REGULAR ARTICLE

Soil depth detection by seeds and diurnally fluctuating temperatures: different dynamics in 10 annual plants

Arne Saatkamp · Laurence Affre ·
Teddy Baumberger · Pierre-Jean Dumas ·
Aïda Gasmi · Sophie Gachet · Fabien Arène

Abstract

Background and Aims Seeds buried in the soil detect burial depth through light and diurnally fluctuating temperatures (DFT) and in this way limit losses due to germination too deep in the soil. DFTs and germination also increase in vegetation gaps. However, dry open environments with high DFTs can also increase seedling mortality, creating conflicting selection pressures for reaction to DFTs. Since this questions the general function of DFT detection, we therefore tested if interspecific differences in DFT detection are related to mortality in different soil depths.

Methods We buried seeds of ten annual plants including species pairs of increasing and decreasing germination in response to DFTs. Seeds were buried in 5, 10 and 25cm soil depth and exhumed after two different burial times. Seed viability was tested using germination in growth chambers and tetrazolium. We also measured DFTs at these depths using temperature data loggers.

Results DFT detection was not related to differences in mortality at three burial depths. Three species showed a clear pattern of depth dependent mortality, however inconsistently related to DFT detection.

Conclusions Depth detection mechanisms are more species-specific than expected. Hence, interspecific differences in seed mortalities are difficult to predict by DFT detection alone and alternative soil depth sensing mechanisms should be explored in future.

Keywords Diurnal temperature range (DTR) · *Centaurea solstitialis* · *Bifora testiculata* · Soil seed bank · Seed size

A. Saatkamp (✉) · L. Affre · T. Baumberger ·
P.-J. Dumas · A. Gasmi · S. Gachet · F. Arène
Institut Méditerranéen d'Écologie et de Paléoécologie
IMEP UMR CNRS 6116 IRD, Université
d'Aix-Marseille III,
FST Saint-Jérôme, case 462,
13397 Marseille, Cedex 20, France
e-mail: arnesaatkamp@gmx.de

F. Arène
e-mail: arene.fabien@gmail.com

Introduction

Seed mortality in soil is one of the most important population dynamic parameters, especially in annual plants (Kalisz and McPeek 1992; Adams et al. 2005). It is not astonishing that important effects on local extinction rates could be related to this life history trait (Stöcklin and Fischer 1999). Interspecific differences in soil seed mortality and seed bank formation are also one of the primary mechanisms that promote coexistence in herbaceous plant communities, as conceptualized by the storage effect (Warner and Chesson 1985; Cáceres 1997; Facelli et al. 2005). The promotion of coexistence for subordinate species

and the persistence of local populations both depend crucially on the capacity of species to form persistent soil seed banks by preventing germination in the soil (Warner and Chesson 1985; Stöcklin and Fischer 1999; Facelli et al. 2005). Mechanisms that allow seeds to stay ungerminated and to detect unfavourable conditions for regeneration clearly give important advantages in this context (Grubb 1977; Bullock 2000) and are probably traits that enhance the storage effect.

The detection of burial and soil depth is crucial for seeds to survive in environments where burial due to rain (Benvenuti 2007), disturbances, litter shedding or wet-dry cycles (Burmeier et al. 2010b) is important. The deeper seeds are buried, the lower the chance of seedlings to reach the surface (Grundy et al. 2003; Pearson et al. 2002; Bond et al. 1999). Since maximum emergence depth is related to the resources seedlings have, models have been developed to relate seed size to the depth from which seedlings can still emerge (Bond et al. 1999). These models are important components for prediction of weed emergence from soil seed banks (Grundy 2003).

Plants evolved mechanisms to detect depth of burial (Fenner and Thompson 2005; Bond et al. 1999; Thompson 2000), since their seedlings die by exhaustion when seed germinate in too deep soil layers (Benvenuti et al. 2001a; b; Benech-Arnold et al. 2000; Ghersa et al. 1992). These mechanisms include: (i) detection of light, which enters little into soil and has been shown to trigger germination of small seeds (Ciani et al. 2005; Pons 1992; Milberg et al. 2000) and (ii) diurnally fluctuating temperatures (DFTs) (Ghersa et al. 1992; Thompson 2000). However, light is probably less important for soil depth detection in seeds (see however Pons 1992) than just for the detection of burial. This is corroborated by the complete absence of light beyond the first mm in compact soils (Ciani et al. 2005; Benvenuti 1995) when there are no soil cracks or aggregates (Burmeier et al. 2010b). Light and response to diurnal fluctuating temperatures interact in their effect on germination (Vandelook et al. 2008; Vincent and Roberts 1977), which complicates the picture for the shallowest soil layers.

Since the first suggestions of DFTs as a burial detection mechanism (Grime 1989; Thompson et al. 1977), DFTs have also been proposed to be a gap detection mechanism. Indeed, DFTs decrease with increasing vegetation cover or decreasing gap size,

either through higher day temperatures or lower night temperatures or both (Thompson and Grime 1983; Thompson et al. 1977; Denslow 1987; Bullock 2000). Many plants show therefore lower germination under constant compared to fluctuating temperatures. They germinate to higher proportions when vegetation cover is removed by individual mortality or disturbances. This scheme led to the concept of gap detection (Bullock 2000; Denslow 1980). In many ways, DFTs may serve equally well for both, gap and depth detection (Thompson and Grime 1983). One important exception is the situation of small seeded species that germinate under large DFTs from shallow depths in open areas. The resulting seedlings have disadvantages in gaps due to their lower desiccation tolerance and higher risk of seedling death due to drought (Baker 1972; Leishman and Westoby 1994). This leads to conflicting selection pressures between gap and soil depth detection using the DFT signal and sheds doubt on the generality of depth sensing by DFTs alone. In these situations with strong light, the high irradiance response (HIR) of seeds can be a candidate mechanism to avoid germination (Górski and Górska 1979; Pons 1992). However, the relation of HIR to DFT detection or to seed size has not been studied yet.

DFTs vary according to season, topography, and global climate (Dai et al. 1999), they have been reported to be lower in winter and under cloud cover, to be smaller at coastal than at inland sites, and to decrease during the recent climate change (Dai et al. 1999). Seed germination also varies according to season and is generally limited to a precise germination 'window' by annual dormancy cycles, moisture and temperature requirements (Baskin and Baskin 1998; Merritt et al. 2007). Since both DFTs and germination both vary among seasons, DFTs may serve to detect different things at different times of the year, e.g. moist conditions in winter and vegetation gaps or drought in spring. Hence, even within a local flora, germination cueing by DFTs might differ among species according to phenology. Therefore, independently from the conflicting selection pressures expressed above, we expect that the capacity to detect DFTs is not generally related to depth detection.

Until now, no comparative work related a plant's capacity to detect DFTs to their capacity to detect differential depth of burial across species. This is a significant lack since for quantitative dynamics of soil

seed banks, DFT detection already turned out to be important (Saatkamp et al. 2011). Moreover, under-standing soil depth sensing is a basis for the modelling of soil seed bank dynamics with impor-tance for weed emergence (Grundy 2003) and for plant species coexistence in herbaceous ecosystems (Facelli et al. 2005).

Therefore, our aim was to test if a plant's capacity to detect DFTs is related to its capacity to limit germination in too deep soil layers. Conditions of such a test are to (i) bury seeds of species with contrasting germination features respective to con-stant/diurnally fluctuating temperatures (ii) at defined, different depths and to (iii) study the mortality of seeds buried in the above-cited conditions. Moreover, it is important to study if (iv) the gradient of decreasing DFTs with burial depth is maintained in different seasons, and, furthermore, (v) if seasonal changes in this gradient correlate to differences in germination of buried seeds between DFT-detectors and non-DFT-detectors.

Materials and methods

Choice of species and measurement of DFT detection capacity

According to previous knowledge on species' capacity to detect diurnally fluctuating temperatures (Saatkamp et al. 2011), we chose ten species with contrasting germination in reaction to diurnally fluctuating temperatures. To do so, we first studied germination of seeds in complete darkness at constant temperatures of 12°C and in daily fluctuat-ing temperature cycles of 16°C/8°C at 14 hs/10 hs in a growth chamber using eight replicates of 25 seeds per species. We used germination in darkness, since light can act as an independent mechanism for burial depth detection and we were interested in what happens to already buried seeds. We then calculated an index of relative germination in diurnally fluctu-ating temperatures (G_{DFT}) as the number of seeds that germinated in fluctuating minus the number of seeds germinating under constant temperatures di-vided by the sum of both multiplied by hundred (Saatkamp et al. 2011):

$$G_{DFT} = \frac{G_{fluctuating} - G_{constant}}{G_{fluctuating} + G_{constant}} \times 100 \qquad (1)$$

This value takes +100 when all seeds germinated only under fluctuating conditions and −100 when seeds only germinated under constant temperatures (Table 1). We classified species into two groups according to this index, into DFT detectors, when values were positive and non-DFT detectors when values were negative (Table 1). We preferentially integrated closely related species pairs (at the family level) with contrasting values of G_{DFT} (Table 1). We measured seed mass as mean of three samples of twenty seeds divided by twenty.

Burial experiment, temperature measurement and viability testing

For the burial experiment, we prepared a 10×20 m plot in the botanical garden of Aix-Marseille Univer-sity (43°20′22″N, 5°24′40″E, 121 m) located at 5 km distance from the Mediterranean Sea. Inside the plot,

Table 1 Relative germina-tion rates for fluctuating compared to constant tem-peratures (G_{DFT}), DFT detection and seed mass according to Saatkamp et al. 2011 for the ten studied species

Species	Family	Seed mass [mg]	G_{DFT}	DFT detection
Anagallis arvensis L.	Primulaceae	0.404	−100	−
Bifora radians M. Bieb	Apiaceae	12.880	35	+
Bifora testiculata (L.) Spreng.	Apiaceae	7.593	−33	−
Centaurea sostitialis L.	Asteraceae	1.682	43	+
Cnicus benedictus L.	Asteraceae	30.897	−80	−
Nigella damascena L.	Ranunculaceae	1.386	16	+
Papaver rhoeas L.	Papaveraceae	0.088	−7	−
Ranunculus arvensis L.	Ranunculaceae	13.496	64	+
Ceratocephalus falcatus (L.) Pers.	Ranunculaceae	14.436	−75	−
Roemeria hybrida (L.) DC.	Papaveraceae	0.157	33	+

we set up five blocks, containing three experimental units at depths of 5 cm, 10 cm and 25 cm from soil surface (Fig. 1). Each experimental unit contained nylon mesh bags with 20 seeds for each of the ten species (Table 1). We collected seeds for the burial experiment from at minimum ten individuals per species in summer 2006 and stored them dry at room temperature until usage and mixed before preparation of seed samples. We randomized position of mesh bags inside experimental units. Along the experiment we measured temperature at hourly intervals using temperature data loggers with a temperature resolution of 0.5°C (i-button DS1921G, Maxim IP Inc, Sunnyvale, CA) which were buried close to samples at the same three depths as seed samples for three blocks, and at the surface (Fig. 1). Rainfall was measured as daily rainfall sum from a nearby weather station.

We buried seeds samples on 29 October 2009 and exhumed the first set on 20 January 2010 and the second set on 14 March 2010. After exhumation, we counted and discarded void or non-firm seeds, while we kept firm, intact looking seeds and put them on moist filter paper in Petri dishes for three weeks at daily fluctuating temperature cycles of 16°C/8°C at 14 hs/10 hs (light/dark) in a growth chamber. We tested ungerminated seeds for viability using a 1% tetrazolium chloride solution on bisected seeds for 12 h, classifying seeds as viable when the embryo was intact and stained pink. During the experiment

we determined viability of 6000 individual seeds by the means of germination tests and tetrazolium testing. This yielded numbers of dead seeds for each buried seed sample, the variation of which we interpret as "fatal germination" according to experimental factors. We are aware that there are other sources of soil seed mortality *i.e.* aging and seed predation (including fungi attack). However, we think that aging is not important at the short time scale of our experiment and we discuss the potential confounding factor of predation.

Data analysis

The experiment yielded numbers of dead seeds as a dependent variable; experimental blocks, species and plant families as random effects and G_{DFT}, depth and season of exhumation as well as their interactions as fixed effects. We therefore used generalised linear mixed models (GLMM) using Laplace approximation to analyse effects of independent variables and their interactions on number of dead seeds. We used a Poisson model appropriate for our data, which are counts of dead seeds. We did not integrate phylogeny as a random effect since for so few species, we do not think that phylogenetic effects are meaningful, but rather included family as a random effect to account for the designed choice of contrasting but related species. We tested random
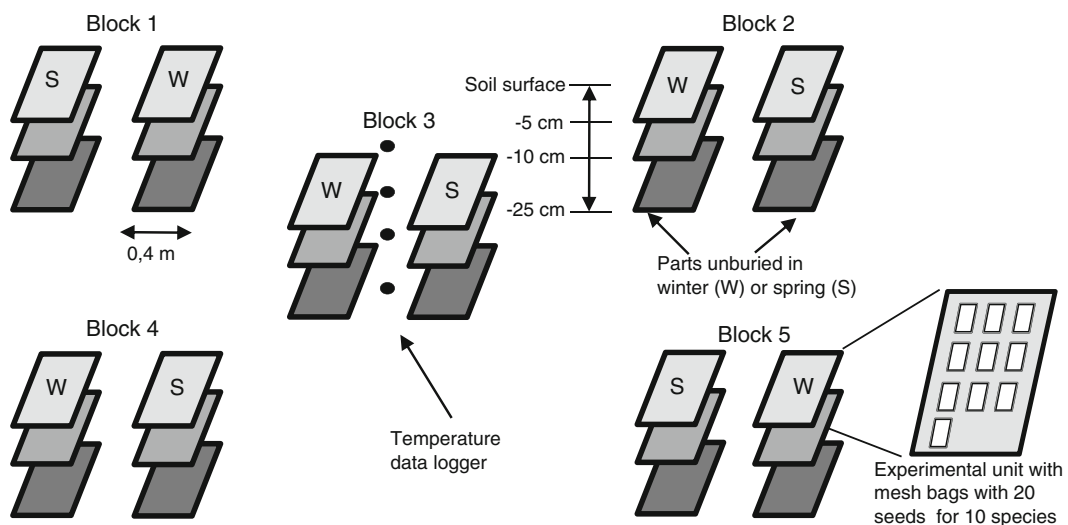

Fig. 1 Experimental setup with five blocks, parts unburied in winter and spring and three depths of burial (5 cm, 10 cm and 25 cm), as well as detail for one depth layer with mesh bags for

seed samples of ten species; black points represent temperature data logger measuring temperatures every hour

effects for significance using likelihood ratio tests (LRT, Pinheiro and Bates 2000), but kept them in the model to account for the experimental design. GLMM were done using lme4 and R (R Development Core Team 2009; Bates and Maechler 2010). We performed a two-way ANOVA on square-root transformed DFTs (calculated as differences between daily maximum and minimum temperatures) according to depth and season of burial.

Results

### Temperature, diurnally fluctuating temperature and rainfall

The temperature course for a soil profile along the experiment (Fig. 2a) shows contrasting phases of high and low DFTs and decreasing temperatures from October to January with an absolute soil surface temperature minimum of −4°C at 12.1.2010, and slowly rising temperatures later on. The mean daily temperature range for 49 rainy days (7.2°C) was significantly lower than the mean for 103 dry days (9.5°; $t=3.34$, $p=0.0011$). Moreover, the depth profile of DFTs according to the two experimental seasons, winter and spring, shows that the decrease of diurnally fluctuating temperature with depth is maintained along of the experiment (Fig. 2b, ANOVA, $F=318.28$, $p<0.001$). DFTs were higher in spring compared to winter for the surface measurements (Fig. 2b). This increase in DFTs from winter to spring was measurable at −5 and −10 cm but not significant.

Mortality of buried seeds at different depths

The GLMM analysis indicates that there was no strong main effect of burial depth or G_{DFT}, but a

Fig. 2 **a** Hourly temperature and daily rainfall during the experiment in 5 cm (*grey*) and 25 cm (*black*) of burial depth ; **b** Diurnally fluctuating temperatures during the first (winter, 29.10.2009-20.1.2010) and second (spring, 20.1. - 14.3.2010) experimental burial phase in the three depths of experimental seed burial at St Jérôme, Marseille, significant differences at $p<0.001$ in Tukey's post-hoc test are denoted by different letters above the boxes; boxes denote interquartile range, broken lines 1.5 × interquartile range, outside of which data points are represented by circles
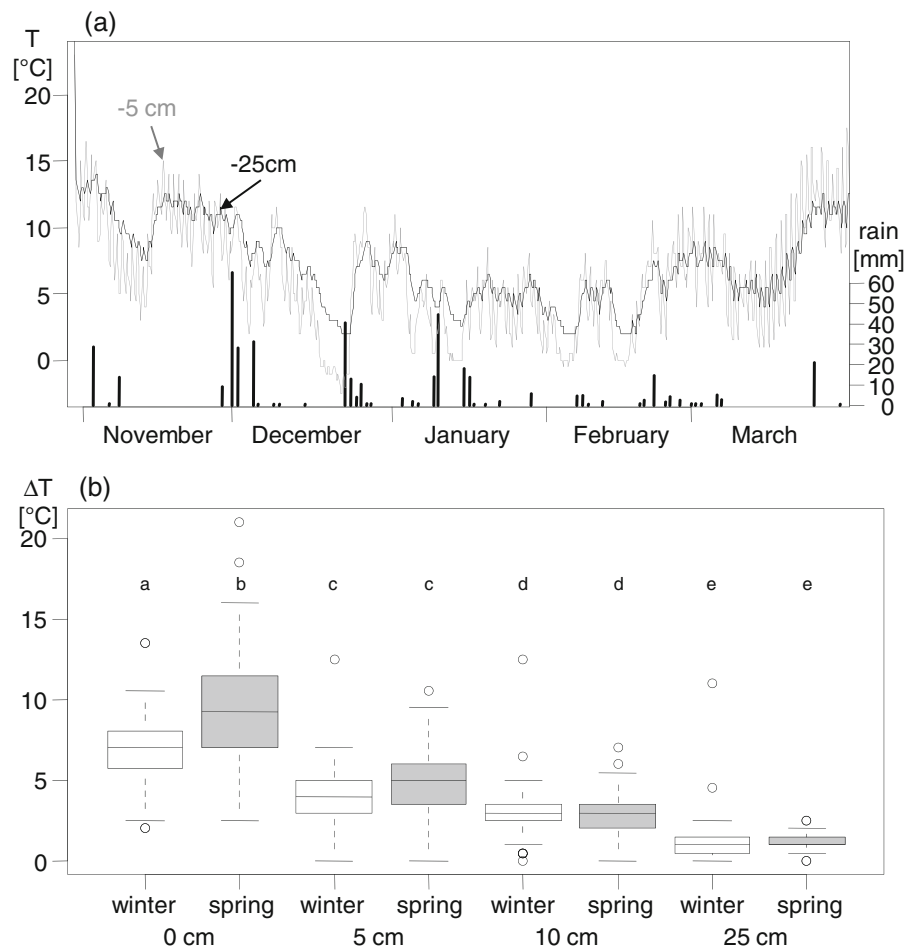
strong effect of season on the mortality of seeds (Table 2). Evidently, more seeds were classified as dead after the longer burial period ending in spring. The significant interaction between G_{DFT} and burial season indicated that in the first burial phase in winter, soil seed mortality was lower than at the end of the experiment for species with high G_{DFT} values (Fig. 3). Moreover, the interaction of depth of burial and G_{DFT} suggested that species with low G_{DFT} values had higher soil seed mortalities with increasing depth, compared to species with negative G_{DFT} which were comparatively indifferent to depth of burial (Fig. 3). There was also a significant interaction of depth of burial and season of burial and a tendency for a three way interaction (Table 2, Fig. 3). This tendency suggests that after the second burial phase, there was decreasing soil seed mortality with depth for species with high G_{DFT}, contrasting with an increasing mortality for species with low G_{DFT}.

For random effects, the likelihood ratio tests indicated that only species had a significant effect (LRT, $\chi^2=342.54$, $p<0.0001$), which was not the case for family (LRT, $\chi^2=0.0067$, $p=0.9349$) and experimental block (LRT, $\chi^2<0.0001$, $p>0.9999$).

Comparing our data on seed mass and on capacity to detect DFTs, we found no relation in a paired U-test ($p>0.1$) for species pairs, grouped by family as indicated in table 1 omitting *Anagallis* and *Nigella*.

In order not to over-parameterize our model we did not include interactions between species and fixed effects, instead we preferred to redo the analysis for each species individually. We therefore fitted mixed models for individual species, with experimental blocks as random effects and season as well as depth as fixed effects to analyse patterns of individual species (Fig 4). These analyses yielded a significant positive effect of burial depth and soil seed mortality for *Cnicus benedictus* ($z=2.394$, $p=0.0166$), a significant interaction of depth and season on soil seed mortality

for *Ranunculus arvensis* ($z=0.089$, $p=0.0002$) and *Ceratocephalus falcatus* ($z=0.054$, $p=0.0181$), indicating that mortality increased with depth in winter and decreased in summer (Fig. 4).

Two species had a significant higher mortality in spring compared to winter: *Bifora radians* ($z=-3.299$, $p=0.0010$) and *Roemeria hybrida* ($z=1.369$, $p=0.0015$). The remaining species showed no significant effect ($p>0.05$) of burial depth, season or their interactions on soil seed mortality in a mixed model with experimental blocks as random effects.

Discussion

Our measurements of temperatures at different burial depths show that the gradient of diurnally fluctuating temperatures with depth is maintained along of the experiment (Fig. 2b). Our data also confirm that rain is accompanied by lower DFTs, which has been shown for larger areas by climatologic works (Dai et al. 1999). Moreover, DFTs are generally lower in early winter compared to late winter and spring (Dai et al. 1999).

Considering all depths, our data showed no clear pattern of seed mortality due to germination under burial for species with different G_{DFT} values (Table 2, Fig. 4). We were surprised about absence of a clear relationship given the strong experimental constraints in terms of DFT gradient in soil and the contrasting values of G_{DFT} among species.

A potential explanation for this might be the burial depth in the experiment, which is deeper compared to data on seed depth distributions (Benvenuti 2007; Gruber and Claupein 2006). An aspect that is sustained by the fact that DFT detecting species have a tendency to lower mortality in winter, with little differences according to depth of burial (Fig 4). For one single species, *Ranunculus arvensis*, with one of

Table 2 Effects of season, G_{DFT} and burial depth and their interactions on soil seed mortality in a generalised linear mixed model, using species, plant family and experimental blocks as random effects

| Factor	Estimate	Standard error	z-value	p
Burial depth	−0.0075	0.0037	−2.040	0.0413*
G_{DFT}	0.2217	0.6710	−0.330	0.7411
season	−0.3852	0.0867	−4.441	<0.0001***
depth: G_{DFT}	−0.0217	0.0076	−2.842	0.0045**
depth: season	0.0121	0.0055	2.187	0.0288*
G_{DFT}: season	−0.7511	0.1771	−4.242	<0.0001***
depth: G_{DFT}: season	0.0182	0.0110	1.649	0.0991

Fig. 3 Interaction of season, depth of burial and detection of diurnally fluctuating temperatures (DFTs) on mortality of buried seed across all species; species are grouped according to their germination in response to DFTs (high: $G_{DFT} > 0$, or low: $G_{DFT} < 0$, see text for details); boxes denote interquartile range, broken lines 1.5 × interquartile range, outside of which data points are represented by circles
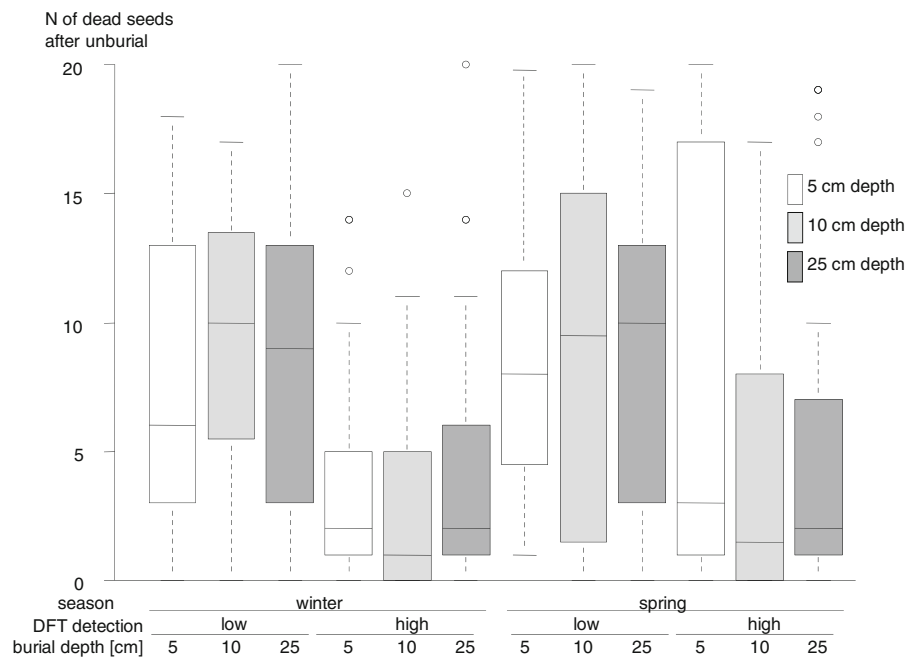
the largest seeds, there was a clear pattern of germinated/dead seeds being clearly negatively correlated with depth. This let us think that we probably missed the relevant burial depths in our experiment since the studied species cannot emerge from more than 10 cm according to the allometric relationship reported in Bond et al. (1999). This allometric relationship suggests maximum emergence depth of our species to range from 1.2 cm (*Papaver rhoeas*) to 8.5 cm (*Cnicus benedictus*) according to their mean seed

Fig. 4 Effects of season and depth of burial on soil seed mortality for two large seeded species, a non DFT detector, *Cnicus benedictus* with a positive effect of depth on mortality (GLMM, $p = 0.0166$) and a DFT detector *Ranunculus arvensis* with a significant interaction of depth and season on soil seed mortality (GLMM, $p = 0.0002$), showing negative effect of burial depth on soil seed mortality at the end of the experiment ($p < 0.0001$); in both mixed models, experimental blocks were used as random effects; boxes denote interquartile range, broken lines 1.5 × interquartile range, outside of which data points are represented by circles
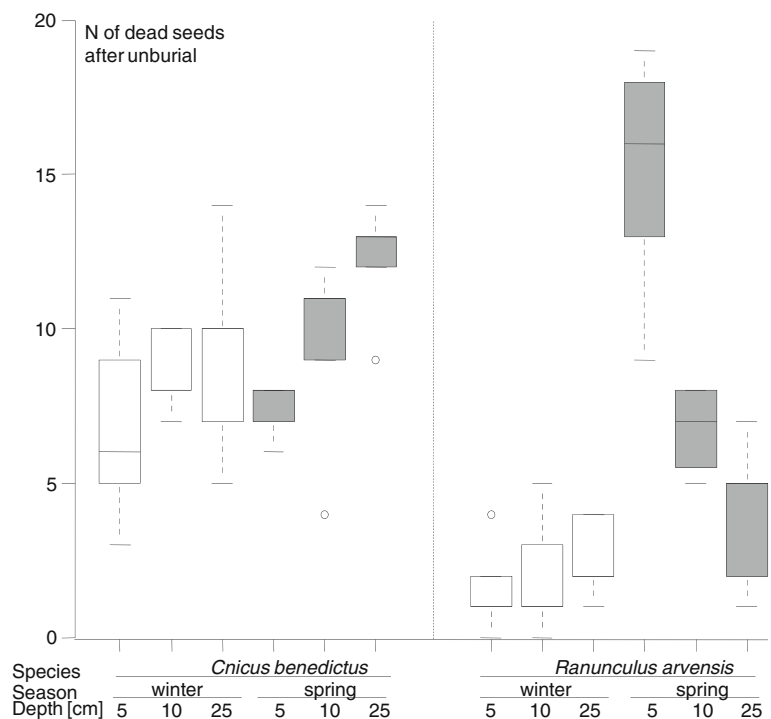
weight. In this context, it is important to note that seed mortality decreases with depth from 5 to 10 cm for combined seed samples of five species with G_{DFT} above zero (DFT detectors) and increases the five non DFT detecting species for both seasons (see Fig. 3). Interestingly, this range of depths corresponds to the range from which seed can emerge according to the model of Bond et al. (1999). It is the mortality data for deeper burial which is not in line with this trend and with the vision that soil burial depth is detected by DFTs. This suggests that DFTs as depth detecting mechanism is conditional on other factors.

In our data set, there is no relation between seed size and G_{DFT}, even when comparing closely related species pair-wise (Table 1). This is unexpected and should be re-evaluated on a larger data basis, since smaller seeds emerge only from shallow depths (Bond et al. 1999; Grundy et al. 2003) but get buried faster and deeper (Benvenuti 2007). They also adapted not to germinate while buried as indicated by the relation between light requirement for germination and seed size (Milberg et al. 2000). An absence of a relation between seed size and G_{DFT} could also result from conflicting selection pressures. This is especially true for seedlings from small seeds which are little drought resistant in semiarid climates (Baker 1972; Leishman and Westoby 1994), where rainfall events are correlated to smaller diurnally fluctuating temperatures (Dai et al. 1999). This suggests that small seeds may sense appropriate moisture conditions for germination through constant temperatures (Pearson et al. 2003), which is in conflict with the burial depth sensing mechanism where germination is triggered by high DFTs. Furthermore, the time of dry storage—comparatively long in our burial experiment—can alter the reaction to temperature conditions through after-ripening (Thompson and Grime 1983; Baskin and Baskin 1998). Evidence on the effect of after-ripening for sensitivity of seed germination to diurnally fluctuating temperatures are equivocal, both decreasing sensitivity (de Valla et al. 1980) or no change (Norsworthy and Oliveira 2007) have been reported. However, since intense after-ripening in Mediterranean summer is what naturally happens to seed of the studied species in the field, we do not expect that our data are biased in a systematic way by our storage conditions.

The alternative roles of temperature fluctuations as a germination cue are underlined by species without DFT detection mechanism, such as *Cnicus benedictus*, where mortality is positively correlated to burial depth in spring (Fig. 4). Probably, for these species, with higher germination under constant temperatures, constant temperatures indicate favourable conditions under natural conditions such as rainy weather, higher soil water content or presence of vegetation cover. Since these low DFTs are also realised in deep burial, here seeds germinate and die, which can be considered as an artefact of our experiment, as also documented by Ghersa et al. (1992) for *Sorghum halepense*.

Since we are left with a comparatively high value of the species random effect in our data, alternative mechanisms for seeds to detect burial depth might further explain variance in soil seed mortality across species. Such mechanisms could include gradients of oxygen availability and related gradients of relative ionic concentrations and redox-potential. Nitrate and oxygen concentration decrease with increasing soil depth and both concentrations are correlated due to microbial activity in soil (Jensen et al. 1994; Davidsson et al. 1997; Jobbágy and Jackson 2001).

We are aware that in our experimental design, we cannot separate mortality due to 'fatal germination' or due to predation including fungi attack, a likely alternative source of seed losses in our experiment. It can be expected that the activity of soil organisms does change in the depth profile, it is however unlikely that this depth-related-change differs consistently among plant species according to their capacity to detect DFTs. In future experiments, this can be more tightly controlled by comparing seed emergence and mortality in buried seed samples (Burmeier et al. 2010a). Nevertheless, we think that predation (including fungi attack) plays only a minor role at the time scale and temperatures of our experiment and that thus most variance in mortality can be attributed to fatal germination.

Conclusion

Our work confirms that seeds of several species do not germinate while buried in too deep soil depths. However, the mechanism through which seeds are thought to primarily detect burial, *i.e.* declining DFTs, only prevents DFT detecting species from germination buried in soil. Beyond shallow burial depths, this effect no longer discriminates among species according to their DFT detection mechanism.

Whereas seeds of DFT detectors persist according to a depth profile, non DFT detecting species tend to decline in abundance with depth, since they lack a requirement of fluctuating temperatures which could prevent fatal germination. This has important consequences for the capacities of non DFT detecting species to form persistent seed banks: persistence of their seeds will be much more limited in time and probably only be possible at the soil surface. Since burial depths of seeds change with soil environment and seed characteristics (Benvenuti 2007), we advocate to study DFT detection mechanisms in relation to a species' habitat requirement and seed traits. Such studies can further enhance our understanding on quantitative temporal seed bank dynamics as well as on specific detection mechanisms for regeneration opportunities (Grubb 1977; Vandelook et al. 2008). Our data highlight how DFT detection can determine size and persistence of the storage compartment, the soil seed bank. Therefore, we think that interspecific differences in the detection of burial depth combined with differences in emergence depth promote coexistence under the storage effect model (Warner and Chesson 1985; Facelli et al. 2005).

In future studies, we need to address the role of burial depth on germination across species on the scale of burial and emergence depths occurring in the field. Furthermore, the way how germination in response to DFTs is assessed can be a source of error. The reaction to DFTs in germination screenings can be closer to the one observed in the field and cover different amplitudes. Finally, alternative burial detection mechanisms should be considered, this could include nitrate concentration or redox-potential, which can be manipulated experimentally either in the field or in germination experiments.

References

Adams VM, Marsh DM, Knox JS (2005) Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. Biol Conserv 124:425–436

Baker HG (1972) Seed weight in relation to environmental conditions in California. Ecology 53:997–1010

Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography and evolution of dormancy and germination. Academic, San Diego

Bates D, Maechler M (2010) Linear mixed-effect models using S4 classes. R package version 0.999375-35 2010

Benech-Arnold RL, Sánchez RA, Forcella F, Kruk BC, Ghersa CM (2000) Environmental control of dormancy in weed seed banks in soil. Field Crops Res 67:105–122

Benvenuti S (1995) Soil light penetration and dormancy of jimsonweed (Datura stramonium) seeds. Weed Science 43:389–393

Benvenuti S (2007) Natural weed seed burial: effect of soil texture, rain and seed characteristics. Seed Sci Res 17:211–219

Benvenuti S, Macchia M, Miele S (2001a) Light, temperature and burial depth effects on Rumex obtusifolius seed germination and emergence. Weed Res 41:177–186

Benvenuti S, Macchia M, Miele S (2001b) Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. Weed Sci 49:528–535

Bond WJ, Honig M, Maze KE (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. Oecologia 120:132–136

Bullock JM (2000) Gaps and seedling colonization. In: Fenner M (ed) The ecology of regeneration in plant communities. CABI, Wallingford, pp 375–395

Burmeier S, Donath TW, Otte A, Eckstein RL (2010a) Rapid burial has differential effects on germination and emergence of small-and large-seeded herbaceous plant species. Seed Sci Res 20:189–200

Burmeier S, Eckstein RL, Otte A, Donath TW (2010b) Desiccation cracks act as natural seed traps in flood-meadow systems. Plant Soil 333:351–364

Cáceres CE (1997) Temporal variation, dormancy, and coexistence: a field test of the storage effect. Proc Natl Acad Sci USA 94:9171–9175

Ciani A, Goss KU, Schwarzenbach RP (2005) Light penetration in soil and particulate minerals. Eur J Soil Sci 56:561–574

Dai A, Trenberth KE, Karl TR (1999) Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. J Climate 12:2451–2473

Davidsson TE, Stepanauskas R, Leonardson L (1997) Vertical patterns of nitrogen transformations during infiltration in two wetland soils. Appl Environ Microbiol 63:3648–3656

Denslow JS (1980) Gap partitioning among tropical rainforest trees. Biotropica 12:47–55

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Evol Syst 18:431–451

de Valla L, Sanchez RA, Soriano A, Ghersa CM (1980) Influencia de algunos factores externos e internos sobre la germinación de las semillas de Sorgo de Alepo. Revista de Investigaciones Agropecuarias 15:549–560

Facelli JM, Chesson PL, Barnes N (2005) Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86:2998–3006

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge

Ghersa CM, Arnold RLB, Martinez-Ghersa MA (1992) The role of fluctuating temperatures in germination and establishment of sorghum halepense. Regulation of germination at increasing depths. Funct Ecol 6:460–468

Górski T, Górska K (1979) Inhibitory effects of full daylight on the germination of *Lactuca sativa* L. Planta 144:121–124

Grime JP (1989) Seed banks in ecological perspective. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. London Academic, London, pp xv–xxii

Grubb PJ (1977) Maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev Camb Philos Soc 52:107–145

Gruber S, Claupein W (2006) Effect of soil tillage intensity on seedbank dynamics of oilseed rape compared with plastic pellets as reference material. J Plant Dis Protect 273–280

Grundy AC (2003) Predicting weed emergence: a review of approaches and future challenges. Weed Res 43:1–11

Grundy AC, Mead A, Burston S (2003) Modelling the emergence response of weed seeds to burial depth: interactions with seed density, weight and shape. J Appl Ecol 40:757–770

Jensen K, Sloth NP, Risgaard-Petersen N, Rysgaard S, Revsbech NP (1994) Estimation of nitrification and denitrification from microprofiles of oxygen and nitrate in model sediment systems. Appl Environ Microbiol 60:2094–2100

Jobbágy E, Jackson R (2001) The distribution of soil nutrients with depth: Global patterns and the imprint of plants. Biogeochemistry 53:51–77

Kalisz S, McPeek MA (1992) The demography of an age-structured annual: resampled projection matrices, elasticity analyses and seed bank effects. Ecology 73:1082–1093

Leishman MR, Westoby M (1994) The role of seed size in seedling establishment in dry soil conditions—experimental evidence from semi-arid species. J Ecol 82:249–258

Merritt DJ, Turner SR, Clarke S, Dixon KW (2007) Seed dormancy and germination stimulation syndromes for Australian temperate species. Aust J Bot 55:336–344

Milberg P, Andersson L, Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. Seed Sci Res 10:99–104

Norsworthy JK, Oliveira MJ (2007) Light and temperature requirements for common cocklebur (*Xanthium strumarium*) germination during after-ripening under field conditions. Weed Sci 55:227–234

Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW (2002) Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. Ecology 83:2798–2807

Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW (2003) Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view. Funct Ecol 17:394–402

Pinheiro J, Bates D (2000) Mixed effect models in S and S-Plus. Springer, New York

Pons TL (1992) Seed responses to light. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CABI, Wallingford, pp 259–284

R Development Core Team (2009) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org. Vienna.

Saatkamp A, Affre L, Dutoit T, Poschlod P (2011) Germination traits explain soil seed persistence across species: the case of Mediterranean annual plants in cereal fields. Ann Bot - London 107:415–426

Stöcklin J, Fischer M (1999) Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950–1985. Oecologia 120:539–543

Thompson K (2000) The functional ecology of seed banks. In: Fenner M (ed) Seeds. CABI, Wallingford, pp 215–235

Thompson K, Grime JP (1983) A comparative study of germination responses to diurnally fluctuating temperatures. J Appl Ecol 20:141–156

Thompson K, Grime JP, Mason G (1977) Seed germination in response to diurnal fluctuations of temperature. Nature 267:147–149

Vandelook F, Van de Moer D, Van Assche JA (2008) Environmental signals for seed germination reflect habitat adaptations in four temperate Caryophyllaceae. Funct Ecol 22:470–478

Vincent EM, Roberts EH (1977) The interaction of light, nitrate and alternating temperature in promoting the germination of dormant seeds of common weed species. Seed Sci Technol 5:659–670

Warner RR, Chesson PL (1985) Coexistence mediated by the recruitment fluctuations: a field guide to the storage effect. Am Nat 125:769–787