explicit hypotheses concerning ancestral states but rather wanted to control statistically for phylogenetic

correlation, so Grafen's (1989) method of branch length estimation was used to cope with missing branch lengths.

The data contained both random variables, such as experimental blocks, phylogeny and species, as well as fixed variables such as ΔG_{light}, ΔG_{DFT}, T_{50}, season and time after burial. GLMMs were therefore used in a Bayesian framework to analyse their effect on mortality proportions. The posterior probability distribution for effects was estimated using a Markov chain Monte Carlo algorithm and we only considered and illustrated effects for which their 95 % credible interval (CI) excluded zero (Figs 3 and 4). All possible interactions were analysed initially, and then interaction terms for which the 95 % CI included zero were omitted. Standardized fixed variables were used to compare effects, and mode and 95 % CIs were plotted for fixed (Fig. 3) and random effects (Fig. 4). Since only overall effects were interpreted post-hoc tests were not carried out between particular groups for Figs 5–7.

All analyses were run using the MCMCglmm-package and the R environment (Hadfield, 2010; R Development Core Team, 2009). We applied the analyses with a non-informative prior, 13 000 MCMC iterations, burn-in after 3000 iterations and a thinning interval of ten iterations according to the documentation in Hadfield (2010).

RESULTS

The burial revealed that the proportion of dormant seeds varied across burial dates and among species (Fig. 1). There was a marked seasonal effect: there were high levels of germination after sampling in autumn compared with spring. Most species were non-dormant in autumn but dormant in spring. Figure 1A–C illustrates another effect; here three contrasting species with high levels of immediate germination after

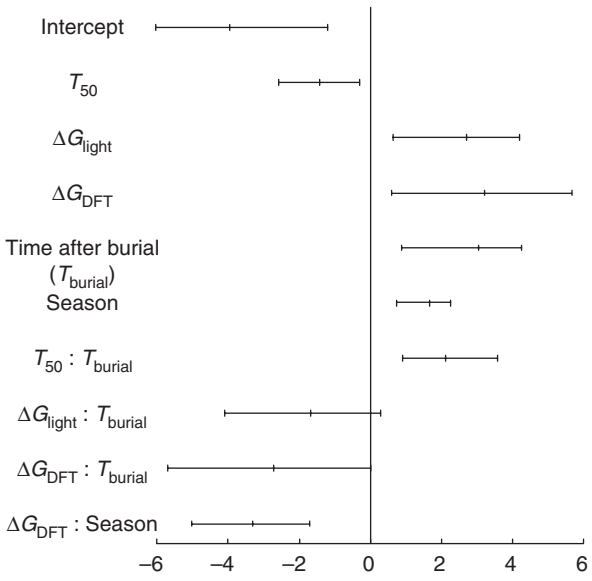

FIG. 3. Effect of germination traits, burial phase and season on soil seed mortality analysed as fixed effects in a generalized linear mixed model (GLMM): the middle tick mark denotes the posterior mode and the line extends to the 95 % credible intervals of the posterior distribution produced by Markov chain Monte Carlo; zero effect is marked by a straight line.

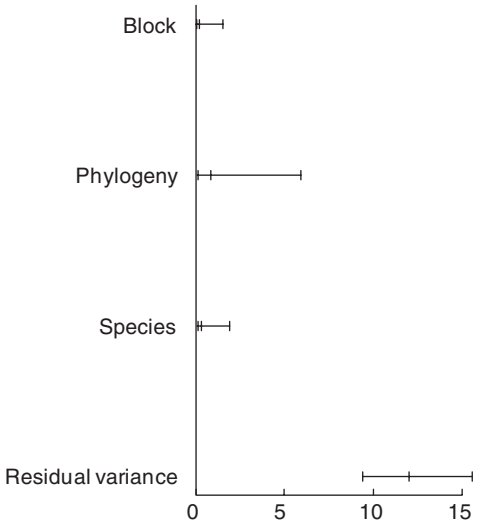

FIG. 4. Effect of experimental blocks, phylogeny, species, all random effects in the GLMM, and residual variance of soil seed mortality: the middle tick mark denotes the posterior mode and the line extends to the 95 % credible intervals of the posterior distribution produced by Markov chain Monte Carlo; for details see the Methods section.

retrieval from the soil either at the beginning (*Nigella damascena*) or at the end (*Cnicus benedictus*) of the burial experiment are present. Additionally, the proportions of seeds germinating in the growth chamber compared with ungerminated but viable seeds detected by tetrazolium varied greatly among species. *Turgenia latifolia* (Fig. 1C and Table 1) illustrates a species with rather high levels of germination compared with other species and a steep decline of viable buried seeds.

Germination tests revealed striking differences in germination speed as measured by T_{50} (Table 1). Species with rapid germination had a low T_{50} such as only 2·7 d for *Centaurea solstitialis* and 3·6 d for *Agrostemma githago*, whereas other species such as *P. hybridum*, *Ranunculus arvensis* and *T. latifolia* had a T_{50} of at least 17 d.

In the germination assays, species differed clearly in their light and temperature requirements. Table 1 illustrates the contrasted patterns revealed by germination experiments in light and darkness. Some species germinated only in light, such as *Anagallis arvensis* or *P. argemone* (Fig. 2A), whereas other species germinated better in darkness, such as *Neslia paniculata* or *Vaccaria hispanica* (Fig. 2C).

In a similar way, the germination at constant vs. fluctuating temperatures varied markedly between species. There were clear 'gap detectors' germinating better under DFTs such as *Androsace maxima* (Fig. 2B). Astonishingly, some species germinated better under constant than under fluctuating temperatures, e.g. *Vaccaria hispanica* (Fig. 2C).

The GLMM analysis of germination traits as fixed effects indicated that all fixed effects had an interaction with time after burial (Fig. 3), meaning that their effect is different at the beginning compared with the end of the experiment. These interactions are illustrated in Figs 5–7. Furthermore, the results of the GLMM (Fig. 4) showed that the block effect as a random factor for soil seed mortality was close to zero. Moreover, there were clear effects of species as a

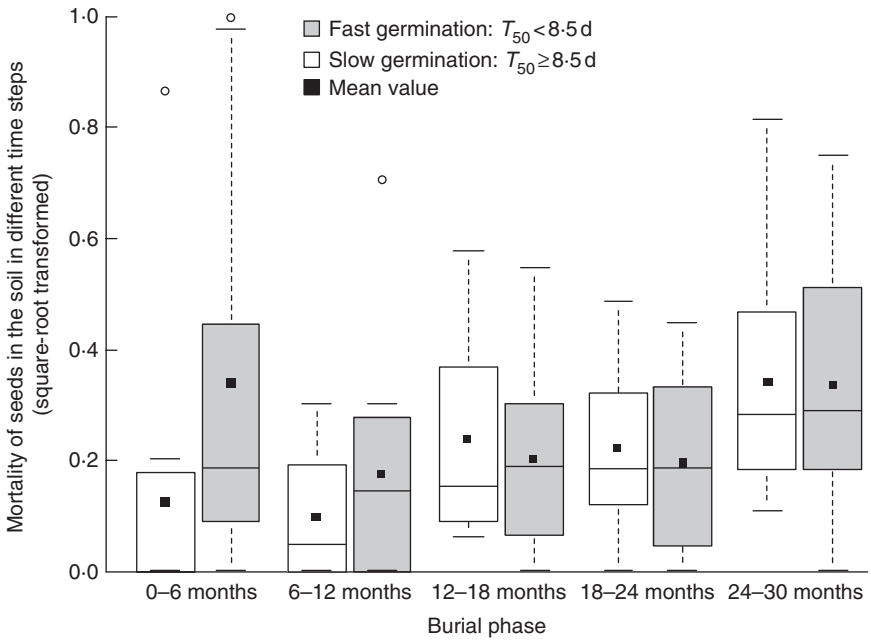

FIG. 5. Interaction of burial phase and germination speed (T_{50}): box plots of the soil seed mortality of slow germinating species ($T_{50} \geq 8{\cdot}5$ d) and fast germinating species ($T_{50} < 8{\cdot}5$), where T_{50} is the number of days necessary for germination of 50 % of all seeds. Note that mortality is square-root transformed.

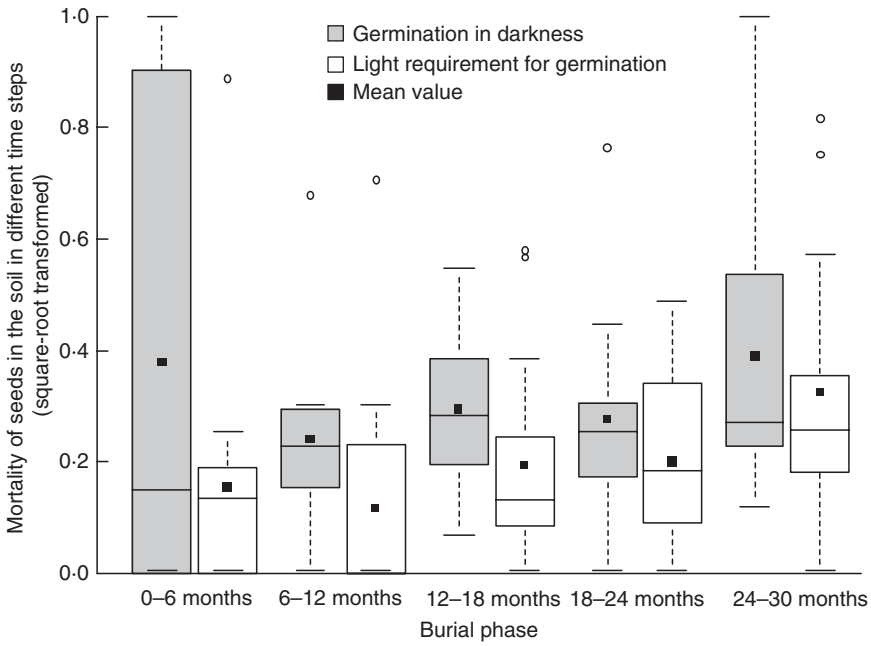

FIG. 6. Interaction between time of burial phase and light requirement for germination: box plots of soil seed mortality of species germinating in darkness and light in five burial periods of 6 months each. Note that mortality is square-root transformed, and the indifferent species *Carthamus lanatus*, *Camelina microcarpa*, *Cnicus benedictus* and *Papaver hybridum* have been excluded here.

random factor; in contrast, the effects of phylogeny were very weak. There was a comparatively high residual variance.

The comparison of soil seed mortality between slow and fast germinating species along the time steps illustrated that fast germinating species have much higher soil seed mortality after 6 and 12 months of burial. After longer periods of burial, there was little or no difference between these groups of species (Fig. 5). Fast germinating species for which seeds were strongly depleted in the first burial phases included *A. githago* and *Centaurea cyanus*, with no or only 21 % survival of seeds after 6 months of burial. Species with very high T_{50}, such as *P. hybridum*, *R. arvensis* or *Bifora radians*, had comparatively high survival after 6 months (all three species >90 %). However, some species that also had very low T_{50},

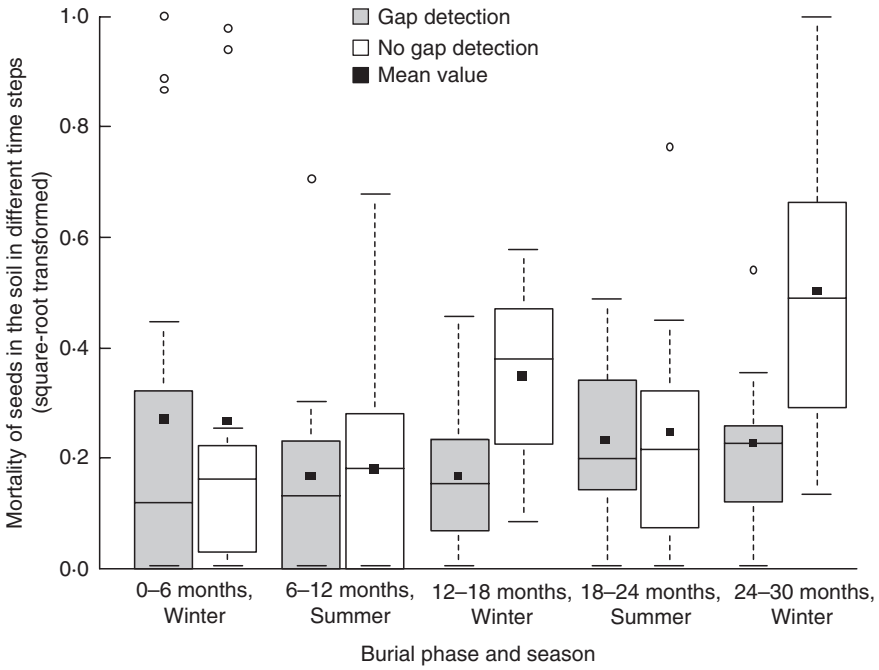

FIG. 7. Interaction between burial season, burial phase and gap detection: box plots of soil seed mortality of species germinating better under diurnally fluctuating temperatures (grey) than under constant temperature (white) in five burial periods of 6 months each. Note that mortality is square-root transformed, and the indifferent species *Agrostemma githago*, *Carthamus lanatus*, *Camelina microcarpa* and *Papaver hybridum* have been omitted from this graph.

such as *C. solstitialis* (2·7 days), had 97 % of viable seeds after 6 months and 82 % after 2·5 years of burial.

The mortality of species germinating in darkness was higher than soil seed mortality for species with a light requirement for germination in all five burial phases. Figure 6 illustrates the significant interaction of time after burial and light requirements for the mortality of seeds buried in the soil: with increasing time of burial the differences in seed mortality between species with and without light requirements declined. Whereas the GLMM revealed the significant interactions among the continuous variables 'time after burial' and 'ΔG_{light}', the grouping into species with and without a light requirement made it possible to present this graphically. Species with an important light requirement as measured by ΔG_{light} that also showed low mortality just after burial or after longer periods were: *C. solstitialis*, *A. arvensis* and *L. speculum-veneris* with seed survival until 6 months (and 2·5 years) of 97 % (82 %), 99 % (89 %) and 99 % (69 %). Species without a light requirement such as *N. damascena* and *V. hispanica* were depleted quickly after 6 months of burial to only 25 and 4 %, respectively, of surviving seeds; however, some of their seeds survived until the end of the burial experiment with 11 and 2 % of living seeds. The declining differences in seed mortality between species with and without a light requirement can be attributed to the declining mortality over longer periods of burial for species that had a high initial mortality and low light requirements, such as *N. damascena* (Fig. 1) and *V. hispanica.* These species maintained a small proportion of seeds with very low soil seed mortality for longer periods of burial: 70 % of the seeds that were viable after 2 years were still viable after 2·5 years for both species.

Comparison of Figs 5 and 6 shows that the differences in soil seed mortality between groups of species according to light requirement lasted for a longer time than between groups of species according to germination speed as measured by T_{50}. In other words, species with a light requirement still had lower soil seed mortalities between 2 and 2·5 years of burial than species without a light requirement (Fig. 5), whereas slow and fast germinating species did not differ in their mortalities of seeds at the end of the burial experiment (Fig. 6).

The effect of the reaction to DFTs on soil seed mortality (Fig. 7) showed that there was initially no difference in mortality for species with higher vs. lower germination percentages in fluctuating temperatures, but there was a marked effect after the first 6 months of burial. This clear interaction with burial phase (Fig. 3) indicates the increasing effect of this factor with time after burial. Moreover, there was a clear seasonal effect (Figs 3 and 7). Comparing 'gap detectors' with 'non-gap detectors' in the two seasons (Fig. 7) shows that 'gap detectors' had significantly lower soil seed mortality in winter than in summer.

DISCUSSION

Germination speed and soil seed persistence

The statistically strong effect of T_{50} illustrates the importance of germination speed for mortality of buried seeds: a high percentage of unsuccessful germination just after burial of fast germinating species markedly reduced the number of viable seeds in the initial stages of our experiment (Fig. 5). In contrast, slow germinating species had much lower mortality in

the soil just after burial. These slow germinating species needed to experience a longer period of favourable conditions before germination was induced. It is evident that slow germination in these species can be related to morphological dormancy, as some of the species with the highest T_{50} or the slowest germination, such as *B. radians*, *C. regalis* and *P. hybridum*, belong to plant families (Apiaceae, Ranunculaceae and Papaveraceae) that have underdeveloped embryos (morphological dormancy) and, in the case of *Papaver*, that have morphophysiological dormancy (Baskin *et al.*, 2002; Baskin and Baskin, 1998, 2004; Karlsson and Milberg, 2007*a*).

The time that germination is delayed by these mechanisms was quantified by T_{50} in the present study. The data suggest that a long time until germination can be sufficient for other factors such as darkness and low oxygen concentration to prevent germination, to induce secondary dormancy or to induce a secondary light requirement (Thanos and Georghiou, 1988; Noronha *et al.*, 1997). In our experiment, seeds were all buried experimentally at the same time, but under field conditions slow germination (high T_{50}) may also lead to a higher probability of seeds becoming buried (Fig. 8).

These findings support experimentally the view that dormancy, one way to prevent germination until burial in soil, is relevant for interspecific differences in soil seed persistence, a fact for which previous evidence was relatively weak (Baskin and Baskin, 1998, 2006; Thompson *et al.*, 2003). The difference in methodology between data from seed burial experiments compared with data on seed persistence compiled from seedling emergence studies is probably sufficient to explain why this pattern is much clearer here than in previous work. In the present work, soil seed depletion and T_{50} were both studied on a quantitative scale. The close relationship between germination speed as measured by T_{50} and soil seed survival is also clear from an evolutionary point of view. Bet-hedging predicts that plants should spread their germination to disperse risks in reproductive success, which can be achieved by slow germination (Venable, 2007). Since seeds that did not germinate on the first occasion have to stay viable until the next germination opportunity, slow germination should be correlated to other traits that enhance seed survival in the soil. T_{50} does not reflect different dormancy types but it measures, in the present case, the degree to which a seed population germinates in the conditions corresponding to the first main germination season for the studied habitat in autumn. However, this T_{50} is a typical quantitative bet-hedging trait that can be related to the risk in reproductive success for each species (Venable, 2007). The close relationship of T_{50} to soil seed persistence reported here illustrates the usefulness of this quantitative trait. Germination speed is especially important for soil seed mortality just after seed burial, as exemplified by the difference between fast and slow germinating species in Fig. 5. In the first burial phase, seeds of some non-dormant and fast germinating species, such as *A. githago*, *V. hispanica* and *C. cyanus*, decrease rapidly to a low level, which results in big differences between fast and slow germinating species. The high soil seed mortality, resulting from immediate germination and missing light requirement (Table 1) of these species, seems disadvantageous at first sight. However, the seed losses due to rapid germination while buried in soil or in unfavourable environments can be compensated for. Rapidly germinating species have more time for development and this may lead to a higher performance in terms of biomass production, competitive ability and plant size, resulting in relatively high seed production. Even if T_{50} is no measure of dormancy our data indicate how it can contribute to delay germination and to the formation of soil seed banks.

Light requirement and soil seed persistence

Light requirement is a second possibility to achieve seed survival during burial (Baskin and Baskin, 1989, 1998), which was clearly corroborated by our data (Figs 6 and 8). Species, such as *C. solstitialis*, with a light requirement showed a lower decline of soil seed survival rate in our data set than species capable of germinating in darkness (Fig. 6, Table 1). This is in agreement with the view that a light requirement can be sufficient to form persistent seed banks in the absence of dormancy (Baskin and Baskin, 1989, 2006) because light decreases to $<0{\cdot}01$ % at only 4 mm of depth for most soils (Benvenuti, 1995) and because emergence of seedlings declines with burial depth (Grundy *et al.*, 2003). The interaction between ΔG_{light} and times after burial (Fig. 6) shows that the importance of a light requirement

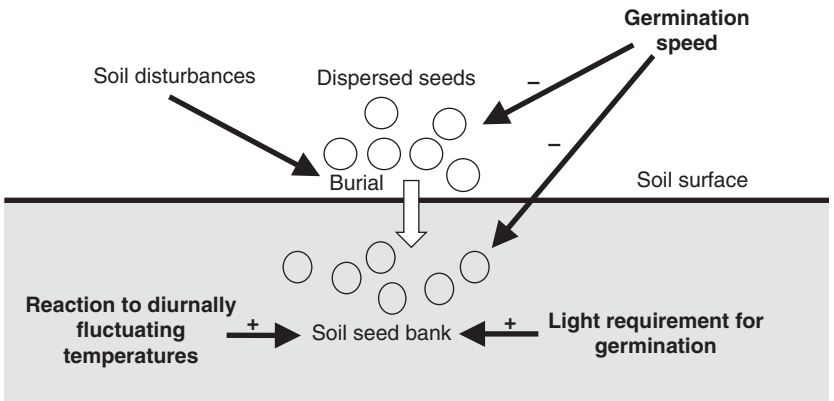

FIG. 8. Germination traits (bold) that explained the differences in survival of buried seeds between species in this study; a higher germination speed leads to lower survival, whereas high germination in response to fluctuating temperatures or to light leads to higher survival of seeds buried in soil.

decreased with time of burial. This can be so for several reasons: some dark germinating species disappeared completely after short times of burial, as was the case with *A. githago*. However, this cannot explain why the effect lasts so long and does not completely break down after the first burial phase as is the case with the effect of T_{50} (Fig. 5). Species germinating in darkness must have developed alternative strategies to stay ungerminated in soil: these may include (*a*) secondary dormancy induced by falling temperatures after dispersal in autumn (Baskin and Baskin, 1998); (*b*) a secondary light requirement (Thanos and Georghiou, 1988; Noronha *et al.*, 1997); (*c*) reaction to diurnally fluctuating temperatures (this study); or (*d*) dependence on oxygen (Benvenuti *et al.*, 2001). Some species with higher germination rates in darkness, such as *N. paniculata* or *B. radians*, had relatively high soil seed survival. In these cases, the T_{50} was comparatively high, illustrating the complementary strategies of light requirement and delayed germination to control germination below ground (Table 1).

Diurnally fluctuating temperatures and soil seed persistence

The inspection of soil seed mortality during different seasons (Fig. 7) illustrated that soil seed mortality of species that germinated better without DFTs was higher during burial in winter than in summer and that this effect increased with time. At least sometimes, species with a 'gap detection' mechanism had clearly lower soil seed mortalities than non-gap detectors (Fig. 8). We think that in this case the role of gap detection (high ΔG_{DFT}) is to trigger germination as a function of depth and vegetation cover in the main germination season, whereas cycling dormancy and drought prevent germination in spring when drought can be a serious cause of death in juveniles. Species without a gap detection mechanism (low ΔG_{DFT}) may have germinated easily in winter and in this way were depleted from the soil seed population (Fig. 7). An alternative explanation is that relatively constant temperatures in winter buffered by high soil water content induce differences between these two groups. With increasing depth, diurnally fluctuating temperatures are lower. Since we use a relatively deep burial depth (10 cm), our data therefore add evidence to underpin the role of DFTs in the timing of germination (Bullock, 2000), and to show how germination in soil layers which are too deep can be prevented by DFTs in groups of species that detect this factor (Fig. 7). This role of DFTs in triggering germination (Thompson *et al.*, 1977; Grime *et al.*, 1981; Thompson and Grime, 1983) leads to the hypothesis that the role of DFTs to detect burial depth should be correlated to seed size, a trait that is strongly correlated to depth of seed emergence (Bond *et al.*, 1999; Grundy *et al.*, 2003).

We did not study explicitly the shape of seed decay curves in soil across species, since our experiment had a limited temporal resolution. However, the interactions between germination traits and time after burial shown in this study suggest that seed decay curves are influenced by functional aspects that differ between the moment of integration in the soil seed bank and after longer periods of burial. We showed that differences in germination speed heavily influence seed decay curves, sustaining the view that the shape of seed decay curves can be determined by the dormancy type of a species (Baskin and Baskin, 1989, 1998; Rees and Long, 1993). Subsequently, we have shown that the reaction to DFTs has an effect that increases with time after burial and that differs among seasons of burial. Germination in reaction to DFTs can thus be a trait that shapes the tail of a seed decay curve, whereas light requirement and T_{50} determine seed decay just after burial.

CONCLUSIONS

Based on our study, we propose to use germination features measured on dry stored seeds after dispersal to predict soil seed longevity. Germination features constitute an independent data source compared with seed size which has previously been proposed as a predictor for soil seed longevity, but which turned out to be of contradictory value (Bekker *et al.*, 1998*a*; Moles and Westoby, 2006; Saatkamp *et al.*, 2009). Our work not only illustrates that different germination traits are correlates of soil seed persistence but also highlights their adaptive role to schedule germination and hence to limit soil seed mortality through fatal germination (Fig. 8), linking the data on soil seed persistence to germination cues (Merritt *et al.*, 2007). Since germination traits are specific to a species' habitat, climatic zone and life form (Baskin and Baskin, 1998), our data apply best to highly disturbed Mediterranean habitats and annual plants, as exemplified by the 25 species studied here. We have shown that T_{50} and a light requirement for germination inform our functional understanding of soil seed survival, notably the changing importance of these traits according to the time after burial.

Additionally, we have illustrated that the reaction to DFTs known as 'gap detection' is a factor that acts independently of time after burial on soil seed persistence. This gives guidelines on how future works should study soil seed mortality: when short time scales of <1 year are the focus, T_{50} is helpful as a quantitative measure of a germination speed. Light requirements can be predictive for initial and intermediate burial times. On longer time scales, DFTs may be more interesting. In future works, early and late burial phases should thus be separated to understand better how germination traits can trigger soil seed bank formation. We also advocate focusing on mechanisms acting after longer burial periods, using experimental data on soil seed mortality. Therefore, seed germination traits and seed coat thickness (Gardarin *et al.*, 2010) are promising easy-to-measure traits that can be used to predict soil seed longevity. Since T_{50}, light requirement and germination in reaction to DFTs were correlated to high soil seed persistence, and since soil seed persistence is related to local population extinction (Kalisz and McPeek, 1992; Stöcklin and Fischer, 1999), they can contribute to identify vulnerability of species in the context of changing land use.

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