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The role of fluctuations in soil water content on the regulation of dormancy changes in buried seeds of *Polygonum aviculare* L.

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Abstract

It has been hypothesized that fluctuations in soil water content may affect the dormancy status of weed seed banks under field conditions. In this paper, we present results showing that fluctuations in soil water content affect the dormancy status of buried seeds of *Polygonum aviculare* L. stored at dormancy-releasing temperatures. Effects of fluctuations in soil water content on the dormancy status of *P. aviculare* seeds were evaluated by comparing changes in the range of temperatures and water potentials permissive for germination, and in the sensitivity to fluctuating temperatures, between seeds subjected to a moist soil regime (MS) or to a fluctuating soil water content regime (FS). In comparison to the dormancy release pattern observed for seeds subjected to MS, seeds subjected to FS generally showed an increase in their dormancy level after periods of storage under dry soil conditions, and a decrease in their dormancy level after periods of storage under moist soil conditions. These effects were more pronounced during early stages of the storage period, producing larger changes in the thermal and water potential range for seed germination than in the sensitivity of seeds to fluctuating temperatures. Seeds subjected to FS generally exhibited a lower mean low-limit temperature, lower mean thermal time and hydrotime requirements for germination, and a higher proportion of the seed population with the capacity to germinate *in situ*, than seeds subjected to MS. The results obtained suggested that fluctuations in soil water content could be an additional factor affecting dormancy and weed emergence patterns under field conditions.

Keywords: buried seeds, dormancy, germination, *Polygonum aviculare*, soil water content, soil water content fluctuations, weeds

Introduction

Temperature has been identified as one of the critical environmental factors regulating dormancy changes in buried seeds of many weed species (Baskin and Baskin, 1988). For example, Kruk and Benech-Arnold (1998) showed that dormancy changes in buried seeds of the summer annual weed, *Polygonum aviculare* L., were mainly governed by seasonal changes in soil temperature; low winter temperatures alleviated dormancy, while high summer temperatures reinforced dormancy. In many weed species, dormancy alleviation is characterized by a widening of the range of temperatures and water potentials permissive for seed germination (Batlla *et al.*, 2004). Batlla and Benech-Arnold (2003, 2004) showed that storage of *P. aviculare* seeds under low 'winter' temperatures produced a widening of the range of temperatures and water potentials permissive for germination through a decrease of the lower temperature limit for germination of the seed population (T_l) and the base water potential of the seed population (Ψ_b), respectively. Consequently, if soil water potential is not restrictive for germination, emergence of *P. aviculare* in the field usually occurs in late winter–early spring, when increasing soil temperatures surpass T_l (Kruk and Benech-Arnold, 1998; Batlla and Benech-Arnold, 2003).

In addition, Batlla *et al.* (2003) showed that *P. aviculare* seeds, depending on the dormancy status of the population, also required the stimulus of

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temperature fluctuations to terminate dormancy and allow germination to be completed. Changes in the degree of dormancy of the seed population are associated with changes in the sensitivity of the seeds to the effect of fluctuating temperatures.

Although the role of temperature as the critical environmental factor driving seasonal changes in the dormancy status of natural seed banks is widely accepted, under certain environmental conditions fluctuations in soil water content may also affect the dormancy status of buried seeds (Egley and Duke, 1985; Batlla and Benech-Arnold, 2004). Under field conditions, seeds buried near the soil surface are generally subjected to cyclic fluctuations in soil water content, which in turn determine cyclic changes in seed water content (Downs and Cavers, 2000). Exposure of seeds to cycles of hydration–dehydration under laboratory conditions increased germination percentage and velocity (Hegarty, 1978; Bouwmeester, 1990). Under natural conditions, fluctuations in soil water content can affect the dormancy status of buried seeds and be an additional environmental factor regulating emergence fluxes observed in the field (Stoller and Wax, 1973; Vleeshouwers, 1997). On the other hand, in some species seed desiccation and re-hydration can have an opposite effect, i.e. inducing seeds into secondary dormancy (Staniforth and Cavers, 1979; Downs and Cavers, 2000).

Limited experimental evidence supports the hypothesis that fluctuations in soil water content can change the seasonal pattern of weed emergence under field conditions. For example, *Sisymbrium officinale* seeds usually display a cyclic seasonal pattern in dormancy, but are not induced into secondary dormancy when they are exposed to a desiccation treatment immediately after exhumation from soil (Bouwmeester and Karssen, 1993a). Similar changes in the seasonal dormancy pattern of buried seeds, due to seed dehydration treatments, have also been reported for other weed species (Karssen, 1980/81; Karssen *et al.* 1988; Bouwmeester, 1990). However, few studies have investigated the effects of fluctuations in soil water content on the dormancy status of buried weed seed populations in detail.

Our previous studies with *P. aviculare* seeds stored constantly at field capacity soil water content described changes in the thermal range permissive for germination, in base water potentials, and in the sensitivity to fluctuating temperatures in relation to dormancy loss (Batlla and Benech-Arnold, 2003, 2004; Batlla *et al.*, 2003). Here, we present a comparative analysis of changes in these seed population parameters (thermal range, base water potential and sensitivity to fluctuating temperatures) for seeds stored at dormancy-releasing temperatures under fluctuating or constant soil water content environments.

Materials and methods

Storage treatments

Seeds of *P. aviculare* were collected in a wheat field at Balcarce (latitude 37°45′S, longitude 58°15′W), Argentina, at the time of their natural dispersal (March 2000). After collection, the seeds were air-dried, winnowed with a seed blower (Burrows model 1836-3, Evanston, Illinois, USA) to eliminate unfilled or immature seeds, and stored at 0.1 g/g fresh weight water content in glass jars at ambient temperature (*c*. 20°C) for 40 d until the experiment commenced. In May 2000, groups of approximately 350 seeds, determined by weighing, were placed inside bags made of fine-mesh nylon gauze, and buried at 5 cm depth in 12 cm diameter black plastic pots filled with soil (Vertic Argiudoll according to the USDA taxonomy), previously oven-dried at 70°C for 3 d. Then, pots containing bags with seeds were stored at three dormancy-releasing temperatures (1.6, 7 and 12°C) (Batlla and Benech-Arnold, 2003), under three different soil water content regimes: dry soil (DS), moist soil (MS) and fluctuating soil water content (FS).

Dry soil regime (DS)

Soil in the pots was maintained dry (2% gravimetric water content) during the entire storage period.

Moist soil regime (MS)

Pots were irrigated to saturation and sealed at the top with solid black nylon to prevent water evaporation. Afterwards, pots were allowed to drain for 48 h, following which the nylon that sealed the pots was removed, and the pots were weighed to determine the weight corresponding to field capacity for each pot. Pots were kept without the nylon cover during storage. At regular intervals during the storage period, pots were re-weighed, and water was added until they reached their original weight, to maintain their initial field capacity status (gravimetric water content 36%). Regular watering maintained soil water content above 27% during the experiment.

Fluctuating soil water content regime (FS)

Pots were irrigated to saturation and sealed at the top with solid black nylon to prevent water evaporation. Afterwards, they were allowed to drain for 48 h, following which the nylon that sealed the pots was removed, and the pots were weighed to determine the weight corresponding to field capacity for each pot. Pots were kept without the nylon cover during

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storage. At regular intervals of approximately 15 d during the storage period, nylon bags containing seeds were moved (in total darkness) from pots containing moist soil to pots containing dry soil and vice versa. During periods of storage under moist soil, pots were re-weighed every 5 d, and water was added to restore their original weight. Regular watering maintained soil water content above 27% during storage under moist conditions.

Soil temperature in the pots was recorded hourly during the storage period, using temperature sensors (LI-COR model 1015, Lincoln, Nebraska, USA) connected to a DataLogger (LI-COR model 1000, Lincoln, Nebraska, USA). At the beginning of the experiment, three replicates of 35 seeds that had not been buried were tested for germination to quantify the initial dormancy of the seed population. At intervals of approximately 15 d throughout the storage period, three nylon mesh bags containing seeds (three replications) were exhumed from pots placed at each storage temperature under each soil water regime, and were exposed to the germination tests. For seeds subjected to FS, germination tests were conducted each time seeds were transferred. The entire experiment lasted 110 d. The moisture content of exhumed seeds was determined in subsamples by weighing, before and after drying for 24 h in an oven at 100°C.

Germination tests

Seeds were removed from the mesh bags under laboratory fluorescent white light and were rinsed with distilled water to remove adhering soil particles. Seeds were then tested under different germination conditions (see below). Seeds were exposed to white fluorescent light during germination counting, but otherwise were maintained in the dark inside temperature-controlled chambers. Germinated seeds, defined as having visible radicle protrusion (radicle length ≥ 1 mm), were removed after they were counted.

Determination of the thermal range permissive for germination

Three replicates of 35 seeds each were placed on two discs of Whatman No. 3 filter paper in 9-cm diameter plastic Petri dishes containing 5 ml of distilled water. They were exposed to a gradually increasing temperature regime ranging from 6 to 25°C. Since germination rate is generally faster at higher temperatures in the permissive range, the duration of exposure to each temperature differed, depending on the prevailing incubation temperature (Washitani, 1987; Batlla and Benech-Arnold, 2003): 6 d at 6°C, 5 d at 10°C, 4 d at 15°C, 3 d at 20°C, and 2 d at 25°C. Another three replicates were incubated at constant 15°C in a controlled temperature chamber for 15 d. This incubation temperature was near the optimum germination temperature (16°C) reported previously for this species (Kruk and Benech-Arnold, 1998). After 24 h of incubation in either regime, seeds were exposed to a 15 min red-light pulse to satisfy the light requirement for germination (Batlla and Benech-Arnold, 2003). The number of germinated seeds was recorded immediately before each temperature change in the increasing temperature regime and at approximately 2 d intervals during incubation at constant 15°C. Distilled water was added, when necessary, to maintain water level inside the dishes during germination tests.

Determination of the water potential range permissive for germination

Three replicates of 35 seeds each were placed on two Whatman No. 3 filter papers in 9-cm diameter plastic Petri dishes and moistened with 5 ml of distilled water or different polyethylene glycol solutions, establishing water potentials of -0.4, -0.8 and -1.2 MPa. Petri dishes were sealed with plastic film to prevent water evaporation and were incubated in a chamber at 15°C for 15 d. After 24 h of incubation, the seeds were exposed to a 15 min red-light pulse to satisfy their light requirement for germination. Solutions of polyethylene glycol (PEG 6000) were prepared according to Michel (1983), and water potential values of the solutions were verified using a vapour pressure osmometer (VAPRO 5520, Wescor Inc., Utah, USA) calibrated against NaCl standards. Seeds incubated on solutions containing PEG were transferred to fresh solutions after the first 24 h, and then weekly thereafter (Ni and Bradford, 1992), to maintain a constant water potential in the germination medium. Seed germination was recorded at intervals of approximately 2 d during the incubation period.

Determination of the sensitivity to fluctuating temperatures

Replicates of 35 seeds each were placed on two discs of Whatman No. 3 filter paper in 9-cm diameter plastic Petri dishes containing 5 ml of distilled water. Seeds were incubated for 24 h at 15°C and were exposed to a 20 min red-light pulse. Subsequently, three replications of 35 seeds each were incubated for 15 d at constant 15°C, or exposed to 12 cycles of a fluctuating temperature regime of 10°C (14 h)/24°C (10 h). Seeds that did not germinate after exposure to 12 cycles of fluctuating temperatures were further incubated at constant 15°C for 15 d. The number of germinated seeds was recorded at the end of the first incubation period (15 d at 15°C or 12 d at 10/24°C), and at the end of the

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second incubation period (15 d at 15°C), for seeds previously subjected to fluctuating temperatures. Distilled water was added when necessary to maintain water level inside the dishes during germination tests.

Determination of thermal parameters

Thermal parameters for seeds exhumed during the storage period were quantified using a mathematical germination model described in detail by Washitani (1987). The model predicts germination time courses of a seed population as a function of time and temperature. Thus, germination time-course curves obtained for seeds stored at each temperature (1.6, 7 and 12°C), using the previously described germination tests (germination curves from seeds incubated at the increasing temperature regime and at the constant 15°C regime), were reproduced by simulation for each exhumation. The model allows the estimation of two kinds of population thermal parameters in relation to observed data: (1) those describing dormancy status of the seed population, i.e. those parameters determining the thermal range for seed germination [the lower (T_l) and the higher (T_h) limit temperature for seed germination, and their corresponding standard deviations σ_{Tl} and σ_{Th} respectively]; and (2) those describing the relationship between germination rate and temperature of individual seeds [base temperature (T_b), optimal temperature (T_o), maximal temperature (T_m), thermal time required for 50% germination ($\theta_{(50)}$) and the thermal time accumulated between the germination of the first seed (just after 0% germination) and 50% germination (D)]. The assumptions of these models are described in detail by Kruk and Benech-Arnold (1998, 2000) and Batlla and Benech-Arnold (2003).

A program incorporating the equations of the germination model was developed using Squeak Smalltalk software (Anonymous, 2000). It has an optimization module that optimizes values for each seed population thermal parameter to maximize the fit of simulated curves with experimentally obtained ones. Optimization of the fit between simulated and experimentally obtained germination curves was performed by a dynamic hill-climbing global optimization algorithm (Russell and Norvig, 1995). The criterion used for thermal parameter optimization was minimum root mean square error (RMSE). The value of RMSE used for optimization was the average of the RMSE resulting from the fit of both germination regime curves of the germination test.

Determination of hydrotime parameters

Germination time course data under different osmotic potentials (0, −0.4, −0.8 and −1.2 MPa), for seeds exhumed during the storage period at the three temperatures (1.6, 7 and 12°C), were analysed by repeated probit regressions to calculate seed population hydrotime parameters: mean base water potential [$\Psi_{b(50)}$], hydrotime required for germination [θ_H] and standard deviation of Ψ_b [$\sigma_{\Psi b}$]. This approach is described in detail by Bradford (1990, 1995), Dahal and Bradford (1990) and Dahal *et al.* (1990).

Effects of fluctuations in soil water content upon seed dormancy level were evaluated by comparing results obtained for seeds stored under FS with those previously reported by Batlla *et al.* (2003) and Batlla and Benech-Arnold (2003, 2004) for seeds stored under MS. Comparison between previously published results and results presented in the present paper are justified because experiments were carried out simultaneously and using the same seed lot.

Results

Seeds stored under DS

Seed samples exhumed from pots containing dry soil (DS) had very low germination percentages (<5%) following storage at the three temperatures, and remained highly dormant during the entire 110 d storage period (data not shown). The moisture contents of exhumed seeds showed little change during storage, relative to that determined for recently dispersed seeds (Fig. 1). Mean stratification temperatures during dry storage periods were 2.4, 9 and 14°C, 0.8–2°C greater than those registered in pots containing soil at field capacity.

Seeds stored under MS

The results obtained for seeds stored under MS were published in Batlla *et al.* (2003) and Batlla and Benech-Arnold (2003, 2004). Moisture contents of exhumed seeds stored under MS are presented in Fig. 1.

Seeds stored under FS

Changes in soil water content during storage resulted in significant changes in the water contents of seeds buried 5 cm deep (Fig. 1). Seeds exhumed after periods of storage in moist soil maintained an average water content of 39 ± 6%, while seeds exhumed after periods of storage in dry soil averaged 12.5 ± 3%. Mean stratification temperatures during moist periods were 1.6, 7 and 12°C. For convenience, these will be referred to as the stratification temperatures, recognizing that temperatures were somewhat higher during the dry storage periods.

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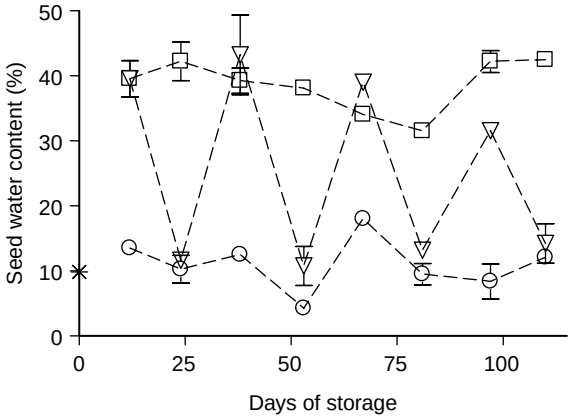

Figure 1. Water content (percent, fresh weight basis) of *Polygonum aviculare* seeds stored under different soil water content regimes in relation to days of storage. Symbols correspond to seeds stored under a moist soil regime (squares), under a fluctuating soil water content regime (inverted triangles) and under a dry soil regime (circles). The asterisk indicates the water content of recently dispersed seeds. Vertical bars indicate standard errors if larger than the symbols.

In situ germination

A significant increase in the percentage of seeds germinating *in situ* was observed for seeds stored at 1.6 and 7°C subjected to FS, in comparison to values observed for seeds stored under MS (Fig. 2). While seeds stored at 1.6°C under MS had less than 11% germination *in situ*, seeds stored at 1.6°C under FS had more than 40% germination *in situ* towards the end of the storage period. Similarly, seeds stored at 7°C under MS exhibited almost no germination during storage, while seeds stored under FS for 97 and 110 d had more than 10% germination *in situ*. Finally, seeds stored at 12°C did not germinate *in situ* under any storage moisture regime (data not shown).

A comparative analysis of changes in seed population thermal parameters

Seed population thermal parameters that maximize the fit of simulated germination curves with curves obtained from experimental data were estimated for each exhumation date for seeds stored at the different temperatures under FS (Table 1). To estimate seed population thermal parameters for seeds stored at 1.6 and 7°C, the fraction of seeds germinated *in situ* was added to the cumulative germination time-course curves obtained for exhumed seeds in the germination tests. This was basically achieved by estimating the germination time course for the fraction of seeds germinated *in situ*, using population thermal parameters previously estimated by Batlla and Benech-Arnold (2003) for the same seed lot stored under a constant moist soil regime ($\theta_{(50)} = 60$°Cd and $D = 60$°Cd).

To run the model it was assumed that T_b and T_o did not vary during the stratification period, so fixed values of 0 and 16°C respectively, were used for parameter optimization (Kruk and Benech-Arnold, 1998). The assumption of no variation in T_b and T_o during storage was based on previous reports for *P. aviculare* and other annual weed species, which found no variation of these parameters during burial in the soil (Vleeshouwers, 1997; Bauer *et al.*, 1998; Kruk

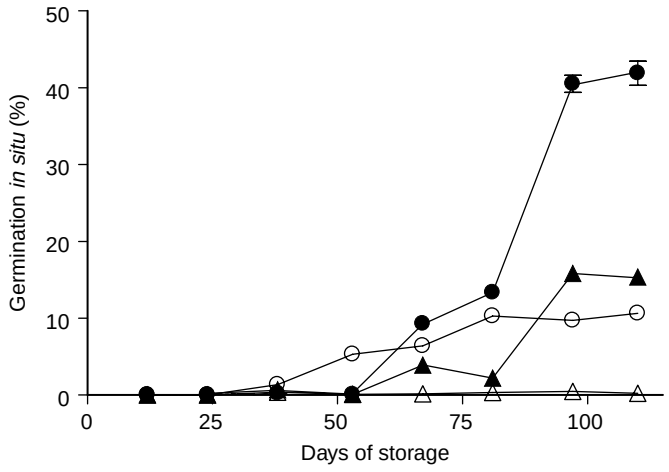

Figure 2. *In situ* germination of *Polygonum aviculare* seeds during storage at either 1.6 (circles) or 7°C (triangles) and under a continuously moist (open symbols) or a fluctuating soil moisture regime (filled symbols). Vertical bars indicate standard errors if larger than the symbols.

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Table 1. Estimated population thermal parameters for *Polygonum aviculare* seeds stored at (a) 1.6°C, (b) 7°C and (c) 12°C, under a fluctuating soil water content regime [periods of storage under moist (36% gravimetric water content) and dry (2% gravimetric water content) soil conditions are indicated]. T_l = lower limit temperature for germination, T_h = higher limit temperature for germination, σ_{Tl} = standard deviation of T_l, σ_{Th} = standard deviation of T_h, $\theta_{(50)}$ = thermal time required for 50% germination, D = the thermal time accumulated between the germination of the first seed (just after 0% germination) and 50% germination, and RMSE = the root mean square error of model simulation. Parameters were obtained by simulation of the germination time-course curves for seeds incubated at the increasing temperature regime and at the constant 15°C regime for each exhumation day. To estimate thermal parameters values of the higher limit temperature (18°C), base temperature for germination (0°C), optimum temperature for germination (16°C) and maximum temperature for germination (30°C) were assumed to be constant. Dashes mean that estimation of population thermal parameters was not possible, due to 0% germination under these conditions

Days of storage	Storage soil condition	$T_{l(50)}$ (°C)	σ_{Tl}	$T_{h(50)}$ (°C)	σ_{Th}	$\theta_{(50)}$ (°Cd)	D (°Cd)	RMSE
(a) At 1.6°C								
0	–	–	–	–	–	–	–	–
12	Moist	15.5	6.2	18	0.9	57	55	2.4
24	Dry	17.8	4.5	18	1.4	80	65	4
38	Moist	8.8	13	18	5	34	23	5.2
53	Dry	12	13	18	6	45	30	8.9
67	Moist	7.4	8.4	18	0.1	21	16	2.5
81	Dry	6.7	10.4	18	4.7	25	15	2.9
97	Moist	5.5	11	18	4.5	30	30	4.8
110	Dry	4	9	18	6	35	35	6.6
(b) At 7°C								
0	–	–	–	–	–	–	–	–
12	Moist	18	1.8	18	0.2	77	20	0.3
24	Dry	18	2.4	18	0.7	75	54	0.8
38	Moist	17	9	18	1.3	75	75	2.7
53	Dry	17.8	7	18	1.7	78	77	5
67	Moist	13.5	8	18	0.1	38	27	8.9
81	Dry	8	12	18	5	40	37	7.3
97	Moist	5.8	7	18	1.8	44	42	3.7
110	Dry	6	7.7	18	1.4	57	49	3.2
(c) At 12°C								
0	–	–	–	–	–	–	–	–
12	Moist	–	–	–	–	–	–	–
24	Dry	–	–	–	–	–	–	–
38	Moist	17.9	1.9	18	0.1	70	70	2.4
53	Dry	18	1.3	18	0.5	70	70	0.3
67	Moist	17.5	3.9	18	0.1	70	60	8.9
81	Dry	17	2.1	18	0.1	55	20	4.6
97	Moist	16	3	18	0.1	72	30	13.1
110	Dry	15	1	18	0.1	95	90	19.9

and Benech-Arnold, 1998, 2000; Batlla and Benech-Arnold 2003). Values for other parameters were allowed to vary over a reasonable range, based on previously reported data for *P. aviculare* or related summer annual species (Washitani, 1987; Bouwmeester, 1990; Kruk and Benech-Arnold, 1998; Batlla and Benech-Arnold, 2003). Results of an initial quantification of seed population thermal parameters at the three storage temperatures showed little variation in T_h (18°C) and T_m (30°C) during the storage period, as reported previously for this species (Batlla and Benech-Arnold, 2003). Nearly complete germination of remaining non-germinating seeds during both germination tests, with further incubation for extended periods ($\cong$ 11 months) at 6 and 10°C, showed that non-germinating seeds were viable, but dormant (data not shown). Hence, final estimation of optimum seed population thermal parameters was performed using constant values of T_b (0°C), T_o (16°C), T_h (18°C) and T_m (30°C).

Almost no seeds germinated in the initial germination test (data not shown), indicating that the seed population was deeply dormant shortly after dispersal. This precluded the quantification of initial seed population thermal parameters (Table 1). On the other hand, seeds buried at 12°C did not germinate

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until 38 d of storage, thus impeding the calculation of seed population thermal parameters for shorter storage periods in this treatment (Table 1).

Seeds stored under both soil water regimes (FS and MS) showed a decrease of $T_{l(50)}$ during storage under the different dormancy-releasing temperatures (Fig. 3). However, seeds stored under MS showed an almost linear decrease of $T_{l(50)}$ in relation to storage time, while the rate of $T_{l(50)}$ decrease for seeds stored under FS was affected by fluctuations in the soil water content during storage. The effects of fluctuating soil water content depended upon the temperature at which seeds were stored. Seeds stored at low temperatures (i.e. 1.6 and 7°C) showed greater changes in $T_{l(50)}$ in response to fluctuations in soil water content than did seeds stored at higher temperatures (12°C). An increase in $T_{l(50)}$ was observed for seeds stored at 1.6°C after periods of storage under dry soil conditions during initial phases of the storage process (Fig. 3). In contrast, seeds exhumed after periods of storage under moist soil conditions, following periods of storage under dry conditions, showed a steep decrease of $T_{l(50)}$, reaching values lower than those obtained with seeds stratified for the same number of days under MS. Seeds exhumed after 67 d of storage had reached $T_{l(50)}$ values that were lower than those observed for seeds stored under MS towards the end of the storage period.

Seeds stored at 7°C under FS did not show significant changes during the first 53 d of storage. The $T_{l(50)}$ value of seeds exhumed after 67 d storage under this soil water content regime was lower, similar to that obtained with seeds stored for the same number of days under MS (Fig. 3). Later exhumations showed a continuous decrease of $T_{l(50)}$, reaching values similar to those estimated for seeds stored at 1.6°C, and substantially lower than those observed for seeds stored at 7°C under MS. Finally, seeds stored at 12°C under FS showed a slight decrease of $T_{l(50)}$, resulting in values relatively higher than those obtained for seeds stored under MS.

Changes in $T_{l(50)}$ for seeds stored at 1.6 and 7°C under FS were positively correlated with changes in $\theta_{(50)}$ ($P < 0.0001$; $R^2 = 0.7$) (Fig. 4). A positive correlation, although weaker than under FS, was also observed between both parameters for seeds stored under MS ($P = 0.012$; $R^2 = 0.37$) (Fig. 4). On the other hand, seeds stored at 12°C under FS did not show significant changes in $\theta_{(50)}$ (Table 1), producing values relatively higher than those determined for seeds stored at 12°C under MS (see Batlla and Benech-Arnold, 2003).

In several exhumations, high values of σ_{Tl} (i.e. a wide distribution of T_l within the seed population) were estimated for seeds stored at 1.6 and 7°C (Table 1a, b). This resulted in a fraction of the population presenting T_l values lower than T_b (0°C) or higher than T_h (18°C). Seeds with a T_l lower than 0°C would be part of the germinable fraction; however, they would not germinate until thermal time is accumulated above T_b (0°C). On the other hand, a T_l higher than T_h means that seeds are fully dormant (i.e. their thermal range permissive for seed germination is null), and they will not germinate until they have been stored long enough to decrease T_l below T_h.

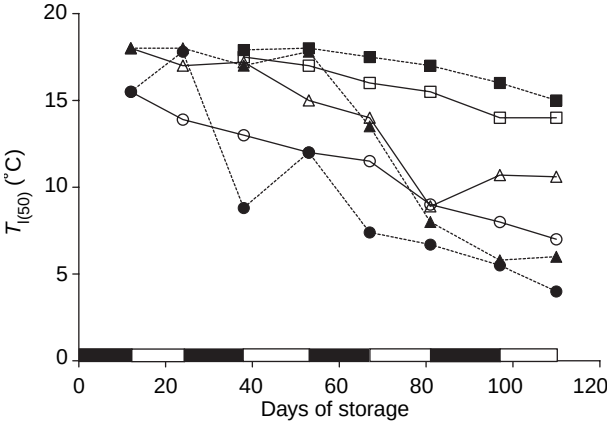

Figure 3. Estimated mean lower limit temperature ($T_{l(50)}$) values for *Polygonum aviculare* seeds stored at 1.6°C (circles), 7°C (triangles) and 12°C (squares) under a moist (open symbols) and a fluctuating soil water content regime (filled symbols). Bars above the *x*-axis indicate periods of storage under moist (black bars) and dry (white bars) soil conditions in the fluctuating soil water content regime. Missing values of $T_{l(50)}$ for seeds stored at 12°C under the fluctuating soil water content regime prior to 38 d were due to little (<5%) or no germination in the germination test. Data for MS from Batlla and Benech-Arnold (2003).

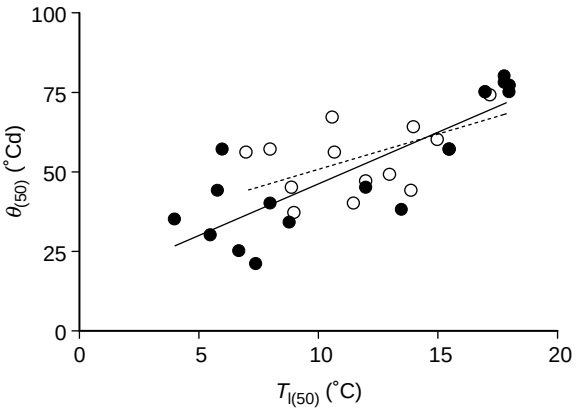

Figure 4. Relationship between mean thermal time for germination ($\theta_{(50)}$) and the mean lower limit temperature ($T_{l(50)}$) for *Polygonum aviculare* seeds stored at 1.6°C and 7°C under a moist (open circles) and a fluctuating soil water content regime (filled circles). Lines were best-fit linear models, corresponding to data obtained for seeds stored under a moist soil regime (dashed line; $P = 0.012$, $R^2 = 0.37$) and seeds stored under a fluctuating soil water content regime (solid line; $P < 0.0001$, $R^2 = 0.7$).

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A comparative analysis of changes in seed population hydrotime parameters

Hydrotime parameters of the seed population were estimated for seeds exhumed during storage at different temperatures under FS (Table 2). To estimate the population hydrotime parameters, the percentage of seeds germinated *in situ* when stored at 1.6 and 7°C under FS (Fig. 2) were added to the germination curves obtained for seeds incubated at 0 MPa (distilled water) in the germination test for each exhumation, as explained above for the determination of population thermal parameters.

Table 2. Estimated population hydrotime parameters for *Polygonum aviculare* seeds stored at (a) 1.6°C, (b) 7°C and (c) 12°C, under a fluctuating soil water content regime [periods of storage under moist (36% gravimetric water content) and dry (2% gravimetric water content) soil conditions are indicated]. $\Psi_{b(50)}$ = mean base water potential, $\sigma_{\Psi b}$ = standard deviation of Ψ_b, θ_H = hydrotime required for germination and R^2 = the coefficient of determination for probit regressions. Dashes mean that estimation of population hydrotime parameters was not possible, due to little (<5%) or no germination in the germination test

Days of storage	Storage soil condition	$\Psi_{b(50)}$ (MPa)	$\sigma_{\Psi b}$ (MPa)	θ_H (MPa h)	R^2
At 1.6°C					
0	–	–	–	–	–
12	Moist	−0.07	0.46	43	0.91
24	Dry	0.36	1.1	108	0.75
38	Moist	−0.61	0.84	68	0.96
53	Dry	−0.09	0.58	22	0.93
67	Moist	−0.74	0.67	28	0.98
81	Dry	−0.47	0.81	32	0.91
97	Moist	−0.62	0.73	39	0.90
110	Dry	−0.44	0.5	35	0.90
At 7°C					
0	–	–	–	–	–
12	Moist	0.75	0.75	85	0.85
24	Dry	–	–	–	–
38	Moist	0.12	0.81	61	0.95
53	Dry	0.41	0.68	43	0.92
67	Moist	−0.4	0.47	36	0.9
81	Dry	−0.51	0.54	40	0.87
97	Moist	−0.65	0.42	45	0.92
110	Dry	−0.6	0.4	58	0.91
At 12°C					
0	–	–	–	–	–
12	Moist	–	–	–	–
24	Dry	–	–	–	–
38	Moist	–	–	–	–
53	Dry	–	–	–	–
67	Moist	−0.04	0.61	71	0.96
81	Dry	−0.03	0.57	71	0.74
97	Moist	−0.38	0.34	57	0.74
110	Dry	−0.31	0.35	55	0.89

The values of $\Psi_{b(50)}$ estimated for seeds exhumed during storage at the three temperatures under FS are shown (Fig. 5) in comparison to those reported for seeds stratified at similar temperatures under MS (Batlla and Benech-Arnold, 2004). Seeds stored under both soil moisture regimes showed a decrease of $\Psi_{b(50)}$ during storage under the three dormancy-releasing temperatures (Fig. 5). However, seeds stored at 1.6°C under FS showed an increase in $\Psi_{b(50)}$ values after periods of storage under dry soil conditions, while a decrease of $\Psi_{b(50)}$ values was observed after exhumations of seeds stored under moist soil conditions. As observed for changes in $T_{l(50)}$, the magnitude of these effects decreased as time of storage progressed. Initially, seeds exhumed after periods of storage under moist soil conditions, following periods of storage under dry soil conditions, showed $\Psi_{b(50)}$ values lower than those estimated for seeds stored under MS, while seeds exhumed after periods of storage under dry soil conditions showed $\Psi_{b(50)}$ values higher (i.e. less negative) than those estimated for seeds stored under MS. Towards the end of the storage period, seeds stored under FS had values of $\Psi_{b(50)}$ that were similar to those obtained for seeds stored under MS.

Seeds stored at 7°C under FS showed a similar pattern of response to that observed for seeds stored at 1.6°C during initial phases of the stratification process: an increase in the values of $\Psi_{b(50)}$ for seeds exhumed

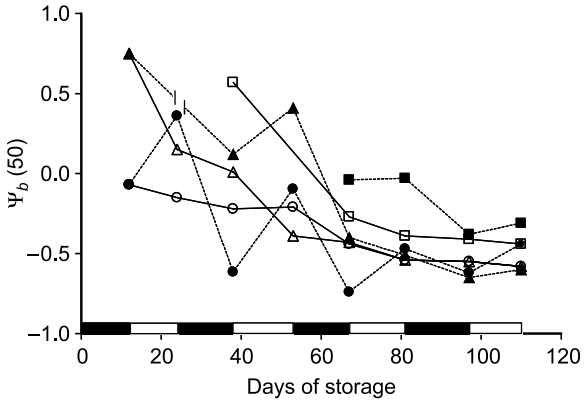

Figure 5. Estimated values of the mean base water potential ($\Psi_{b(50)}$) for *Polygonum aviculare* seeds stored at 1.6°C (circles), 7°C (triangles) and 12°C (squares) under a moist soil regime (open symbols) and a fluctuating soil water content regime (filled symbols). Bars above the *x*-axis indicate periods of storage under moist (black bars) and dry soil (white bars) conditions in the fluctuating soil water content regime. Missing values of $\Psi_{b(50)}$, for seeds stored under the fluctuating soil water content regime for 24 d at 7°C and prior to 67 d at 12°C, were due to little (<5%) or no germination in the germination test. Data for MS from Batlla and Benech-Arnold (2004).

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after periods of storage under dry soil conditions and a decrease of $\Psi_{b(50)}$ for seeds exhumed after periods of storage under moist soil conditions. Seeds exhumed after the first period of storage under dry soil conditions (24 d of storage) showed less than 5% germination in water, precluding the determination of hydrotime parameters (Table 2; Fig. 5). Seeds exhumed at 67 d or later showed a constant decrease of $\Psi_{b(50)}$, reaching values similar to those obtained for seeds stored at a similar temperature under MS.

Seeds stored at 12°C under FS did not reach germination percentages that allowed the estimation of hydrotime parameters until 67 d of storage (data not shown). Seeds exhumed after 67 and 81 d of storage did not show significant changes in $\Psi_{b(50)}$, with values close to 0 MPa (Table 2; Fig. 5). After the last period of storage under moist soil conditions (seeds exhumed after 97 d of storage), a decrease of $\Psi_{b(50)}$ was observed, reaching values similar to those obtained for seeds stored at a similar temperature but under MS.

A comparative analysis of changes in seed population sensitivity to fluctuating temperatures

Exposure of seeds to 12 cycles of 10/24°C stimulated germination in comparison to those kept at constant 15°C, for seeds exhumed during storage at the different dormancy-releasing temperatures under both soil water content regimes (Fig. 6). An increase in the germination percentage of seeds subjected to fluctuating temperatures and incubated at constant 15°C was observed as storage time under dormancy-releasing temperatures progressed. However, seeds stored under lower temperatures (Fig. 6a, b) showed a higher rate of increase in response to fluctuating temperatures and in germination at constant temperature than did seeds stored under higher temperatures (Fig. 6c).

Differences in germination response between seeds stored under FS and MS were observed, particularly during early stages of the storage process. Seeds stored at 1.6°C, exhumed after the first period of storage under dry soil conditions (24 d of storage), had lower germination percentages, for seeds incubated either at constant 15°C or exposed to fluctuating temperatures, than seeds stored for the same period of time under MS (Fig. 6a). However, values obtained for later exhumations were similar for seeds stratified under both soil water content regimes.

Lower germination percentages than those observed under MS for both situations (seeds incubated at constant 15°C and seeds exposed to fluctuating temperatures), were also observed for seeds stored at 7°C under FS exhumed after the two first periods of storage under dry soil conditions (seeds exhumed after 24 and 53 d of storage) (Fig. 6b). No significant differences were observed between soil water content regimes for later exhumations.

Seeds stored at 12°C under FS had lower germination percentages under both incubation temperature regimes than those obtained for seeds stored at a similar temperature under MS, during most of the storage period (Fig. 6c). Moreover, seeds stored

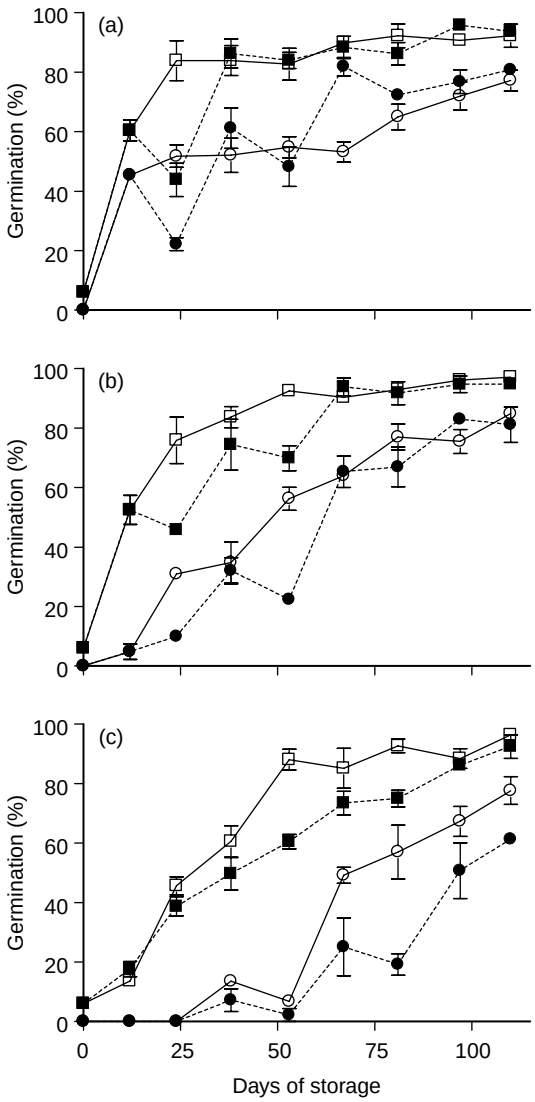

Figure 6. Germination percentages of *Polygonum aviculare* seeds exhumed after different days of storage under a moist soil regime (open symbols) and under a fluctuating soil water content regime (filled symbols) at 1.6°C (a), 7°C (b) and 12°C (c). Circles represent seeds incubated at 15°C for 15 d, and squares represent seeds exposed to 12 cycles of fluctuating temperatures of 10°C (14 h)/24°C (10 h) followed by incubation for 15 d at constant 15°C. Vertical bars indicate standard errors when larger than the symbols.

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under FS at this temperature had a higher fraction of the seed population with requirements for fluctuating temperatures for dormancy termination than did seeds stored under MS during the whole storage period.

Discussion

In most cropping systems the largest part of the weed seed bank that could successfully emerge is located in the upper layer of the soil (Radosevich *et al.*, 1997). Shallowly buried seeds are usually subjected to cycles of hydration–dehydration, depending on the temporal rain pattern (Egley and Duke, 1985; Downs and Cavers, 2000). Usually, seeds are hydrated during a rain event, after which a dehydration phase begins as the soil dries out, until a new rain event allows re-imbibition of the seeds (Karssen, 1982). Based on results obtained under laboratory conditions, many investigators have suggested that these hydration–dehydration cycles would affect the dormancy status of buried weed seeds and, thus, the annual pattern of weed emergence under field conditions (Stoller and Wax, 1973; Bouwmeester, 1990; Vleeshouwers, 1997).

In this paper, we present results showing that fluctuations in soil water content certainly affect the dormancy status of buried seeds of *P. aviculare* stored at dormancy-releasing temperatures under controlled conditions. To evaluate the effect of fluctuations in soil water content on the dormancy status of *P. aviculare* seeds, dormancy-release dynamics for seeds subjected to a moist soil regime (MS) and a fluctuating soil water content regime (FS) were compared.

In comparison to the dormancy release pattern observed for seeds subjected to MS, seeds subjected to FS generally showed an increase in dormancy level after periods of storage in dry soil, while a decrease in the dormancy level was observed after periods of storage in moist soil (soil at field capacity) (Figs 3, 5 and 6). These results showed that re-hydration of seeds (which took place during the germination test) that had been stored in dry soil for approximately 15 d was not enough to produce a decrease in their dormancy level, as reported upon hydration of previously dehydrated seeds by many authors for other species (e.g. Vincent and Cavers, 1978; Karssen, 1980/81; Bouwmeester and Karssen, 1989, Bouwmeester and Karssen 1993a, b). Conversely, an increase in the dormancy level of the seed population was observed after periods of storage in dry soil. A longer period of storage in moist soil (approximately 15 d) was required to produce a decrease in the dormancy level of the seed population. This decrease in some cases was more pronounced than that observed for seeds stored in constantly moist soil at the same temperature for the same length of time.

The apparent sensitivity of seeds to fluctuations in soil water content varied depending on the indicators used to evaluate the dormancy level of the seed population (thermal range permissive for seed germination, water potential range permissive for seed germination or sensitivity of the seed population to fluctuating temperatures). For example, seeds stored at 1.6°C showed significant changes in $\Psi_{b(50)}$, due to the effect of changes in soil water content during storage (Fig. 5), while there were smaller changes in the response of seeds to fluctuating temperatures (Fig. 6a). In addition, the sensitivity of seeds to fluctuations in soil water content varied in relation to their dormancy level at the time they were subjected to soil moisture fluctuations. For example, seeds subjected to periods of storage in dry soil at 1.6°C had a significant increase in $T_{l(50)}$ during early stages of the storage process (seeds exhumed after 24 and 38 d of storage), but there was no increase in $T_{l(50)}$ after periods of storage in dry soil conditions for seeds exhumed in later stages of the storage period (more than 60 d of storage), where a gradual decrease in the value of this parameter was registered (Fig. 3).

Seed populations subjected to FS had a greater proportion with the capacity of germinating *in situ* during the storage period than was recorded for seeds stored under MS (Fig. 2). This effect was closely related to the dormancy level of the seed population (days of storage under dormancy-releasing temperatures). Thus, seeds with a lower dormancy level (more storage time) have higher values of germination *in situ* than seeds with a higher dormancy level (less storage time). Since seeds germinated while buried in the soil, the capacity of germinating *in situ* must be related to the loss of the light requirement for germination of a considerable fraction of the population (Batlla and Benech-Arnold, 2005). Similar results were obtained by Bouwmeester (1990), who observed that *Polygonum lapathifolium* subsp. *lapathifolium* seeds, which usually require light stimuli for germination, were capable of germinating in darkness, after being subjected to hydration–dehydration cycles under laboratory conditions. In addition, Araki *et al.* (1998) observed that *Persicaria lapathifolia* L. seeds, buried at 5 cm depth, showed 66% germination *in situ* if they were subjected to a fluctuating moisture regime, while seeds buried at the same depth, but subjected to a constant moisture regime, had almost no germination *in situ*. In addition, germination *in situ* of seeds stored at 1.6°C can be associated with the capability of seeds to germinate under extremely low temperatures; this means that at least a fraction of the seed population presents a T_l lower than the storage temperature ($T_l < 1.6$°C).

To calculate thermal parameters (Table 1) and hydrotime parameters (Table 2) of the seed population for seeds stored at 1.6 and 7°C, we assumed that thermal time and hydrotime requirements (θ°Cd and

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θ_H MPa h) for the fraction of the seed population, which germinated *in situ*, were the same as those reported previously by Batlla and Benech-Arnold (2003, 2004), for the same seed lot stored under MS. This assumption may have caused some errors in the estimation of population parameters for seeds exhumed in the late stages of the storage process, where more than 40% of the population germinated *in situ*. On the other hand, variations in the soil water content involved changes in the storage temperature to which seeds were exposed. It is possible that these fluctuations in the thermal environment could have

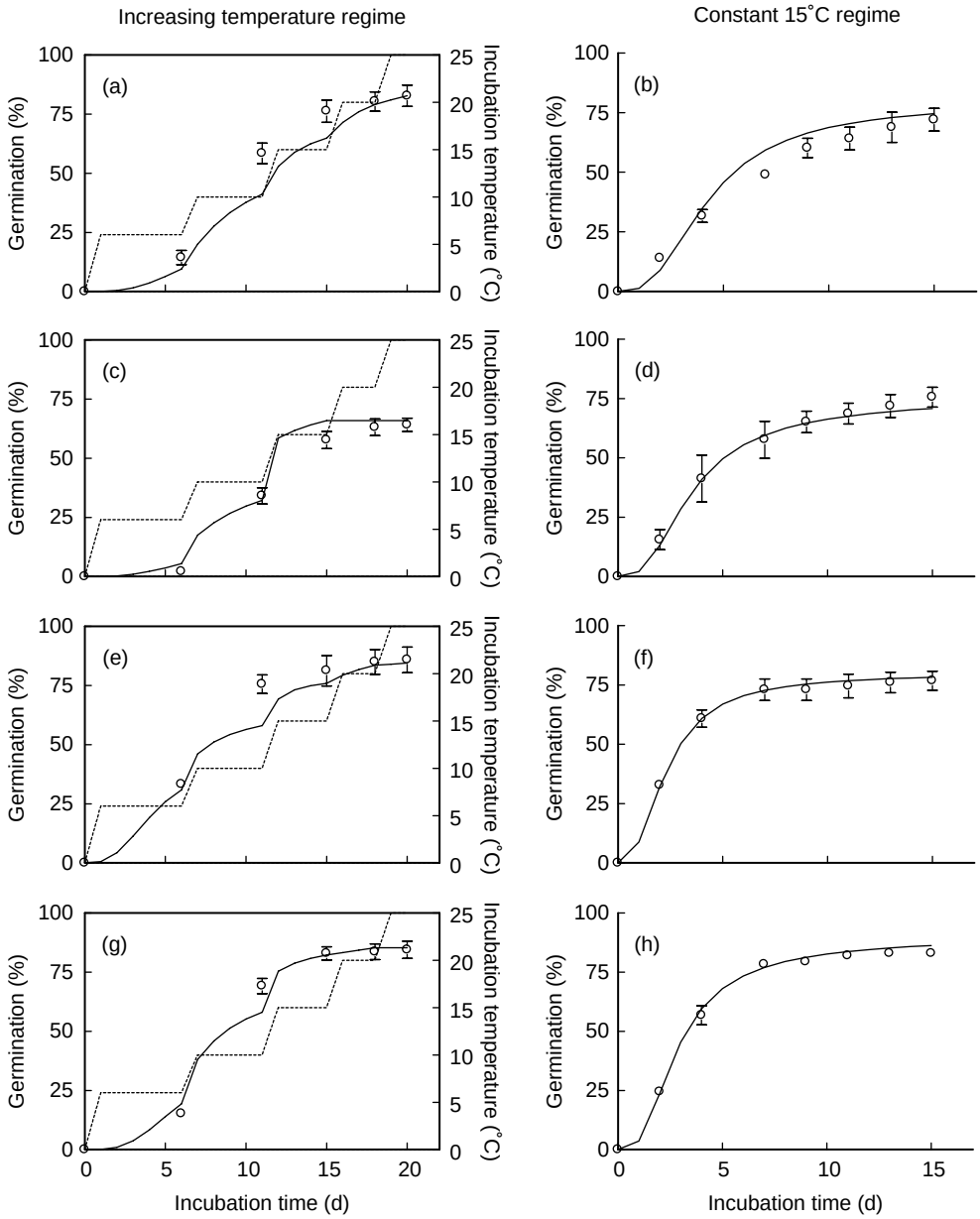

Figure 7. Cumulative percentage germination of *Polygonum aviculare* seeds stored for 97 d under a moist soil regime (panels a, b, c and d) and under a fluctuating soil water content regime (panels e, f, g and h) at 1.6°C (panels a, b, e and f) and at 7°C (panels c, d, g and h). Left panels correspond to seeds incubated at the increasing temperature regime and right panels to seeds incubated at the 15°C constant regime. In all panels, the symbols are the actual data and the solid curves are predicted by the germination model, using the values in Table 1a and b for seeds stored at 1.6 and 7°C, respectively. The dotted line in the left-hand panels (right axis) represents the course of temperature change during incubation of seeds at the increasing temperature regime. Vertical bars indicate standard errors when larger than the symbols.

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had an effect on the dormancy level of the seed population, beyond the effect of fluctuations in soil water content. However, results obtained by Batlla *et al.* (2003) showed that the thermal amplitude of fluctuating temperature regimes should be at least 6°C or greater to affect the dormancy of *P. aviculare* seeds; thus, the low amplitude variations in temperature registered during the storage period (0.8–2°C in 15 d cycles) could hardly have affected the dormancy level of the seeds.

Seeds stored at 1.6 and 7°C subjected to FS showed lower values of $T_{l(50)}$ and $\theta_{(50)}$ than those observed for seeds stratified at 1.6 and 7°C under MS (Figs 3 and 4). The consequence of this was that seeds subjected to FS germinated in a wider range of temperatures, and more rapidly and synchronously, than did seeds stored under MS. An example of this can be observed comparing time-course germination at the constant and the increasing temperature regime for seeds stored under both soil water content regimes for 97 d (Fig. 7). An increase in the rate and uniformity of germination following exposure to hydration–dehydration cycles has been reported previously (Hegarty, 1978; Allen *et al.*, 1993). It has been proposed that, under natural conditions, this mechanism could reduce the time interval between a rain event, after a dry period, and germination of the seed population (Dubrovsky, 1996; Adams, 1999). Rapid germination following onset of prolonged water availability would give a seed a competitive advantage during early establishment (Allen *et al.*, 1993).

Changes in soil water content also affected the germination response of seeds to fluctuating temperatures (Fig. 6). However, fluctuations in soil water content did not produce an increase in the sensitivity of the seed population to the fluctuating temperature stimuli; on the contrary, a decrease in the sensitivity of seeds to the effect of fluctuating temperatures was observed after periods of storage under dry soil conditions. This effect was large during the initial stages of the storage process, while low or null effects were observed for seeds exhumed at later stages. As indicated in the methods section, seeds exposed to fluctuating temperatures were incubated for a longer time period (12 d at 10/24°C + 15 d at 15°C) than were seeds incubated under constant temperatures (15 d at 15°C). However, higher germination observed under the fluctuating temperature regime cannot be regarded as a consequence of a longer period of incubation since: (1) seed germination under constant 15°C had almost finished after 10 d of incubation, as can be seen in Fig. 7 (right panels); thus, further incubation would have not yielded higher germination; and (2) almost 95% of final germination for seeds exposed to fluctuating temperatures occurred during the first 12 d of incubation at 10/24°C (data not shown).

Our results clearly show that fluctuations in soil water content affect the dormancy level of buried *P. aviculare* seeds, which could influence the temporal patterns of weed emergence under field conditions. Consequently, the effects of fluctuations in soil water content on the dormancy level of the seed bank should be taken into account if weed emergence patterns are to be predicted with precision. Additionally, when seeds require light to terminate their dormancy and germinate, fluctuations in soil water content could allow a fraction of the seed population to bypass this requirement. Steep changes in soil water content, to which seeds were exposed during storage in the present experiments, could only take place in the topmost centimetres of the soil profile, where fluctuations of environmental variables, such as water and temperature, are larger. From an ecological viewpoint, this loss of light requirement for germination, as a result of soil water content fluctuations, could represent a depth detection mechanism (in addition to the previously reported requirements for light and fluctuating temperatures).

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