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Temperature-dependent regulation of induction into secondary dormancy of *Polygonum aviculare* L. seeds: A quantitative analysis

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ABSTRACT

In seeds of many summer annuals low temperatures under moist conditions provoke dormancy release while high temperatures induce secondary dormancy. Seed dormancy level establishes the range of temperatures under which germination is possible. The range of temperatures permissive for seed germination is determined by two threshold limit temperatures: Lower limit temperature (T_l) and High limit temperature (T_h). Numerous studies have been conducted to characterize the effect of temperature on dormancy release, but there is very few information on how temperature regulates secondary dormancy induction. Seeds of *Polygonum aviculare* were stratified at 1.6, 5 and 10 °C until achieving a minimum dormancy, and then were induced into secondary dormancy by further storage at 10, 15, 20, 25 and 30 °C. Based on obtained germination time course-curves we quantified changes in the thermal range permissive for seed germination through variations in the mean lower limit temperature for seed germination ($T_{l(50)}$) using a mathematical simulation germination model. Our data suggest that induction into secondary dormancy in *P. aviculare* seeds can be assessed quantitatively through changes in $T_{l(50)}$. This changes could be described through a Dormancy Induction Thermal-Time Index (DI_{tt}), in which thermal time units are accumulated above a threshold temperature from which secondary dormancy is induced (7.9 °C). Additionally, the induction-rate into secondary dormancy was affected by the stratification temperature during dormancy release. We conclude that the effect of temperature on the rate of dormancy induction is not only dependent on prevailing temperature, but also on temperature experienced by seeds during previous dormancy release and the resulting dormancy status of the seed population.

1. Introduction

Seed dormancy has been defined as "an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions" (Benech-Arnold et al., 2000). Depending on the timing of occurrence, dormancy is classified in primary and secondary dormancy (Karssen, 1982). Primary dormancy refers to the innate condition presented by the seeds when they are dispersed from the mother plant (Bewley and Black, 1994). Secondary dormancy refers to a dormant state that is induced in non-dormant seeds, or re-induced in once-dormant seeds after a sufficiently low dormancy had been attained (Hilhorst, 1995, 1998). *Polygonum aviculare* L. (Knotgrass, yard knotweed) belongs to the Polygonaceae family and is a cosmopolitan common summer annual herbaceous weed of temperate climates (Holm et al., 1997). Under natural conditions, *P. aviculare* seeds tend to form persistent seed-banks in the soil and show cyclic changes in dormancy status according to the predominant season (Courtney, 1968; Baskin and Baskin, 1985, 1990; Forcella et al., 2000). *P. aviculare* seeds usually display a high dormancy level (primary dormancy) at the moment of dispersal which normally takes place at the end of the summer (Kruk and Benech-Arnold, 1998; Batlla and Benech-Arnold, 2003). This high dormancy level is evidenced by the fact that germination does not occur at any temperature in recently dispersed seeds (Batlla and Benech-Arnold, 2003). The seeds are released from dormancy if moistened, through the exposition to low temperatures (stratification); these conditions normally prevail in the soil during the months following dispersal (i.e. autumn and winter), thus determining a minimum dormancy level at the

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end of the winter which, in turn, may allow for emergence in the field (Courtney, 1968; Baskin and Baskin, 1998; Batlla and Benech-Arnold, 2003). During spring, those seeds that for different reasons did not germinate are exposed to the rising temperatures and induced into secondary dormancy thereby preventing germination until the seeds are again released from dormancy at the end of the next winter. As mentioned, these seasonal changes in dormancy level in *P. aviculare* seeds are mainly driven by temperature, though this effect is possibly modulated by other factors (i.e. the level of seed hydration).

Seed dormancy can vary over a continuous dormancy degree-scale between some point where dormancy is maximal and some other point where it is minimal (Batlla et al., 2004). The level of dormancy of a seed population establishes the width of the range of environmental factors that allows germination (Vegis, 1964). For example, as dormancy is relieved, the temperature range permissive for germination gradually widens until it is maximal while, as dormancy is induced, the range of temperatures under which germination takes place narrows until germination is no longer possible at any temperature and full dormancy is reached (Karssen, 1982; Bouwmeester and Karssen, 1992). Therefore, except for seed populations (or a fraction of a seed population) that display absolute dormancy and consequently do not germinate under any condition, dormancy is a relative phenomenon which, depending on the dormancy level of the seed population, can be expressed under certain temperatures but not at others (Hilhorst, 2007). In summer annual species like *P. aviculare,* changes in the temperature range for seed germination during dormancy release and induction are mainly a consequence of an increase or decrease, respectively, in the capacity of seeds to germinate at low temperatures, while germination at high temperatures can proceed even when the seeds still have high dormancy levels (Courtney, 1968) (Fig. 1A). The concepts of "lower limit temperature (T_l)" and "higher limit temperature (T_h)" introduced by Washitani (1987) can deal with this temperature-dependent expression of dormancy and have been extensively used in previous work with this species (Batlla and Benech-Arnold, 2003, 2015). When a seed population displays temperature-dependent expression of dormancy, final germination percentages decrease gradually as temperature departs from that one at which no (or less) dormancy is expressed, a temperature sometimes erroneously regarded as "optimum temperature". This gradual decrease can be regarded as a consequence of a different dormancy level in the individuals composing the population (Batlla and Benech-Arnold, 2015). This different dormancy level among individuals would be manifested as a different temperature at which dormancy starts to be expressed or, in words of Washitaniís equation, as a different "lower limit (T_l)" or "higher limit temperature (T_h)" (Fig. 1A). For this reason, it is considered that both T_l and T_h are normally distributed within the population, with mean $T_{l(50)}$ and $T_{h(50)}$ and their standard deviations σ_{Tl} and σ_{Th} respectively (Washitani, 1987; Kruk and Benech-Arnold, 1998, 2000; Batlla and Benech-Arnold, 2003) (Fig. 1). For the case of *P. aviculare*, Batlla and Benech-Arnold (2003) showed that during dormancy release (i.e. cold stratification at 0–10 °C), the range of temperature for seed germination widened as a consequence of a decrease in the lower limit for seed germination (T_l). This decrease has been shown to be linearly related to the accumulation of "stratification thermal time" (S_{tt}), an index built on the accumulation of cold temperatures below a threshold temperature above which dormancy release does not take place (Batlla and Benech-Arnold, 2003). Although the stratification temperature does not modify the relationship between dormancy release (assessed through changes in T_l) and S_{tt}, it does affect T_l distribution (σ_{Tl}) within the seed population, thus affecting the germination behaviour at temperatures close to the $T_{l(50)}$ of the seed population (Fig. 1 B, C) (Batlla and Benech-Arnold, 2003). During induction into secondary dormancy (which results from exposition to temperatures higher than 10 °C) the opposite as described in the case of dormancy release possibly occurs: a narrowing in the range due to an increase in $T_{l(50)}$ as shown preliminarily by Batlla and Benech-Arnold (2003). However, no research has been conducted to formally describe this relationship between $T_{l(50)}$ (and σ_{Tl}) and induction into secondary dormancy as a result of exposition to temperatures higher than 10 °C. Neither has been investigated whether the stratification temperature for dormancy release affects the rate of induction into secondary dormancy or not.

The aims of this study were (i) to establish a quantitative relationship between temperature, duration of exposition and induction into secondary dormancy in *Polygonum aviculare* seeds characterized by changes in $T_{l(50)}$, (ii) to investigate how the different stratification conditions during dormancy release affect the subsequent rate of induction into secondary dormancy. Since environmental control of induction into secondary dormancy and, in particular, its quantitative aspects, has been much less studied than dormancy release, this paper also intends to evidence and discuss the complexities of these responses.

2. Materials and methods

2.1. Seed collection

Seeds of *P. aviculare* (Knotgrass, yard knotweed) were collected in a wheat field located at Balcarce (latitude 37°45′ S, longitude 58°18′ W), Buenos Aires, Argentina, at the time of their natural dispersal (March 2013). After collection, the seeds were winnowed with a seed blower (Burrows model 1836-3, *Evanston, IL, USA*) to eliminate light seeds and stored (moisture content at harvest 12% fresh wet basis) in black glass jars in dry conditions at 20 °C for 30 days until the experiment commenced. At the beginning of the experiment, four replicates of 40 seeds were exposed to an initial germination test (see "Germination test") to quantify the initial level of dormancy of the population (observed germination <2%).

2.2. Thermal conditions during storage

2.2.1. Dormancy release

In May of 2013, groups of approximately 300 seeds were placed inside mesh nylon bags and buried at 4 cm depth in 8 cm diameter black plastic pots filled with soil (40%), sand (40%) and vermiculite (20%). Pots were irrigated to saturation and allowed to drain for 48 h, and were weighed to determine the weight corresponding to field capacity for each pot. The constancy of substrate moisture content was checked regularly during the experiment and the pots were re-weighed, and water was added until they reached their original weight to maintain their initial field capacity status. Trays with pots were stored at three stratification temperatures: 1.6, 5 and 10 °C. The seeds stratified at each temperature were exhumed when they had accumulated the same amount of stratification thermal time units (°Cd) according to the model proposed by Batlla and Benech-Arnold, (2003):

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

where S_{tt}, is stratification thermal time (°Cd), T_c is the dormancy release temperature (i.e. 17 °C, for *P. aviculare,* temperature at, or over which, dormancy release does not occur) and T_s is the daily mean stratification temperature (Batlla and Benech-Arnold, 2003).

The seeds were exhumed with the same accumulated S_{tt} units (i.e 500, 1000 and 1500 °Cd), four nylon mesh bags containing seeds (four replicates) were extracted from pots placed at each stratification temperature and tested for germination as described in section "Germination test". The soil temperature in the pots was

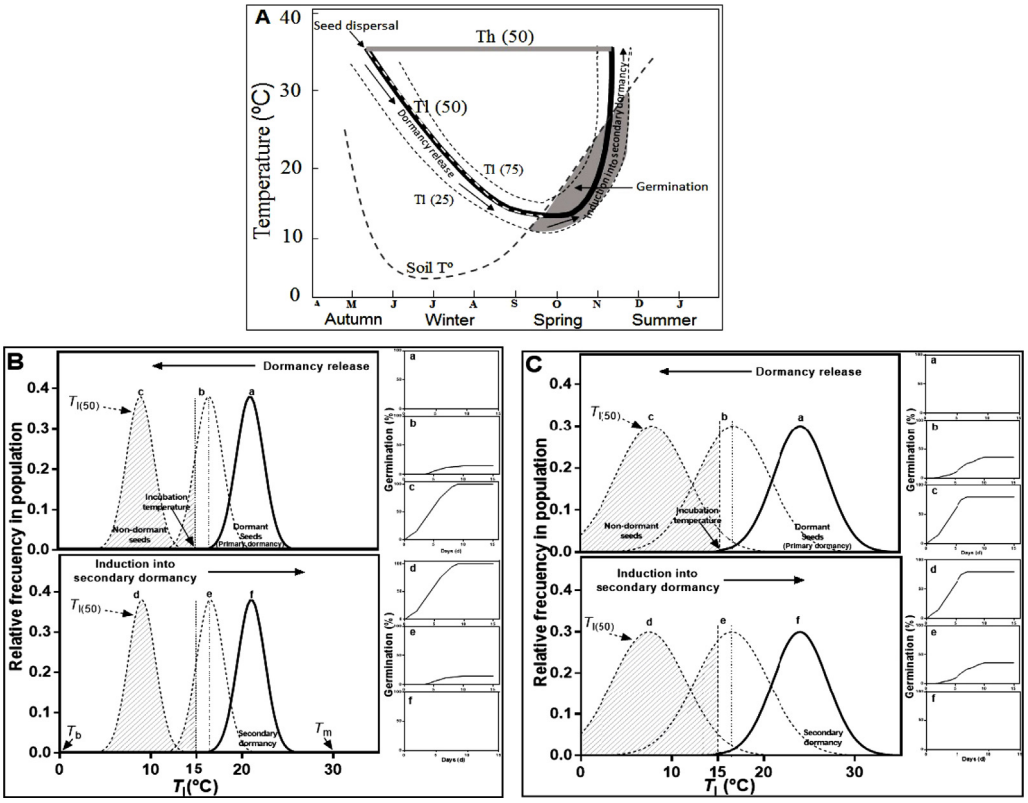

Fig. 1. (A) Schematic representation of seasonal changes in the permissive germination thermal range and its relation with soil temperature dynamics for *P. aviculare* seeds. Solid black lines indicate the mean lower ($T_{l(50)}$) and mean higher ($T_{h(50)}$) limits temperatures of the permissive thermal range allowing germination. Dashed black lines indicate T_l for the 25 and 75 seed population percentiles. Dashed gray line indicate the soil temperature (soil T°). The gray zone represents the moment when germination occurs once the soil temperature enters in the permissive thermal range. Black arrows indicate the lowering and increase in T_l during dormancy release and induction, respectively. (B and C) Schematic representation of changes in the normal distribution of T_l during dormancy release and dormancy induction. The solid and dashed lines curves are the normal distribution of T_l values among individual seeds, which is characterized by $T_{l(50)}$ and its corresponding standard deviation (σ_{Tl}), while the vertical dash line indicates the incubation temperature in the x-axis. The normal distribution shaded area represents the fraction of the population not expressing dormancy (those with a T_l lower than incubation temperature). Panels B and C show changes in the distribution of the T_l and its consequences on germination behaviour during dormancy release (higher panels) and dormancy induction (lower panels), for a seed population showing a $\sigma_{Tl(50)} = 1.5$ in panel B and $\sigma_{Tl(50)} = 4$ for panel C. Germination thermal parameters are indicated by arrows: base temperature for seed germination (T_b) = 0 °C, maximum temperature for seed germination (T_m) = 30 °C, optimum temperature for seed germination (T_o) = 20 °C.

recorded hourly during storage using temperature sensors (RC-30 B *Temperature Data Logger, Schwyz,* China).

2.2.2. Induction into secondary dormancy

To induce secondary dormancy, we used the trays with pots containing only seeds previously stratified at 5 °C that had reached a minimum dormancy level (accumulated 1500 °Cd according to Eq. (1)). Then, the trays with pots were stored at different temperatures (10, 15, 20, 25 and 30 °C) which, according to preliminary experiments (Malavert et al., 2014), induce secondary dormancy in *P. aviculare* seeds. At time intervals throughout the storage period (i.e. 10 °C = 0, 9, 14, 20, 27, 34 days; 15 °C = 0, 6, 13, 18, 24, 30 days; 20 °C = 0, 2, 4, 8, 12, 16 days; 25 °C = 0, 1, 3, 5, 7 days and 30 °C = 0, 1, 3 days), four nylon mesh bags containing seeds (four replicates) were exhumed from pots placed at each of the temperatures and tested for germination as described below, until no germination was observed (i.e. full dormancy). The soil temperature in the pots was recorded hourly during storage using temperature sensors (RC-30B *Temperature Data Logger, Schwyz,* China).

2.3. Germination test

Seeds were exhumed from the mesh bags under dim fluorescent green light and were rinsed with distilled water to remove adhered soil particles. Four replicates of 40 seeds were placed in 9 cm diameter Petri dishes containing 5 ml of distilled water on two discs of filter paper (Whatman No. 3). Then, the seeds were exposed to a saturating pulse of red-light (calculated proportion of phytochrome as Pfr [Pfr/Pt] = 87%, 35 μmol-m^{-2} s^{-1}) provided by red fluorescent tubes (Philips 40/15, Germany) for 20 min (Casal et al., 1991; Batlla and Benech-Arnold, 2005). After this, replicates were placed in germination chambers set at 10, 15, 20, 25 °C to determine the dormancy status of the seeds. Germinated seeds were counted every 2 days during 15 days. Seeds were exposed to white fluorescent light during germination counting, but otherwise were maintained in dark inside the germination chambers. The criterion for germination was radicle growth more than 2 mm and germinated seeds were removed after counting. Temperature in each germination chamber was recorded hourly using temperature sensors (RC-30B *Temperature Data Logger, Schwyz,* China).

2.4. Determination of thermal parameters that characterize the dormancy status of the population

Changes in seed dormancy status in summer annual species can be quantified by changes in the lower limit temperature (T_l) for seed germination, which is assumed to be normally distributed in the population with mean ($T_{l(50)}$) and standard deviation (σ_{Tl}). Therefore, these thermal parameters ($T_{l(50)}$ and σ_{Tl}) were used as an indicator of the dormancy status of the seed population (Washitani, 1987; Batlla and Benech-Arnold, 2015).

Germination time course-curves obtained in each sampling moment throughout the storage period at different temperatures (either at the end of the cold stratification treatment for dormancy release, or during induction into secondary dormancy through warm stratification) were analysed using the mathematical model proposed by Washitani (1987) and subsequently developed by Kruk and Benech-Arnold (1998, 2000) and Batlla and Benech-Arnold (2003). The model developed by Washitani was used as a tool to quantify changes in seed dormancy level. Model thermal parameters were derived by fitting simulated time-course cumulative germination curves to those obtained experimentally for seeds incubated at 10 and 15 °C (germination temperatures) during induction into secondary dormancy at 10, 15, 20, 25 and 30 °C. The model predicts germination dynamics of a seed population as a function of time and temperature and allows the estimation of two kinds of population thermal parameters in relation to germination observed data: 1) those describing the dormancy status of the seed population (i.e. mean lower limit temperature ($T_{l(50)}$) and mean higher limit temperature ($T_{h(50)}$) for germination and their standard deviations σ_{Tl} and σ_{Th}, and 2) those describing the relationship between germination rate and temperature of individual seeds. Model assumptions are as follows (Washitani, 1987):

(1) The fraction of seeds with lower limit temperature (T_l) and higher limit temperature (T_h) than prevailing temperature (T) can be given by the following distribution function:

$$G_i(T) = \left\{ \Phi \left[\left(T - T_{l(50)} \right) / \sigma_{Tl} \right] - \left\{ 1 - \Phi \left[\left(T - T_{h(50)} \right) / \sigma_{Th} \right] \right\} \right\} \quad (2)$$

where G_i is proportion of germinating seeds at a given temperature T and Φ is the normal probability integral.

(2) The temperature dependency of the mean germination rate (r) of individual seeds is assumed to be approximated by two linear equations with four germination parameters, i.e. T_b, T_o, T_m, and θ. The base temperature (T_b) is the temperature at or below which germination will not proceed. The optimum temperature (T_o) is the temperature at which germination is most rapid. The maximum temperature (T_m) is the temperature at or above which germination will not proceed, and (θ) is the thermal time required for germination.

for the suboptimal range,

$$r = 1/\theta \cdot (T - T_b) \quad (3)$$

while for the supraoptimal range,

$$r = 1/\theta * (T - T_b) \cdot \left[(T_m - T) / (T - T_o) \right] \quad (4)$$

The distribution of θ within a seed population can be described by the following distribution function:

$$F_t(\theta) = 1 - \left[3D^3 \left(\theta - m + D \right)^3 + 1 \right]^{-1/2} \quad (5)$$

where m is the median of the distribution, i.e. the required thermal time for the seeds that germinate at the cumulative percentage of 50%, and D is the differential thermal time between 0 and 50% germination.

To estimate seed population thermal parameters, it was assumed that T_b, T_o and T_m did not vary during the stratification period and subsequent induction, so fixed values of 0, 25 and 35 °C, respectively, were used for parameter optimization. These assumptions were based on previous reports for *P. aviculare* and other annual weed species, which suggested no variation of these parameters during different burial periods in the soil (Vleeshouwers, 1997; Bauer et al., 1998; Kruk and Benech-Arnold, 1998, 2000; Batlla and Benech-Arnold, 2003). On the other hand, values for other parameters (T_l, σ_{Tl}, T_h, σ_{Th} and θ) were allowed to vary over a reasonable range, based on previously reported data for *P. aviculare* or related summer annual species found in the literature (Washitani, 1987; Bouwmeester, 1990; Kruk and Benech-Arnold, 1998; Batlla and Benech-Arnold, 2003).

2.5. Evaluation of fit between observed and predicted data

Optimal thermal parameters for the germination model were obtained by a non-linear curve-fitting method using an optimization program (Solver for Nonlinear Programming 0.9, *Sun Microsystem, Inc.*). Maximum fit between simulated and experimentally obtained data was achieved by an iterative technique using a DEPS *Evolutionary algorithm*. The statistical criterion used for thermal parameters 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:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (X_{obs,i} - X_{model,i})^2}{n}} \quad (6)$$

where, X_{obs} is observed values and X_{model} is predicted values at time i.

2.6. Generation of the dormancy induction model

To mathematically describe the dependency on temperature of induction into secondary dormancy, a functional relationship between the induction timing in the seed population and temperatures that induce dormancy (10–30 °C) was established. As pointed out above, induction into secondary dormancy in *P. aviculare* seeds was quantified through changes in $T_{l(50)}$, so this thermal parameter was used as an indicator of the dormancy status of the seed population (Batlla and Benech-Arnold, 2003). The process of model development is summarized below:

(1) Determine seed population thermal parameters that maximize the fit between experimentally obtained germination time-course curves using the germination protocol described above for seeds induced into secondary dormancy at 10, 15, 20, 25 and 30 °C and simulated germination curves obtained from the mathematical germination model for each induction time.
(2) Characterize changes in $T_{l(50)}$ of the seed population over time for seeds induced into secondary dormancy at different temperatures; on the basis of this characterization, the responses at different temperatures were unified using a thermal time scale. The model does not consider significant changes in σ_{Tl} during dormancy induction.
(3) Validate model developed in (2) using data from an independent experiment data, as is explained below.

2.7. Evaluation of the model

Model performance was evaluated with an independent data set from experiments carried out under controlled temperature conditions. Seeds of *P. aviculare* were collected in Balcarce, Argentina during March 2014 at the time of natural dispersal. In September 2014, groups of approximately 200 seeds were placed inside nylon mesh bags and buried at 5 cm depth in pots (as in the treatments of storage conditions: Dormancy release section) and exposed to three stratification temperatures (1.6, 5 and 10 °C). Seeds were exhumed (four replicates per exhumation) after the accumulation of similar stratification units (i.e. 500, 1000 and 1500 °Cd) according to Eq. (1). After the seeds had accumulated 1500 °Cd (i.e. achieved a minimum dormancy level) they were induced into secondary dor-

Table 1
Estimated population thermal parameters for *P. aviculare* seeds during dormancy release at different stratification temperatures (1.6, 5 and 10 °C). Thermal parameters ($T_{l(50)}$, σ_{Tl}, $T_{h(50)}$, σ_{Th}) were obtained from germination experimental data at constant temperature of 10 and 15 °C through adjusting simulated germination curves for seeds stratified at 1.6, 5 and 10 °C that accumulated the same amount of stratification thermal time (S_{tt} = °Cd). Simulation was performed using the equation described in the germination model developed by Washitani (1987) (Eqs. (1)–(5)). It was assumed that T_b, T_o and T_m did not vary during the stratification period, so fixed values of 0, 25 and 35 °C, respectively, were used. A dash means that the estimation of population thermal parameters was not possible due to very low germination in the initial test (observed germination <2%). RMSE was calculated as an estimator of the goodness of curve fitting for the estimated thermal parameters (Eq. (6)).

Temp (°C)	S_{tt} (°Cd)	$T_{l(50)}$	σ_{Tl}	$T_{h(50)}$	σ_{Th}	*RMSE*
1.6	0	–	–	18	–	–
	500	14.5	1.5		1.8	39.5
	1000	12.5	1.5		0.9	41.2
	1500	7.5	1.5		0.8	10.1
5	0	–	–	18	–	–
	500	15.0	4		0.2	22.1
	1000	12.0	4		2.0	27.1
	1500	7.57	4		0.7	22.2
10	0	–	–	18	–	–
	500	15.1	5.2		2.0	21.8
	1000	12.6	5.2		0.8	37.7
	1500	7.53	5.2		0.6	27.3

mancy at 20 °C during 20d. During time at 20 °C seed germination at constant temperatures of 10 and 15 °C was tested (see "Germination test" section) at different time intervals (0, 2, 4, 8, 12 and 20d). The soil temperature in the pots was recorded hourly during storage using temperature sensors (RC-30B *Temperature Data Logger, Schwyz,* China). Germination time course-curves obtained from independent data during dormancy induction were used to evaluate the model performance.

3. Results

3.1. Seed population thermal parameters during release and induction into secondary dormancy

Germination dynamics at 10 and 15 °C for seeds that accumulated different amount of stratification thermal time according to Eq. (1) (0, 500, 1000 and 1500 °Cd) during stratification at 1.6, 5 and 10 °C are shown in Fig. 2. Increasing exposure to all three stratification temperatures resulted in a progressive increase in germination values and therefore, a progressive decrease in $T_{l(50)}$ was observed during stratification (Fig. 2; Table 1). At the end of the stratification period at the three temperatures (S_{tt} = 1500 °Cd), seeds achieved a "minimum" level of dormancy reaching the highest germination percentages at both tested germination temperatures and a low value of $T_{l(50)}$ = 7.5 °C (Fig. 2; Table 1); this point represents 0 days for all the experiments of induction into secondary dormancy.

For inducing seeds into secondary dormancy seeds previously stratified at 5 °C were stored at 10, 15, 20, 25 and 30 °C for different time periods. The germination percentage values observed for seeds exhumed at different times during storage and incubated at 10 and 15 °C were dependent on storage temperature (Fig. 3). Lower storage temperatures (10 and 15 °C) induced seeds into secondary dormancy more slowly than higher temperatures (20, 25 and 30 °C) (Slope test, *P-value* = < 0.0001, Fig. 4a). A temperature-dependent progressive increase in $T_{l(50)}$ was observed for seeds stored at all temperatures during dormancy induction (10–30 °C) while the values of σ_{Tl} showed just minor changes (Fig. 4a; Table 2). However, seeds stored at 10 °C displayed a different pattern of behaviour: during the first 20 days of storage the seeds were slightly induced into secondary dormancy (i.e. slight increase in $T_{l(50)}$); from there on and until 34 days of storage, dormancy release took place again, thus increasing the germination values (27d at 10 °C = 35%; 15 °C = 23% and 34d at 10 °C = 48%; 15 °C = 35%) and reversing the increase in the value of $T_{l(50)}$.

Table 2
Estimated population thermal parameters for *P. aviculare* seeds during dormancy induction at different temperatures of storage (10, 15, 20, 25 and 30 °C). Thermal parameters ($T_{l(50)}$, σ_{Tl}, $T_{h(50)}$, σ_{Th}) were obtained from germination experimental data at constant temperature of 10 and 15 °C through adjusting simulated germination curves for seeds induced into secondary dormancy at the different temperatures (10 °C–30 °C) and days. Simulation was performed using the equation described in the germination model developed by Washitani (1987) (Eqs. (2)–(5)). It was assumed that T_b, T_o and T_m did not vary during the induction into secondary dormancy, so fixed values of 0, 25 and 35 °C, respectively, were used. The day 0 represent the point with minimum dormancy level at the moment of induction. RMSE was calculated as an estimator of the goodness of curve fitting for the estimated thermal parameters (Eq. (6)). A dash means that estimation of population thermal parameters was not possible, due to zero germination in the germination test.

Temp (°C)	Induction days	$T_{l(50)}$	σ_{Tl}	$T_{h(50)}$	σ_{Th}	*RMSE*
10	0	7.5	4	18	0.8	22.2
	9	9.3	2.8		1.2	26.5
	14	11	4		1.0	27.6
	20	12.7	4.3		1.1	31.3
	27	12	4.6		1.1	28.4
	34	10.2	3.3		1.6	33.8
15	0	7.5	4	18	0.8	22.2
	6	10.8	3.4		0.8	31.9
	13	14.7	4.8		1.2	20.6
	18	15.6	4.6		0.6	23.3
	24	16.8	3.5		0.8	21.1
	30	17.7	4.1		1.3	19.2
20	0	7.5	4	18	0.8	22.2
	2	9.8	4.1		2.9	30.9
	4	12.4	3.8		2.9	31.0
	8	14.8	4		3.0	31.8
	12	16.5	4.6		1.8	19.8
	16	18	3.2		0.8	–
25	0	7.5	4	18	0.8	22.2
	1	10.2	4.7		0.9	41.6
	3	14.5	4.9		2.1	25.6
	5	17.1	4.5		1.6	28.4
	7	18	4.1		2.3	–
30	0	7.5	4	18	0.8	22.2
	1	12.5	4.3		3.6	14.4
	3	17.8	4.1		4.8	–

Model equations (Eqs. (2)–(5)) were able to give a good description of changes in germination curves during dormancy release (Fig. 2; Table 1). During dormancy induction, in contrast, model equations gave a good description of changes in germination curves but only for seeds incubated at 15 °C, while it underestimated germination at 10 °C (data not shown). This under-estimation could have been probably a consequence of the occurrence of dormancy release during incubation at 10 °C, as has been previously reported for *P. aviculare* by Batlla and Benech-Arnold (2015). When seeds are incubated at low temperatures, dormancy release during the incubation period might take place thus stimulating germination beyond what might have been expected if no changes had occurred in the dormancy status during incubation (Batlla and Benech-Arnold, 2015). In order to correct this situation, we simulated germination at 10 °C again, but considering that seeds accumulated a certain amount of stratification thermal time units (S_{tt}) during the incubation period according to Eq. (1). The accumulation of these S_{tt} units determined a decrease of $T_{l(50)}$ in relation to that previously considered without taking into account a dormancy release effect during incubation. Using this new value of $T_{l(50)}$ germination curves simulated by the model showed a better fit to changes in germination behaviour during dormancy induction for seeds incubated at 10 °C (i.e. simulation for 9d of induction at 10 °C showed an initial R^2 = 0.35, and with the correction an R^2 = 0.85) (Figs. 2 and 3). Over-

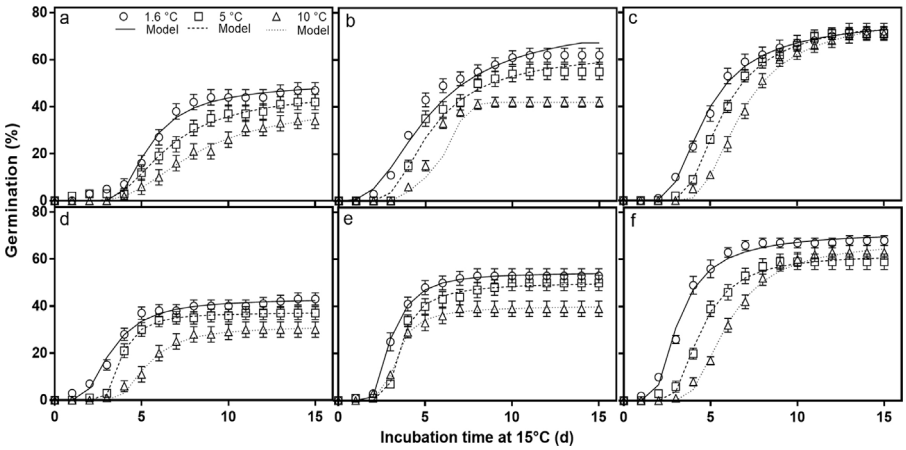

Fig. 2. Cumulative germination time course-curves at incubation temperatures of 10 °C (a, b and c) and 15 °C (d, e and f) for *P. aviculare* seeds stratified at 1.6 °C (◯), 5 °C (□) and 10 °C (Δ) that had accumulated different amounts of stratification thermal time: 500 °Cd (a, d), 1000 °Cd (b, e) and 1500 °Cd (c, f)). Solid and dotted lines represent germination curves simulated using equations described for the germination model developed by Washitani (1987) (Eqs. (1)–(6)). Vertical bars indicate standard error and where no bars are shown the value of standard error of the mean is less than the size of the symbol.

all, this demonstrates that the model is robust enough and supports the reliability of the thermal parameters than can be derived from it. Due to this multiple effect of 10 °C as an incubation temperature (i.e. effect on both dormancy release and germination rate), only parameters derived from incubations at 15 °C (i.e. $T_{l(50)}$ and σ_{Tl}) were used to construct the model described below.

3.2. Model of induction into secondary dormancy

A quantitative relationship between induction temperature, storage time and dormancy level was established for *P. aviculare* by assessing changes in $T_{l(50)}$ during induction into secondary dormancy (Fig. 4a). The quantification of thermal parameters obtained for seeds stratified at 5 °C and then re-induced into dormancy at 10, 15, 20, 25 and 30 °C, allowed the development of a simple thermal time model that is based on the accumulation of degree days above a threshold temperature for the induction into secondary dormancy to take place. This model is analogous to the model of stratification thermal time (S_{tt}) developed by Batlla and Benech-Arnold (2003). To account for the effect of induction temperatures on seed population dormancy status, changes in $T_{l(50)}$ were quantified as a function of the accumulation of Dormancy Induction thermal time units (DI_{tt}) according to the following equation:

$$DI_{tt} = Days \cdot (T_s - T_{uDI}) \quad (7)$$

where DI_{tt} is Dormancy Induction thermal time (°Cd), T_{uDI} is the threshold temperature for induction into secondary dormancy (temperature at or below which dormancy induction does not occur) and T_s is the daily mean storage temperature. Optimal T_{uDI} was obtained using different values of this parameter until the best fit of the bi-linear regression between $T_{l(50)}$ and DI_{tt} was attained. The best fit ($R^2 = 0.88$) between $T_{l(50)}$ and DI_{tt} was obtained with at $T_{uDI} = 7.9$ °C (Fig. 4b). With the following equation it should be possible to predict changes in $T_{l(50)}$ for *P. aviculare* population during induction into secondary dormancy:

$$T_{l(50)} = 0.12 \cdot DI_{tt} + 7.5 \quad (8)$$

where 7.5 °C is initial $T_{l(50)}$ for a seed population after the accumulation of $S_{tt} = 1500$ °Cd (i.e. with a minimum dormancy level).

3.3. Model performance

The performance of the dormancy induction model was evaluated using data from an independent experiment under controlled conditions in which the seeds were stratified at different temperatures (1.6, 5 and 10 °C) and afterwards induced into secondary dormancy at 20 °C during 20d (Fig. 5). To contrast model output against experimental independent germination data, changes in $T_{l(50)}$ during dormancy induction at 20 °C were simulated using equations of the dormancy induction model (Eqs. (7) and (8)). Once $T_{l(50)}$ values were estimated, changes in final germination percentages of seeds incubated at 10 and 15 °C for 15d during dormancy induction at 20 °C were predicted using the previously described germination model equations (Eqs. (2)–(5)). During the simulation of germination, the germination parameters values were assumed constant during dormancy induction, so fixed values of $T_b = 0$ °C, $T_o = 25$ °C and $T_m = 35$ °C (Washitani, 1987; Bouwmeester, 1990; Kruk and Benech-Arnold, 1998; Batlla and Benech-Arnold 2003, 2015). On the other hand, the model assumes that σ_{Tl} does not vary during dormancy induction, thus σ_{Tl} values obtained at the end of the stratification period at each temperature were maintained constant during the dormancy induction period for simulation. Independent experimental results showed that dormancy induction rate at a storage temperature of 20 °C was dependent on the temperature at which the seeds had been stratified: seeds previously exposed to low stratification temperatures (1.6 °C) displayed a higher dormancy induction rate than seeds that were stratified at higher temperatures (5 and 10 °C) (Figs. 6 and 7). The different values of σ_{Tl} (i.e. 1.6 °C [$\sigma_{Tl} = 1.5$], 5 °C [$\sigma_{Tl} = 4$] and 10 °C [$\sigma_{Tl} = 5.2$]) at the beginning of the induction process as a result of different stratification temperature were not modified during entrance in secondary dormancy (Table. 3). These differences between σ_{Tl} at the beginning of the induction process, together with the increase in $T_{l(50)}$ in seeds that had been stratified at 1.6, 5 and 10 °C (Fig. 7), determined that during the first four days of storage at 20 °C, the rate of induction into secondary dormancy was more rapid in seeds that had been stratified at low temperatures (i.e. 1.6 °C) than in those that had been stratified at high temperatures (i.e. 5 and 10 °C). This remarkable difference in the final germination percentage was clearly explained by the model, both from the shape (i.e. the value of σ_{Tl}) and the displacement of the $T_{l(50)}$ distribution for each storage condition (Fig. 7). These findings suggest that the temperature experienced by the seeds during dormancy release can affect the subsequent rate of induction into secondary dormancy and that these effects could be explained by changes in the σ_{Tl} for seed germination. These parameters could give an understanding of the nature of the effect of

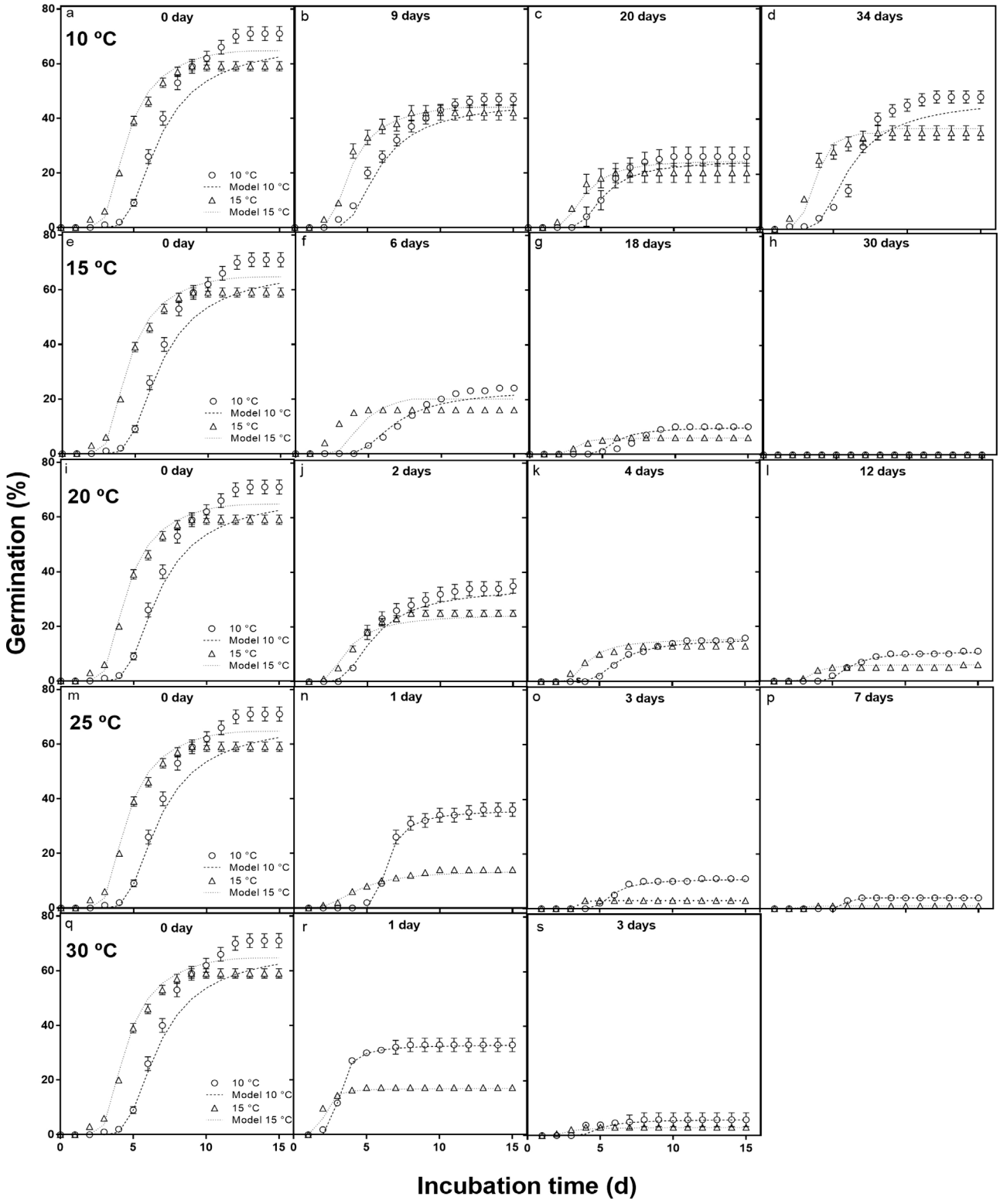

Fig. 3. Seeds of *P. aviculare* induced into secondary dormancy. Predicted (dotted line) and observed (symbols) germination time-course curves of seeds incubated at constant temperatures of 10 °C (○) and 15 °C (Δ) after different days of storage at 10 °C (a, b, c, d), 15 °C (e, f, g, h), 20 °C (i, j, k, l), 25 °C (m, n, o, p) and 30 °C (q, r, s). The panels were selected according to germination curves responses in function of days of induction into secondary dormancy. Previous to storage seed were stratified at 5 °C for 125 days (S_{tt} = 1500 °Cd). Germination data was simulated using equations from the germination model developed by Washitani (1987) (Eqs. (2)–(6)). Vertical bars indicate standard error and where no bars are shown the value of standard error of the mean is less than the size of the symbol.

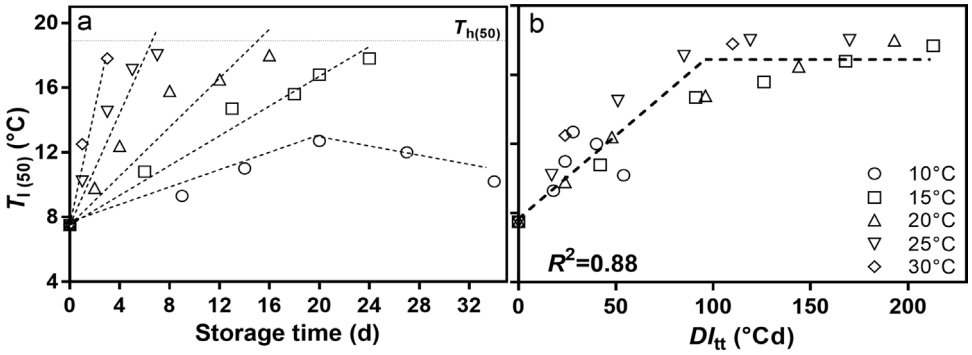

Fig. 4. Estimated values of the mean lower limit temperature ($T_{l(50)}$) for *P. aviculare* seeds stored at 10 °C (○), 15 °C (□), 20 °C (Δ), 25 °C (▽) and 30 °C (◊) (derived from the simulated curves shown in Fig. 2), plotted against days of storage (a), and against Dormancy Induction thermal time (DI_{tt}) (b). The dotted lines in (a) were fitted by linear equations for each storage temperature with R^2 values of 0.96 (10 °C), 0.99 (15 °C), 0.87 (20 °C), 0.89 (25 °C) and 0.96 (30 °C), respectively. *P-value* = < 0.0001, Slope test. The fitted bi-linear line in (b) is the result of repeated regression analysis to obtain the threshold 'dormancy induction temperature' (T_{uDI}) with the best fit according to Eq. (7). The value of parameters corresponding to Eq. (8) are slope ($T_{l(50)}$ increase rate) = 0.12 ± 0.0179 °C per °Cd and y- axis intercept (initial $T_{l(50)}$ of the seed population with minimum dormancy) = 7.5 ± 0.7 °C.

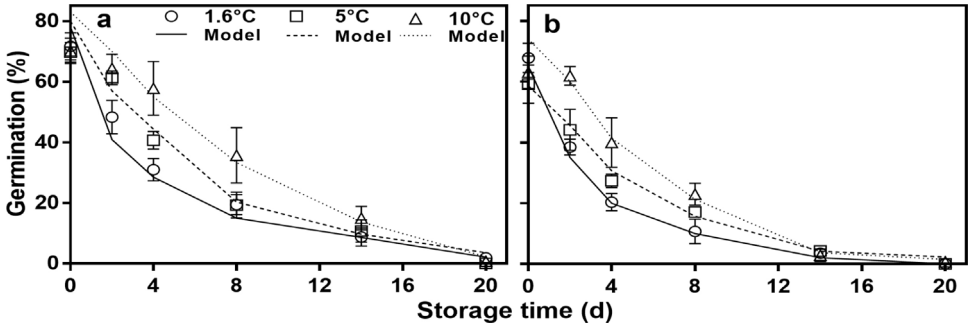

Fig. 5. Predicted (lines) and observed (symbols) final germination percentages at incubation temperatures of 10 °C (a) and 15 °C (b) for *P. aviculare* seeds previously stratified at 1.6 °C (○), 5 °C (□) and 10 °C (Δ) (S_{tt} = 1500 °Cd) and then stored at 20 °C for 20 days. Predicted values were simulated using the equations described in the germination model developed by Washitani (1987) (Eqs. (2)–(6)) for storage temperatures of 1.6 °C (solid line), 5 °C (dashed line) and 10 °C (dotted line). Vertical bars indicate standard error and where no bars are shown the value of standard error of the mean is less than the size of the symbol.

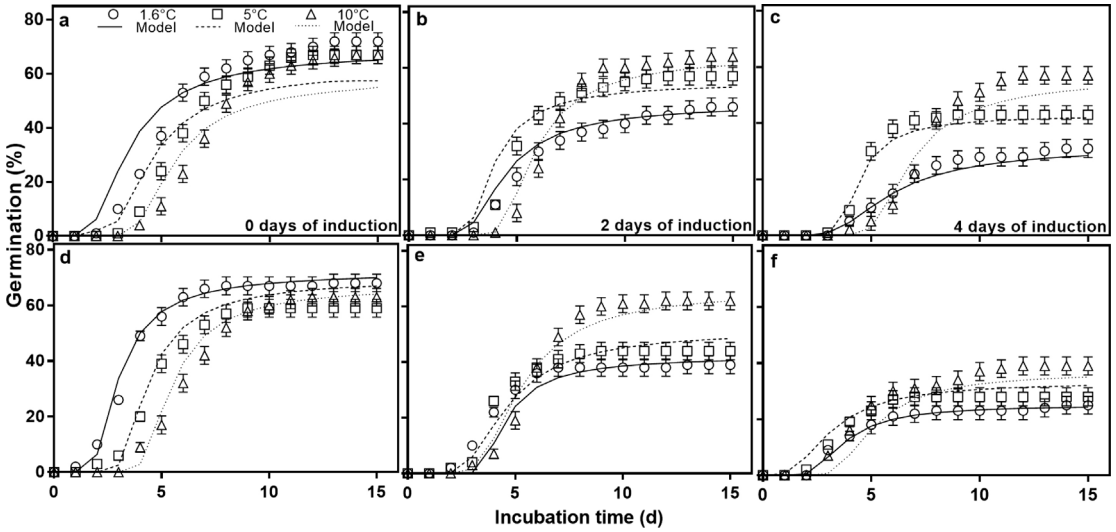

Fig. 6. Simulated germination curves with curves obtained from experimental data during the induction into secondary dormancy at 20 °C for *P. aviculare* seeds previously stratified at 1.6 °C (○), 5 °C (□) and 10 °C (Δ), using the germination test and the equations of the germination model developed by Washitani (1987) (Eqs. (2)–(6)). Predicted (solid and dotted line) and observed (symbols) germination time-course curves for *P. aviculare* seeds incubated at 10 °C (a, b and c) and 15 °C (d, e and f) after storage at 20 °C for 0, 2 and 4 days. Predicted values were simulated using the equations described in the germination model developed by Washitani (1987) (Eqs. (2)–(6)). Vertical bars indicate standard error and where no bars are shown the value of standard error of the mean is less than the size of the symbol.

previous stratification temperature on the rate of induction into secondary dormancy.

4. Discussion

Soil temperature has been regarded out as the main factor governing seasonal changes in dormancy status in *P. aviculare* seeds

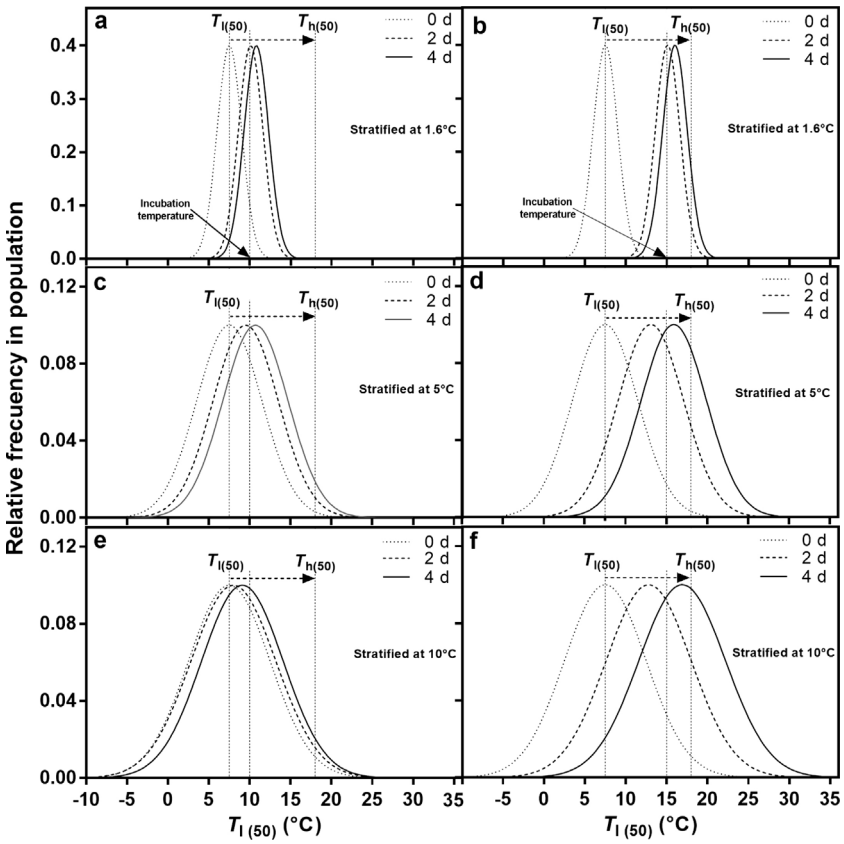

Fig. 7. Changes in the normal frequency distribution of T_l (lower limit temperature for seed germination) within a *P. aviculare* seed population during induction into secondary dormancy. Seeds were previously stratified at 1.6 °C (a, b), 5 °C (c, d) and 10 °C (e, f) until achieving a similar minimum dormancy level (accumulating S_{tt} = 1500 °Cd according to Eq. (1)), and subsequently induced into dormancy through storage at 20 °C for 2 and 4 days. Cero days of storage (first dotted bell shaped curve) correspond to seed population T_l values at the end of the stratification period. T_l values were obtained through simulation of germination time-course curves for seeds stored at 20 °C for 2 and 4 days and then incubated at 10 °C (arrow and vertical dashed line) or 15 °C (arrow and vertical dashed line). Simulations were performed using Eqs. (2)–(6). The initial value of $T_{l(50)}$ prior to storage at 20 °C was 7.5 °C for seeds stratified at all temperatures. The initial value of σ_{Tl} was 1.5, 4 and 5.2 for seeds stratified at 1.6 °C, 5 °C and 10 °C respectively, and were assumed not to change throughout the induction into secondary dormancy (i.e. 20 °C).

Table 3
Estimated population thermal parameters for *P. aviculare* seeds at the end of stratification periods at different temperatures (0 day, represent a point with minimum dormancy level (S_{tt} = 1500 °Cd)) and during induction into secondary dormancy through storage at 20 °C (2 and 4 days). Thermal parameters ($T_{l(50)}$, σ_{Tl}, $T_{h(50)}$, σ_{Th}) were obtained from germination experimental data at constant temperatures of 10 °C (panel **a**) and 15 °C (panel **b**) through adjusting simulated germination curves for seeds induced into secondary dormancy at 20 °C. Simulation was performed using the equation described in the germination model developed by Washitani (1987) (Eqs. (2)–(5)). RMSE was calculated as an estimator of the goodness of curve fitting for the estimated thermal parameters (Eq. (6)).

		(a) Ind at 20 °C (10 °C incubation temp)					(b) Ind at 20 °C (15 °C incubation temp)				
Temp S_{tt} (°C)	Days at 20 °C	$T_{l(50)}$	σ_{Tl}	$T_{h(50)}$	σ_{Th}	*RMSE*	$T_{l(50)}$	σ_{Tl}	$T_{h(50)}$	σ_{Th}	*RMSE*
1.6	0	7.5	1.5	18	4.3	1.1	7.5	1.5	18	4.2	2.7
	2	10.1	1.5	18	0.2	1.5	15.1	1.5	18	0.1	1.7
	4	10.7	1.5	18	0.1	1.6	16	1.5	18	0.1	8.8
5	0	7.5	4	18	0.4	2.4	7.5	4	18	0.4	2.6
	2	9.1	4	18	0.1	1.3	13.4	4	18	4.5	1.6
	4	10.5	4	18	0.2	2.7	16.7	4	18	4.7	2.3
10	0	7.5	5.2	18	3.5	6.6	7.5	5.2	18	3.5	2.3
	2	7.8	5.2	18	1.2	3.2	12.8	5.2	18	4.9	14.3
	4	8.7	5.2	18	4.8	6.5	16.9	5.2	18	2.9	10.8

under field conditions (Courtney, 1968; Kruk and Benech-Arnold, 1998; Benech-Arnold et al., 2000; Batlla and Benech-Arnold, 2003). These seasonal changes in dormancy status are related to changes in the range of environmental conditions within which seeds are able to germinate (Bouwmeester and Karssen, 1992; Vleeshouwers and Kropff, 2000; Bewley et al., 2013). Although several germination models have been developed in order to predict the occurrence of weed emergence with some accuracy as a function of temperature, seldom they consider changes in seed dormancy level; this is mostly due to the difficulty in assessing dormancy quantitatively (Bouwmeester, 1990; Bouwmeester and Karssen, 1992, 1993; Kebreab and Murdoch, 1999). For example, in some works, final germination percentage at a certain stage is regarded as a quantification of dormancy; this leads to serious mistakes since this value not only changes with dormancy but also with the incubation temperature. Indeed, dormancy is a relative phenomenon and it is differentially expressed in different fractions of the seed population depending on the incubation temperature (Batlla and Benech-Arnold, 2015). The concepts of "lower limit temperature (T_l)" and "higher limit temperature (T_h)" introduced by Washitani (1987) can deal with this incubation temperature-dependent expression of dormancy and have been extensively used in previous work with

P. aviculare as a way of assessing dormancy quantitatively (Batlla and Benech-Arnold, 2003). In this way, as seeds are released from dormancy, $T_{l(50)}$ gradually decreases thus denoting the increasing capacity of the population to germinate at low temperatures (Batlla and Benech-Arnold, 2003; Arana et al., 2015). Winter annual species show the reverse dormancy pattern (changes in dormancy level result from fluctuations in $T_{h(50)}$), driven upwards by high temperatures during the summer and downwards leading to secondary dormancy by low temperatures during the winter (Baskin and Baskin, 1976; Karssen, 1982; Probert, 1992).

In this paper we show that induction into secondary dormancy of *P. aviculare* seeds can be also assessed quantitatively through changes in $T_{l(50)}$. Hence, after attaining a "minimum" dormancy level evidenced by a low $T_{l(50)}$ (Table 1; Fig. 2), if seeds are exposed to temperatures above 10 °C, $T_{l(50)}$ increased rapidly until reaching values close to $T_{h(50)}$ (i.e. dormancy is expressed at all temperatures, a situation that can be regarded as a functional definition of "absolute dormancy") (Table 2; Fig. 3). Our results also show that the rate with which $T_{l(50)}$ increased, depended on the temperature to which the seeds were exposed for inducing entrance into secondary dormancy: the higher the temperature the higher the rate of increase of $T_{l(50)}$ (Fig. 4a). The release of dormancy through stratification temperatures in this species was also shown to be temperature-dependent as $T_{l(50)}$ decreases more rapidly (i.e. seeds were released from dormancy at a higher rate) if stratification temperatures are well below a threshold temperature of 17 °C at or above which dormancy release does not take place (Batlla and Benech-Arnold, 2003). The identification of this threshold temperature allowed the development of a "Stratification Thermal Time Index" (S_{tt}); changes in $T_{l(50)}$ were linearly and negatively related to the accumulation of S_{tt}. This relationship is a formal description of changes in dormancy as a function of the thermal environment and can be incorporated to predictive models of *P. aviculare* (Batlla and Benech-Arnold, 2003). In an analogous way, the dependency on temperature of the induction into secondary dormancy could be described formally in this work through: i) the identification of a threshold temperature for secondary dormancy to be induced (7.9 °C); ii) the development of a Dormancy Induction Thermal Time Index (DI_{tt}); iii) the establishment of a bi-linear and positive relationship between $T_{l(50)}$ and the accumulation of DI_{tt} (Fig. 4b). Together, these two thermal time indexes (S_{tt} and DI_{tt}) can be used to assess quantitatively the relationship between temperature and dormancy changes during both release and induction to dormancy, thus allowing to determine the range of temperatures permissive for germination as a consequence of changes in $T_{l(50)}$. In other words, dormancy cycling in the field could be adequately predicted with the combined use of these two indexes. In fact, their performance has been validated against independent data but separately: S_{tt} by Batlla and Benech-Arnold (2003) and DI_{tt} in this paper (Fig. 5).

Thresholds might be expected to vary between summer annual species and even between populations of the same species growing in different environments. The value of the threshold 'dormancy induction temperature' (T_{uDI}) identified in this work was 7.9 °C. This means that seeds would be induced into secondary dormancy if temperature is higher than this value with a rate that would be higher the higher the temperature. Similar threshold values were reported by Batlla et al. (2009) and by Vleeshouwers and Bouwmeester (2001), who determined a minimum value for dormancy induction (the value below which dormancy induction does not occur) of 8.1 °C and 8.9 °C, for *Polygonum persicaria* and *Chenopodium album*, respectively. Surprisingly, this threshold value of 7.9 °C for dormancy induction is well below the threshold temperature for dormancy release which had been determined by Batlla and Benech-Arnold (2003) to be 17 °C. This implies the existence of a temperature range between 7.9 °C and 17 °C within which both processes, dormancy release and induction, take place at the same time. Indeed, not only we were forced to correct $T_{l(50)}$ values when attempting to simulate germination curves of seeds that during the induction into secondary dormancy were incubated at 10 °C (Figs. 3 and 6; Tables 2 and 3), but also induction into secondary dormancy at 10 °C was reverted with further storage at this temperature after a sufficiently "high" dormancy was attained (Fig. 4a). Taken together these results suggest that the relative strength of each process (i.e. dormancy release or dormancy induction) within this temperature range depends, not only on the storage temperature, but also on the dormancy status of the seeds. In this way, when seeds that had begun to enter secondary dormancy were evaluated at 10 °C, this temperature not only drove germination but also had a dormancy release effect which needed to be considered through corrections in $T_{l(50)}$. Similarly, when seeds with a minimum dormancy level were stored at 10 °C, dormancy induction prevailed until the seeds had "enough" dormancy and, from there on, the same temperature promoted dormancy release (Figs. 4a; 8). The idea of induction and release dormancy processes taking place simultaneously at certain temperatures was first proposed by Totterdell and Roberts (1979). More recently, Batlla et al. (2009) and Batlla and Benech-Arnold (2015) suggested that competing forces (i.e. dormancy release, dormancy induction, germination) might be operating at certain temperatures. However, the possibility that the relative strength of these competing forces also depends on the dormancy status of the population is demonstrated for the first time in this paper (Fig. 8).

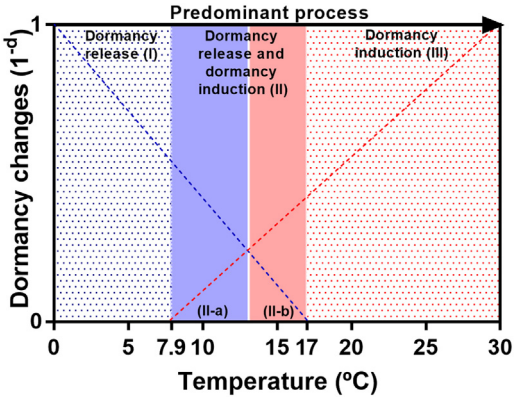

Fig. 8. Conceptual model representing the different processes affecting dormancy level which occur in *Polygonum aviculare* seeds depending on temperature. Zone (I) – Between 0 °C and 7.9 °C dormancy release is the only process taking place. Zone (II) – Between 7.9 °C and 17 °C the two processes (dormancy release and induction into secondary dormancy) can occur. One process will predominate over the other depending on dormancy status and stratification temperature within this range. Therefore, two sub-zones can be identified within this zone (1) – (II-a) A zone where dormancy release is stronger than the induction into secondary dormancy (dim blue zone) and (2) – (II-b) is a zone where the induction into secondary dormancy is stronger than dormancy release (dim red zone). Zone (III) – Above 17 °C induction into secondary dormancy is the only process taking place. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Interestingly enough, our results also show that the induction rate into secondary dormancy is affected by the stratification temperature previously experienced by the seeds during dormancy release, even when the seeds had accumulated the same amount of S_{tt} (in °Cd units) and, consequently, had reached similar $T_{l(50)}$ (Fig. 6; Table 3). These differences in induction rate can be explained to an important extent by the different values of σ_{Tl} observed for seeds stratified at different temperatures before storage under dormancy inductive temperatures; it should be noted that the model assumed that this initial σ_{Tl} does not change during dormancy induction. The different values of σ_{Tl} (i.e. different distribution of $T_{l(50)}$ within the seed population) restrict the fraction of seeds able to germinate as the distribution of $T_{l(50)}$ moves toward higher values during dor-

mancy induction (Fig. 7). Under field conditions this implies that the rate of induction into secondary dormancy due to temperature increase during spring-early summer, would depend on the winter temperatures at which dormancy release occur; the lower the winter temperature the higher the rate of induction at a certain spring thermal scenario.

In the present work we not only developed a model able to predict how the thermal range permissive for seed germination narrows during dormancy induction depending on time and temperature, but we also provide an approach to understand the complexity of the regulation of seed dormancy status by temperature. The obtained results showed that the effect on the rate of dormancy induction was not only dependent on prevailing temperature, but also on temperature experienced by seeds during previous dormancy release and the dormancy status of the seed population.

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