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A predictive model for dormancy loss in *Polygonum aviculare* L. seeds based on changes in population hydrotime parameters

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Abstract

Changes in population hydrotime parameters were determined during stratification in *Polygonum aviculare* L. seeds in order to model dormancy loss. Seeds buried in pots were stored at three temperatures (1.6, 7 and 12°C) for 110 d and were exhumed at regular intervals during the storage period. Exhumed seeds were incubated at different water potentials at 15°C and germination time courses were analysed to determine hydrotime parameters. The population mean base water potential ($\Psi_b(50)$) decreased concomitantly with seed dormancy, while the hydrotime constant (θ_H) and the standard deviation of base water potential ($\sigma_{\Psi b}$) displayed only minor changes. Based on these results, a model for simulating *P. aviculare* seed dormancy loss in relation to low temperature was developed. The model employs $\Psi_b(50)$ as an index of mean seed population dormancy status. While $\Psi_b(50)$ was allowed to vary as seeds were released from dormancy, θ_H and $\sigma_{\Psi b}$ were held constant. Changes in $\Psi_b(50)$ were related to the time and temperature, using a previously developed thermal stratification time index (S_{tt}), which quantifies the accumulation of thermal time units below a threshold temperature required for dormancy loss to occur. Therefore, $\Psi_b(50)$ varied in relation to the accumulation of S_{tt} according to time and temperature. Model performance showed acceptable prediction of timing and percentage of germination of seeds buried in irrigated plots, but did not accurately predict germination of seeds exhumed from rain-fed plots. Thus, environmental factors other than temperature could also be involved in the regulation of dormancy status of buried seeds under field conditions.

Keywords: dormancy, germination, hydrotime, *Polygonum aviculare* L., stratification, temperature, water potential

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Introduction

Dormancy is a common attribute of many weed seed populations (Fenner, 2000). Thus, prediction of emergence from weed seed banks depends largely on understanding the dynamics of dormancy changes in weed species (Benech-Arnold *et al*., 2000). Temperature is one of the main factors governing changes in dormancy status of buried weed seed populations (Bouwmeester and Karssen, 1992). For the summer annual *Polygonum aviculare* L., Kruk and Benech-Arnold (1998) demonstrated that low winter temperatures alleviate dormancy, while high summer temperatures reinforce dormancy in buried seeds. Several models to simulate seasonal changes in dormancy status of buried weed seeds in relation to temperature (Spitters, 1989; Bouwmeester and Karssen, 1992, 1993a, b, c) were based on the concept of dormancy introduced by Vegis (1964), who stated that the dormancy status of a seed population could be related to the width of the thermal range permissive for seed germination. Dormancy release is associated with a widening of the thermal range that permits germination, while conversely, dormancy induction is associated with a narrowing of that thermal range. In *P. aviculare*, as in many other summer annual species, widening or narrowing of the thermal germination range is a consequence of changes in the lower-limit temperature allowing seed germination (Bouwmeester, 1990; Kruk and Benech-Arnold, 1998). Based on this theoretical framework, Batlla and Benech-Arnold (2003) developed a population-based model for simulating *P. aviculare* dormancy loss in relation to the temperature experienced by the seeds during stratification in the soil. The model allows the prediction of the thermal range for seed germination, as a consequence of changes in the lower-limit temperature for germination of the seed population due to the effect of variable stratification times and temperatures. Model simulations gave good descriptions of time and percentage of germination of exhumed seeds

buried under field and environmentally controlled conditions.

However, others have shown that dormancy alleviation could also be correlated with a decrease of the base water potential (Ψ_b) of the seed population (i.e. more negative values), while conversely, dormancy induction could be associated with an increase of Ψ_b (i.e. less negative or even positive values) (Ni and Bradford, 1992, 1993; Dahal *et al*., 1993; Bradford and Somasco, 1994). Based on these findings, Bradford (1995, 1996, 2002) proposed that changes in seed dormancy status could also be quantified and even modelled in relation to variations in Ψ_b, based on the concept of hydrotime proposed initially by Gummerson (1986). Hydrotime models describe seed germination responses to water potential (Ψ) using the following function:

$$\theta_H = (\Psi - \Psi_b(g))t_g, \quad (1)$$

where θ_H is the hydrotime (MPa h) the seeds require for germination, Ψ is the actual water potential of the germination medium (MPa), $\Psi_b(g)$ is the theoretical threshold or base water potential that will just prevent germination of fraction g, and t_g is the germination time (h) of the corresponding fraction g. The model assumes that Ψ_b varies among fractions of a seed population following a normal distribution with its mean, $\Psi_b(50)$, and standard deviation, $\sigma_{\Psi b}$, while θ_H is considered constant for a seed population (Bradford, 1990). These assumptions allow the germination time-course curve for a seed population to be characterized by the following probit equation:

$$\text{probit}(g) = [\Psi - (\theta_H/t_g) - \Psi_b(50)]/\sigma_{\Psi b} \quad (2)$$

Working with the winter-annual weed *Bromus tectorum*, Christensen *et al*. (1996) found that $\Psi_b(50)$, indeed, became more negative as seeds after-ripened under dry conditions. Based on these findings, Bauer *et al*. (1998) developed a simulation model for predicting *B. tectorum* seed dormancy loss as a function of soil temperature and soil water status. The model uses $\Psi_b(50)$ as an index of the seed population dormancy status. This parameter was allowed to vary to account for dormancy changes, while other parameters (i.e. θ_H and $\sigma_{\Psi b}$) were held constant as the dormancy loss process proceeded. Model simulations successfully predicted changes in estimated $\Psi_b(50)$ of buried seeds after-ripened under variable field conditions.

Thus, changes in dormancy status of weed seed populations can comprise changes in the range of temperatures permissive for germination and/or the Ψ_b of the seed population (Benech-Arnold *et al*., 2000; Bradford, 2002). In a previous paper (Batlla and Benech-Arnold, 2003), dormancy loss in *P. aviculare* seeds was assessed through changes in the thermal range permissive for germination, as a consequence of a decrease in the lower-limit temperature for germination of the seed population. In the present paper we report studies performed with the same seed lot, but quantifying the effect of stratification temperature on dormancy loss dynamics assessed through changes in seed population hydrotime parameters. Based on the results obtained with these studies, a simple thermal time model was developed to predict dormancy loss of *P. aviculare* seeds in relation to stratification temperature.

Materials and methods

Stratification 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, seeds were air-dried, winnowed using a seed blower (Burrows model 1836–3, Evanston, Illinois, USA) to eliminate light seeds, and stored (water content 10% fresh wet basis) in glass jars at ambient temperature (*c*. 20°C) for 40 d until the experiment commenced. In May 2000, groups of approximately 350 seeds were placed inside mesh nylon bags and buried at 5 cm depth in 12 cm diameter black plastic pots filled with soil, previously oven-dried at 70°C for 3 d. Pots were irrigated to saturation, sealed at the top with black nylon and stored under different temperatures (1.6, 7 and 12°C) (Batlla and Benech-Arnold, 2003). Pots were allowed to drain for 48 h, following which the black nylon that sealed the pots was removed, and the pots were weighed to determine the weight corresponding to field capacity for each pot. 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. 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). At the beginning of the experiment, three replicates of 35 seeds that had not been buried were exposed to an initial germination test, to quantify the initial dormancy of the population. At intervals of *c*. 15 d throughout the storage period, three mesh nylon bags containing seeds (three replications) were exhumed from pots placed at each storage temperature and were tested for germination. The whole low temperature period lasted 110 d. Afterwards, one pot from each temperature was transferred to a chamber at 22°C to determine whether non-dormant seeds could be re-induced into secondary dormancy at higher storage temperatures. After 12 d of storage at 22°C, seeds were finally exhumed and exposed to the germination test.

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Germination test

Seeds were exhumed from the mesh bags under laboratory fluorescent white-light, and were incubated in groups of 35 in 9 mm plastic Petri dishes on two Whatman No. 3 filter papers 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. This incubation temperature was near the optimum germination temperature reported previously by Kruk and Benech-Arnold (1998) for this species (16°C). After 24 h of incubation, seeds were exposed to a 15 min red light pulse in order to by-pass the light requirement for germination (Baskin and Baskin, 1988; Batlla and Benech-Arnold, 2003). 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 weekly thereafter (Ni and Bradford, 1992) to maintain constant water potential in the germination medium. At regular intervals during the incubation period, seed germination was recorded under laboratory (fluorescent) light. Germinated seeds were removed after they were counted. Seeds were exposed to light during germination counting, but otherwise were maintained in the dark inside temperature chambers. The criterion for seed germination was visible radicle protrusion.

Data analysis

For seeds exhumed during the storage period at the three temperatures (1.6, 7 and 12°C), germination time-course data under the different osmotic potentials (0, –0.4, –0.8 and –1.2 MPa) were analysed by repeated probit regressions to calculate seed population hydrotime parameters ($\Psi_b(50)$, θ_H and $\sigma_{\Psi b}$). This approach is described in detail by Bradford (1990, 1995), Dahal and Bradford (1990) and Dahal *et al*. (1990).

Model development

Our objective was to establish functional relationships between the rate of dormancy loss in seed populations and stratification temperature. As dormancy loss could be quantified through changes in Ψ_b of the seed population, mean population Ψ_b [$\Psi_b(50)$] was used as an indicator of the mean dormancy status of the seed population. Recently, Batlla and Benech-Arnold (2003) developed a thermal time equation that allows the quantification of the effect of variable time and temperature on *P. aviculare* seed population dormancy status. The authors related dormancy changes to the accumulation of thermal time units under a threshold temperature for dormancy loss to occur, using the following function:

$$S_{tt} = \text{Days} \times (T_c - T_s) \quad (3)$$

where S_{tt} is stratification thermal time units (°Cd), T_c is the dormancy release 'ceiling' temperature (the temperature at, or over, which dormancy release does not occur) (°C) and T_s is the daily mean storage temperature (°C). The optimal 'ceiling' temperature for dormancy loss of *P. aviculare* seeds was determined to be 17°C (Batlla and Benech-Arnold, 2003). Thus, in the present model, the same index (S_{tt}) was used to quantify temperature effects on changes in $\Psi_b(50)$ of the seed population. The modelling construction process is summarized as follows:

(1) Determine the population hydrotime parameters for seeds exhumed during storage at 1.6, 7 and 12°C.
(2) Derive equations relating progressive changes in $\Psi_b(50)$ to the accumulation of S_{tt} units during storage.
(3) Using the equation developed in (2), predict changes in $\Psi_b(50)$ of seeds buried under measured temperatures in field and environmentally controlled conditions.
(4) Use predicted values of $\Psi_b(50)$ to simulate germination time-course curves and compare results with experimentally obtained data.

Model evaluation

To evaluate model performance with independent data, results from an experiment carried out under field conditions were used. Seeds of *P. aviculare* were collected in a wheat field at Balcarce, Argentina, at the time of their natural dispersal (March 1999). Seeds were winnowed to eliminate light seeds and stored in glass jars at ambient temperature (*c*. 20°C) for 45 d until experimental set-up. Groups of approximately 300 seeds were placed inside nylon mesh bags and buried 15 and 5 cm deep in 1.5 × 2 m plots in the experimental field of the Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires (latitude 34°25'S, longitude 58°25'W), Argentina. Field plots were subjected to two water regimes: irrigated and rain-fed. In plots assigned to the irrigated water regime, the first 15 cm of the soil profile were maintained moist by a drip-irrigation system controlled by a timer-clock connected to an electric valve. Plots assigned to the rain-fed regime were subjected to the naturally fluctuating soil water status imposed by the natural

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rain pattern. Around the time of the emergence season for this species (late winter–early spring) (Kruk and Benech-Arnold, 1998), seeds were exhumed and tested for germination. Soil temperature in the plots was recorded hourly at 5 and 15 cm deep, using temperature sensors (LI-COR model 1015) connected to a DataLogger (LI-COR model 1000). Plots were hand-weeded throughout the experimental period.

Results

Effect of low temperature on changes in seed population hydrotime parameters

Freshly harvested seeds did not germinate at any tested water potential, preventing the quantification of initial seed population hydrotime parameters and indicating the very high dormancy status of the population shortly after dispersal (Table 1A, B and C). Effectively, all seeds in the population had Ψ_b values greater than 0 MPa.

A progressive decrease in $\Psi_b(50)$ was observed for seeds exhumed during the storage period at all temperatures (Table 1A, B and C; Fig. 1A). However, the rate at which $\Psi_b(50)$ decreased was dependent on the temperature at which seeds were stored. Seeds stored at 1.6°C showed a relatively low value of $\Psi_b(50)$ (–0.07 MPa) after only 12 d of storage (Table 1A; Fig. 1A). From then on, $\Psi_b(50)$ displayed a gradual linear decrease until approximately 81 d of storage, when $\Psi_b(50)$ reached a value of –0.54 MPa. Later exhumations showed only slight changes in $\Psi_b(50)$ with further time at 1.6°C, reaching a value of –0.58 MPa at the end of the storage period.

Seeds stored at 7°C for 12 d exhibited a higher value of $\Psi_b(50)$ (0.75 MPa) than that determined for seeds stored at 1.6°C for the same period (Table 1B; Fig. 1A). However, later exhumations (24, 38, 53 and 67 d after burial) of seeds stored at 7°C yielded a substantial decrease in $\Psi_b(50)$, eventually reaching similar values to those obtained for seeds stored at 1.6°C after 81, 97 and 110 d of burial.

Seeds incubated at 12°C did not germinate until 38 d of storage, precluding the calculation of the seed population hydrotime parameters after short periods in this treatment (Table 1C). After 38 d of storage at 12°C, exhumed seeds had a $\Psi_b(50)$ value of 0.57 MPa (Table 1C; Fig. 1A). Surprisingly, in contrast to the decreasing trend for $\Psi_b(50)$ observed for seeds at the other two temperatures, seeds exhumed 15 d later had a much higher $\Psi_b(50)$ (1.07 MPa). However, subsequent exhumations (after 67 d of storage) showed a substantial shift of $\Psi_b(50)$ to more negative values (–0.27 MPa). Finally, $\Psi_b(50)$ decreased more slowly with further time of storage at 12°C, reaching a value of –0.44 MPa at the end of the storage period. Although no clear reason for the up-shift of $\Psi_b(50)$ observed for seeds exhumed after 53 d of storage at 12°C could be determined, data corresponding to this exhumation were not included in further analyses.

No defined pattern of change in $\sigma_{\Psi b}$ occurred during the incubation period for seeds stored at 1.6°C, showing a mean of 0.65 MPa and a coefficient of variation (CV) of 22% (Table 1A). However, seeds stored for 38 d at 1.6°C had a relatively high value of $\sigma_{\Psi b}$ (0.96 MPa). On the other hand, seeds stored at 7°C (mean 0.59 MPa; CV 24%) and 12°C (mean 0.54 MPa; CV 26%) exhibited a progressive decrease in $\sigma_{\Psi b}$ as storage times progressed, reaching a value of about 0.4 MPa after 110 d of storage at 7 and 12°C (Table 1B and C).

Variations in θ_H occurred between different exhumations for seeds stored at 1.6°C (mean 48 MPa h; CV 35%), while seeds stored at 7°C (mean 62 MPa h; CV 21%) and 12°C (mean 59 MPa h; CV 7%) displayed little variation in this parameter during the entire storage period (Table 1A, B and C).

Storage at 22°C for 12 d of seeds that had been previously released from dormancy through storage at 1.6 and 7°C resulted in a shift of Ψ_b (50) to more positive values, indicating an induction into secondary dormancy due to exposure of seeds to high temperatures (Table 2). Conversely, only slight changes were observed in the values of the other parameters (θ_H and $\sigma_{\Psi b}$). Storage at 22°C of seeds that had been previously held at 12°C showed very low germination percentages (0–7%) at any water potential; the high dormancy status of the seeds precluded quantification of seed population hydrotime parameters (Table 2).

Model development

Values of $\Psi_b(50)$ for seeds stratified at the three tested storage temperatures were related to the accumulation of stratification thermal time units (S_{tt}) during storage, calculated according to equation (3) (Fig. 1B). Results showed that changes in $\Psi_b(50)$ during storage at the three temperatures could be well characterized using the stratification thermal time equation previously developed by Batlla and Benech-Arnold (2003). The $\Psi_b(50)$ decrease in relation to S_{tt} accumulation could be described accurately by the following exponential decay function:

$$\Psi_b(50) = [\Psi_{bi}(50) + \Psi_{bf}(50)] \times \exp(-K \times S_{tt}) + \Psi_{bf}(50) \quad (4)$$

where $\Psi_{bi}(50)$ is the initial mean base water potential [i.e. $\Psi_b(50)$ for recently harvested seeds] (MPa), $\Psi_{bf}(50)$ is the final mean base water potential (MPa) (i.e. $\Psi_b(50)$ for 'fully stratified' seeds) and K is the exponential rate at which $\Psi_b(50)$ decreased in relation to the accumulation of S_{tt} during stratification, until $\Psi_{bf}(50)$ was reached.

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Table 1. Estimated population hydrotime parameters for *Polygonum aviculare* seeds stored at (A) 1.6°C; (B) 7°C; and (C) 12°C. The dash means that estimation of population hydrotime parameters was not possible due to little or no germination in the germination test at 15°C for 15 d. The coefficient of variation (CV) is expressed as a percentage of the mean

(A) 1.6°C

Storage (d)	$\Psi_b(50)$ (MPa)	$\sigma_{\Psi b}$ (MPa)	θ_H (MPa h)	R^2
0	–	–	–	–
12	–0.07	0.46	43	0.91
24	–0.15	0.66	31	0.83
38	–0.22	0.96	59	0.91
53	–0.21	0.64	25	0.92
67	–0.44	0.66	46	0.84
81	–0.54	0.54	44	0.89
97	–0.55	0.71	76	0.91
110	–0.58	0.60	65	0.86
Mean (CV)	–0.34 (60)	0.65 (22)	48 (35)	

(B) 7°C

Storage (d)	$\Psi_b(50)$ (MPa)	$\sigma_{\Psi b}$ (MPa)	θ_H (MPa h)	R^2
0	–	–	–	–
12	0.75	0.75	85	0.85
24	0.15	0.58	40	0.92
38	0.01	0.69	65	0.97
53	–0.39	0.73	75	0.93
67	–0.43	0.67	62	0.92
81	–0.54	0.45	59	0.95
97	–0.55	0.45	54	0.85
110	–0.58	0.39	61	0.88
Mean (CV)	–0.20 (237)	0.59 (24)	62 (21)	0.88

(C) 12°C

Storage (d)	$\Psi_b(50)$ (MPa)	$\sigma_{\Psi b}$ (MPa)	θ_H (MPa h)	R^2
0	–	–	–	–
12	–	–	–	–
24	–	–	–	–
38	0.57	0.76	55	0.91
53[a]	1.07	0.88	68	0.78
67	–0.27	0.60	64	0.94
81	–0.39	0.53	63	0.90
97	–0.41	0.44	60	0.83
110	–0.44	0.40	54	0.87
Mean (CV)	–0.19 (228)	0.54 (26)	59 (7)	0.87

[a]Hydrotime parameters were not used for mean and CV estimation.

Figure 1B clearly shows that $\Psi_b(50)$ decreases exponentially during initial phases of the dormancy loss process, while after the accumulation of approximately 700°Cd, $\Psi_b(50)$ values remain almost constant as stratification time progresses, reaching a constant minimum value of –0.5 MPa.

Model evaluation

Germination data used for the determination of hydrotime parameters of seeds exhumed during storage at the three low temperatures were contrasted with predicted values, using equations (2), (3) and (4), in order to test whether observed changes in $\Psi_b(50)$ could account for variations in seed germination time courses as seeds were released from dormancy. Other studies reported that changes in $\Psi_b(50)$ could account for most of the variation in seed germination time courses when other hydrotime parameters (i.e. $\sigma_{\Psi b}$ and θ_H) were held constant for a seed population during after-ripening (Christensen *et al*., 1996; Bauer *et al*., 1998; Meyer *et al*., 2000). Based on these results,

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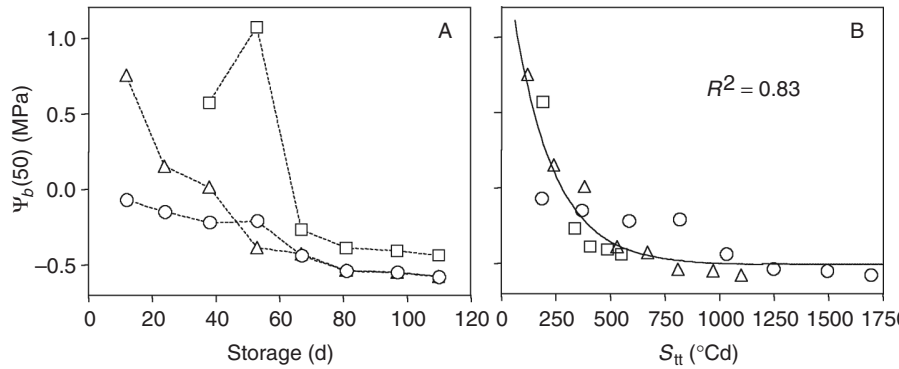

Figure 1. Estimated values of the mean base water potential [$\Psi_b(50)$] for *Polygonum aviculare* seeds stored at 1.6°C (○), 7°C (△) and 12°C (□), plotted against days of storage (A), and against stratification thermal time (S_{tt}) (B). The fitted line in panel (B) corresponds to $Y = 2.235 \times \exp(-5.353^{-3} \times X) - 0.5$.

Table 2. Estimated population hydrotime parameters for *Polygonum aviculare* seeds stored at 1.6 or 7°C for 110 d, followed by storage at 22°C for 12 d. It was not possible to estimate these parameters for seeds stored at 12°C, due to the low germination percentages (less than 7%), even in water

Low storage temperature (°C)	$\Psi_b(50)$ (MPa)	$\sigma_{\Psi b}$ (MPa)	θ_H (MPa h)	R^2
1.6	–0.36	0.40	64	0.88
7	–0.37	0.36	52	0.92

$\sigma_{\Psi b}$ and θ_H were assumed to be constant during seed stratification. $\sigma_{\Psi b}$ and θ_H were calculated by averaging values obtained for seeds stored at the three temperatures during the entire storage period, obtaining values of 0.6 MPa and 56 MPa h, respectively. A good correlation was obtained between predicted and observed data (R^2 = 0.89), showing a root mean square error around 7.3 (Fig. 2). However, the model slightly underestimated experimentally obtained data, showing a slope slightly lower than 1 (0.87). Underestimation was particularly important for high germination percentages observed in seeds incubated at –0.4 MPa.

To see if the model could be used to predict dormancy loss of seeds buried under environmentally variable field conditions, predicted values using equations (2), (3) and (4) were contrasted with independent data obtained from the field experiment described previously. S_{tt} units accumulated during seed burial in the field were calculated using equation (3), in relation to the daily mean soil temperature recorded at 5 and 15 cm deep at the different water-regime experimental plots. Accumulation of S_{tt} after seed burial began when the recorded daily mean soil temperature was below T_c (17°C) (Batlla and Benech-Arnold, 2003). As before, $\sigma_{\Psi b}$ (0.6 MPa) and θ_H (56 MPa h) were assumed to be constant during burial. Seeds exhumed at the beginning of winter (May) did not germinate under any incubation condition. This situation was described accurately by the model, where almost no germination (2%) was predicted (data not shown). For seeds exhumed at the end of the winter (August) from 5-cm deep in irrigated plots, simulated data gave a good description of the observed seed population germination dynamics in water, –0.4 and –1.2 MPa, while slightly overestimating germination at –0.8 MPa (Fig. 3, upper left panel). Prediction of seeds buried at 15 cm in irrigated plots showed that germination was also fairly well estimated by the model, although in this case the model overestimated germination in water (Fig. 3, left lower panel). Conversely, the model was not as accurate in describing germination of seeds buried at the two depths in the rain-fed water regime plots (Fig. 3, right-hand panels).

Discussion

Soil temperature and soil water potential are the two main factors controlling seed-bank germination under field situations. However, because the range of temperatures and water potentials allowing seed germination changes as dormancy status of the seed population changes (Benech-Arnold *et al.*, 2000; Bradford, 2002), dormancy status would determine the fraction of the population that would be able to

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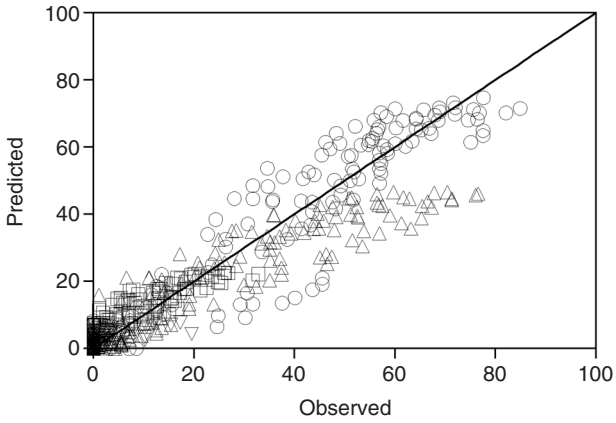

Figure 2. The relationship between observed germination percentages for *Polygonum aviculare* seeds exhumed during the storage period at the different temperatures, and recently harvested seeds, incubated at 0 (○), –0.4 (△), –0.8 (□) and –1.2 MPa (▽) at 15°C for 15d, versus predicted germination percentages [using equations (2), (3) and (4)]. The solid line represents a 1:1 relationship.

germinate in a given soil temperature and water potential condition. Thus, understanding and modelling how environmental factors (i.e. temperature) modify the dormancy status of the seed population are essential for accurately predicting germination under field conditions.

In the present work, a detailed analysis of changes in *P. aviculare* seed population hydrotime parameters, in relation to the temperature experienced by the seeds during burial, was presented. Results showed that $\Psi_b(50)$ shifted progressively to more negative values as dormancy loss progressed due to storage of seeds under three different temperatures (Table 1; Fig. 1A). Similar results have been reported for other species by different authors: *B. tectorum* (Christensen *et al*., 1996; Bauer *et al*., 1998), *Elymus elymoides* (Rafin.) Swezey (Meyer *et al*., 2000) and *Eucalyptus delagatensis* R.T. Baker (Battaglia, 1997). The decrease observed in *P. aviculare* seeds $\Psi_b(50)$ was inversely related to temperature during initial phases of the dormancy loss process; lower temperatures showed higher rates of $\Psi_b(50)$ decrease in relation to those observed at higher storage temperatures. For example, 12 d of storage at 1.6°C allowed seeds to germinate up to 45% in water (data not shown) [$\Psi_b(50)$ = –0.07 MPa], while seeds stored at 12°C, for the same period of time, failed to germinate at any water potential (i.e. all seeds in the population had Ψ_b values above 0 MPa). The same inverse relationship between temperature and *P. aviculare* seed dormancy loss was reported previously by Batlla and Benech-Arnold (2003) and Batlla *et al*. (2003). However, in the present work, a

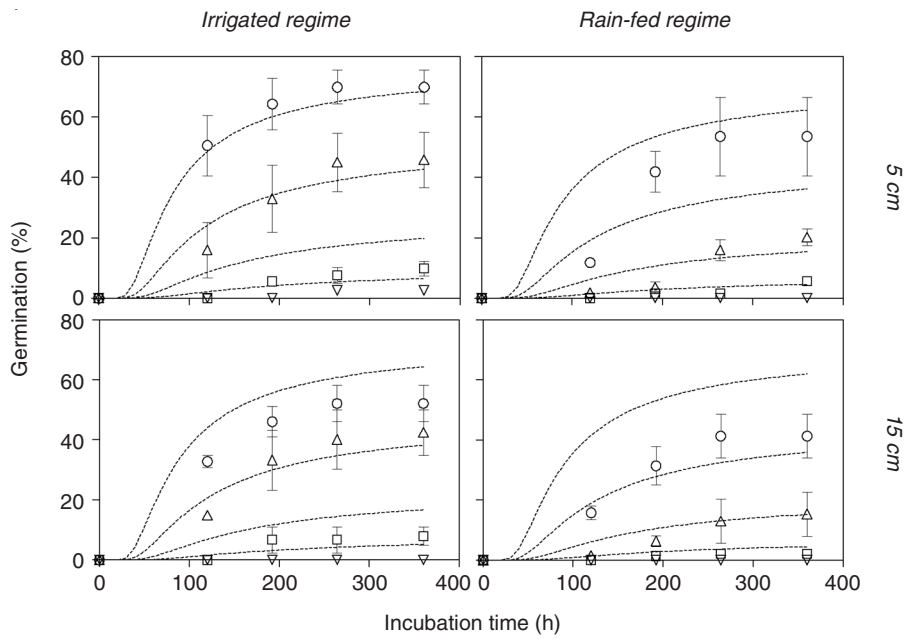

Figure 3. Predicted and observed germination time-course curves for seeds of *Polygonum aviculare*, buried at a depth of 5 or 15 cm, and subjected to a rain-fed or an irrigated water regime. Seeds were exhumed from the field in late winter (August) and incubated at 0 (○), –0.4 (△), –0.8 (□) and –1.2 MPa (▽) at 15°C for 15 d. Symbols represent observed germination percentages for seeds exhumed from the field, while the solid lines represent values predicted from simulation modelling for both panels. Vertical bars indicate standard errors (SE).

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substantial decrease of $\Psi_b(50)$ was observed for seeds stored at 7 and 12°C as stratification time progressed, allowing seeds stored at these higher temperatures to reach values of $\Psi_b(50)$ similar to those determined for seeds stored at 1.6°C towards the end of the storage period (Fig. 1A). Finally, seeds exhumed after 81 d of storage at any temperature showed a slow decrease of $\Psi_b(50)$ with further stratification, almost reaching a minimum constant $\Psi_b(50)$ value. These results agree with those obtained for *B. tectorum* by Christensen *et al*. (1996), who observed that changes in $\Psi_b(50)$ due to dry after-ripening at 20°C followed a negative exponential trend, where changes were more rapid early during after-ripening until a final 'fully after-ripened' $\Psi_b(50)$ constant value was attained. Further work with *B. tectorum* suggests that changes in $\Psi_b(50)$ through time under after-ripening conditions could also show a linear pattern (Bauer *et al*., 1998).

A progressive decrease of $\sigma_{\Psi b}$ was observed for seeds stored at 7 and 12°C during the dormancy loss process, while seeds stored at 1.6°C showed no consistent trend in this parameter (Table 1). On the other hand, θ_H varied little for seeds stored at 7 and 12°C, denoted by the low CV values (Table 1B and C). In contrast, seeds incubated at 1.6°C showed high variation in this parameter during the storage period (Table 1A). The low CV values obtained for θ_H and $\sigma_{\Psi b}$ during the stratification period, in relation to the higher values obtained for $\Psi_b(50)$, strongly suggest that dormancy loss in *P. aviculare* seeds would be characterized by a significant decrease of $\Psi_b(50)$, while the other parameters of the hydrotime model are relatively constant.

As observed previously for *P. aviculare* (Batlla and Benech-Arnold, 2003; Batlla *et al*., 2003), exposure to 22°C induced secondary dormancy in the seed population. In the present work, this was indicated by the shift of $\Psi_b(50)$ to more positive values.

Interestingly, the dynamics of $\Psi_b(50)$ for seeds stored at the three tested temperatures could be easily predicted using a unique function in relation to the thermal time index (S_{tt}) previously developed by Batlla and Benech-Arnold (2003) (Fig. 1B). This index was used satisfactorily to predict changes in the permissive thermal range for germination of a *P. aviculare* seed population, and in the sensitivity of *P. aviculare* seeds to alternating temperatures cycles, as dormancy loss progressed (Batlla and Benech-Arnold, 2003; Batlla *et al*., 2003). Other authors also used similar thermal time approaches to quantify the effect of temperature on seed dormancy loss (Christensen *et al*., 1996; Pritchard *et al*., 1996; Bauer *et al*., 1998; Meyer *et al*., 2000). Thermal time is a useful tool for modelling dormancy changes of weed seed banks exposed to the variable temperature environment under field conditions.

A negative exponential model was used to describe the $\Psi_b(50)$ decrease in relation to S_{tt} accumulation during dormancy loss (Fig. 1B). Choosing this model, instead of a more simple linear model, was supported by the facts that: (1) a linear model showed a lower adjustment to the data (R^2 = 0.79) than the exponential model (R^2 = 0.83) (data not shown); and (2) comparing the two modelling approaches (linear versus exponential) using Akaike's Information Criterion (AIC) (Burnham and Anderson, 1998) indicated that the exponential model had a probability of 87% of being correct.

Changes in $\Psi_b(50)$, while maintaining the other hydrotime parameters (θ_H and $\sigma_{\Psi b}$) constant, could account for most of the variation observed in germination time courses as seeds lost dormancy due to storage under stratification temperatures (Fig. 2). Previous efforts to model seed dormancy loss using $\Psi_b(50)$ as an index of the dormancy status of the seed population (Christensen *et al*., 1996; Bauer *et al*., 1998; Meyer *et al*., 2000) arrived at similar conclusions. These observations, together with the high CV value of $\Psi_b(50)$ in contrast with other parameters, support the present model assumptions of maintaining $\sigma_{\Psi b}$ and θ_H constant during seed stratification. However, although acceptable for modelling purposes, $\sigma_{\Psi b}$ and θ_H could also change during seed dormancy loss, particularly for seeds incubated at extremely low temperatures (i.e. 1.6°C) (Table 1A).

The developed model was used successfully to predict germination of seeds exhumed from irrigated field-plots at two different depths and incubated at constant 15°C under different water potentials (Fig. 3). These results suggest that the model could be used to predict seed dormancy loss under a variable temperature environment. However, the model failed to simulate germination of seeds exhumed from rain-fed plots (Fig. 3). Cycles of hydration–dehydration are known to affect dormancy status of many weed seeds (Hegarty, 1978; Egley, 1995), including *P. aviculare* (Batlla and Benech-Arnold, unpublished results). Seeds exhumed from rain-fed plots certainly had been subjected to soil water content fluctuations, particularly seeds buried at shallow depths (5 cm). This probably affected the dormancy status of buried seeds, leading to the inaccuracy of model predictions for seeds buried under the rain-fed condition.

In a previous paper, Batlla and Benech-Arnold (2003) characterized dormancy loss in *P. aviculare* seeds through changes in the thermal range permissive for seed germination. Results obtained in that work showed that the lower-limit temperature for germination of *P. aviculare* seeds diminishes linearly relative to S_{tt} accumulation during the entire storage period (0–1200°Cd). Results obtained in the present work showed that $\Psi_b(50)$ decreased during initial phases of seed stratification (from 0 to

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approximately 700°Cd), while $\Psi_b(50)$ remained almost constant with further S_{tt} accumulation. However, differences observed between dormancy loss assessed by changes in both seed population threshold parameters could probably be due to the fact that changes in $\Psi_b(50)$ in the present work were determined for seeds germinated at a single temperature (15°C). Previous results, showing that $\Psi_b(50)$ increased below and over the optimum germination temperature range (Dutta and Bradford, 1994; Kebreab and Murdoch, 1999; Allen *et al*., 2000; Alvarado and Bradford, 2002), suggest that changes in dormancy assessed by a decrease in $\Psi_b(50)$ would probably be expressed at lower or higher incubation temperatures as the thermal range for germination widens during seed dormancy loss.

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