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Dormancy, germination and emergence of *Urochloa panicoides* regulated by temperature

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Summary

Urochloa panicoides is an annual weed of summer crops. In Argentina, in subhumid areas with monsoon rainfall, it germinates and establishes in a single flush. To (i) identify the environmental factors that modify its seed dormancy level and germination and (ii) quantify the parameters describing the thermal behaviour of the germination and emergence dynamics of this weed under non-limiting water conditions, we established a set of germination experiments performed (i) under controlled conditions using seeds after ripened for 3 or 6 months in different thermal and hydric conditions and (ii) under field conditions, where the soil temperature was modified by applying different shading levels. Seed dormancy level remained high with 3 months after ripening in all treatments. After 6 months, seeds stored at 4°C in dry conditions did not germinate at any temperature, while seeds stored at 25°C in dry conditions and *in situ* germinated *c*. 20% and 60% respectively. Germination percentage was higher in seeds harvested before their natural dispersal. The base, optimum and maximum temperatures for seed germination were 6, 35 and 45°C respectively. Shading reduced the number of emerged seedlings, possibly by reducing the soil thermal amplitude. The results explained the dormancy-breaking mechanism of *U. panicoides* that allows a high germination rate in the field when rainfall occurs.

Keywords: Liver seed grass, after-ripening condition, base temperature, dormancy release, thermal amplitude, thermal time.

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Introduction

Urochloa panicoides P. Beauv. (liver seed grass), which is native to Africa, has become naturalized in central and north-western Argentina (Morrone & Zuloaga, 1992). It is an annual weed of soya bean (*Glycine max* (L.) Merr.) and maize (*Zea mays* L.) crops and has recently increased its abundance in agricultural fields of central Córdoba, Argentina. In Australia, biotypes resistant to atrazine (Adkins *et al*., 1997) and glyphosate (Boutsalis & Preston, 2008) have been confirmed. Knowledge of the dynamics of germination and establishment of *U. panicoides* and of the factors that regulate these processes is crucial for optimization of long-term weed control. However, there is little information of the bioecology of this species. It is thus necessary to determine the factors that cause changes in the level of seed dormancy, identify the environmental conditions necessary for germination and establish functional relationships between the germination rate and environmental factors (Benech-Arnold & Sánchez, 1995). Walker *et al*. (2010) observed that, in subtropical

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Australia, *U. panicoides* emerges in a single flush that coincides with the onset of precipitation in spring and that the persistence of seeds on the soil surface is very low.

In the field, weed seedlings emerge when seeds reach a low level of seed dormancy (Probert, 1992) and environmental conditions (moisture and aeration) are favourable for germination (Benech-Arnold *et al.*, 2000). It is accepted that the low temperatures of winter are responsible for reducing the level of dormancy in spring–summer seeds and that the high temperatures of late spring and early summer induce increases in the level of seed dormancy (Bouwmeester & Karssen, 1992). However, these responses are complex and low temperature may not be the only factor involved in dormancy breaking in all summer weeds. For example, seeds of *Portulaca oleracea* L. have low seed dormancy at the end of winter, but incubating seeds at low temperatures under controlled conditions does not reduce the level of seed dormancy during the same period, showing that other factors interact in weed dormancy breaking (Kruk & Benech-Arnold, 1998). It has also been observed that high temperatures do not induce secondary dormancy in *P. oleracea*, but rather cause the opposite effect and that the effect of temperature on the level of seed dormancy can be modulated by soil moisture (Kruk & Benech-Arnold, 1998, 2000). Moreover, once they have reached a low dormancy level, most weed seed populations require the termination of dormancy through exposure to light (Kruk *et al.*, 2006) and/or fluctuating temperatures (Thompson *et al.*, 1977).

Once the requirements described above are satisfied, the germination rate becomes predictably modulated by temperature (Forcella *et al.*, 2000). In non-dormant seed populations under non-limiting water conditions, the percentage of germination and emergence of a particular species can be predicted by the thermal time accumulated above a base temperature. Thermal time models have been used to predict the emergence of seedlings and sprouts of various weeds, which improving weed control efficiency and efficacy (Ghersa *et al.*, 1990; Grundy, 2003; Leguizamón *et al.*, 2005; Izquierdo *et al.*, 2013). Using a thermal time (TT) approach to predict weed dormancy breaking and emergence requires estimating the base temperature (T_b), the optimum temperature (T_o), the maximum temperature (T_m) and the thermal time required for germination or emergence (TT_g) of a certain fraction of the seed population. Different methods have been established to quantify these parameters (Arnold, 1959; Washitani, 1987; Steinmaus *et al.*, 2000). The objective of this work was to determine the thermal conditions that modify the seed dormancy level in *U. Panicoides* and to quantify the parameters that describe the thermal behaviour of the dynamics of germination and emergence of this weed under non-limiting water conditions using several methodologies.

Materials and methods

Germination experiments were carried out (i) under controlled conditions using seeds after-ripened under different conditions and different time intervals and (ii) in a field experiment under semicontrolled conditions, where the soil temperature was modified by applying different levels of shading.

Experiments under controlled conditions

Two germination test systems were used: (i) by exposing seed lots to gradual changes in temperature from 4°C to 36°C (*IT-regime*) or from 36°C to 4°C (*DT-regime*) in steps of 4°C as proposed by Washitani (1987) and (ii) by exposing seeds to different constant temperatures.

Germination test system using gradual changes in temperature regimes

Urochloa panicoides panicles were collected from production plots at the National Institute of Agricultural Technology (INTA), Manfredi Experimental Station (31°41′S, 63°46′W), Argentina, during January 2008 (i.e. early summer). These panicles were shaken to release the seeds, which were classified as *dispersed seeds* and *undispersed seeds*, depending on whether or not they had fallen off the panicle. In addition, seeds were also collected *in situ* from the soil surface, which had suffered a severe weed infestation the previous summer (*natural seedbank*) in late August (i.e. late winter). The seeds were subjected to an updraft of air to remove empty seeds. A random sample of high-weight fraction full seed was then selected and evaluated by a tetrazolium test to determine the percentage viability. Seeds were sliced longitudinally and incubated in 0.1% tetrazolium chloride solution for 24 h in the dark at 30°C (ISTA, 1996). Seeds with pink- or red-stained embryos were considered viable. After collection, seeds were bulked and stored in paper bags at room temperature (*c.* 20°C) until they were used for the experiments in February.

After-ripening treatments

Before the germination tests, dispersed seeds were stored under different conditions: (i) dry storage at 25°C in paper bags; (ii) dry storage at 4°C in paper bags; (iii) moist chilling at 4°C on filter paper in Petri

dishes; (iv) *in situ*, on the soil surface under crop residues, where soil temperature and moisture conditions prevail; to this end, the seeds were placed inside transparent polyester 3 cm × 5 cm mesh envelopes with 0.5 mm × 0.5 mm openings, so as to generate a microenvironment within the envelope similar to that of their soil surroundings (adapted from Washitani & Masuda, 1990); and (v) immediately after seed dispersal without any pre-treatment ('initial test'). Seeds were stored under the above-mentioned conditions for 3 and 6 months. The soil temperature under the crop residues was recorded using sensors connected to a data logger (TEMPLOGGER- Cavadevices, Buenos Aires, Argentina) throughout the after-ripening period. Rainfall during the same period was determined from a meteorological station located 800 m from the experiment. Undispersed seeds were only subjected to after ripening in the field on the soil surface under the same conditions as those of dispersed seeds. The percentage of seeds found germinated *in situ* after each exhumation was never higher than 1%.

The germination test system (Washitani, 1987) consisted in exposing one batch of seeds to gradually increasing temperatures from 4°C to 36°C in steps of 4°C (*IT-regime*) and a second batch to gradually decreasing temperatures from 36°C to 4°C (*DT-regime*). As the germination rate is generally higher at higher temperatures in the physiological range, the duration of exposure differed depending on the prevailing temperature: 7 days at 4°C and 8°C, 5 days at 12°C and 16°C, 4 days at 20°C and 24°C, 3 days at 28°C and 2 days at 32°C and 36°C (modified from Kruk & Benech-Arnold, 1998, 2000). The number of germinated seeds was recorded immediately before a temperature change and at the end of the test. The germinated seeds were counted and then removed. The criterion to determine seed germination was radicle protrusion. Four replications of 25 seeds were allocated to each regime (*IT* and *DT*). Seeds were placed on three disks of Whatman N°3 filter paper, with 5 mL of distilled water in 9-cm-diameter Petri dishes, and then exposed to white light during counting or otherwise kept in the dark, inside incubators.

The remaining ungerminated seeds were later exposed to 25°C and daily alternating temperatures of 20°C [12 h]/30°C [12 h] for 7 days at the end of the *DT-* and *IT-regimes* respectively (Kruk & Benech-Arnold, 1998). The germination percentage attained immediately before seeds were incubated at either 25°C or 30°C/20°C was defined as 'final germination percentage' at that regime, while that attained after incubation at 25°C or 30°C/20°C was defined as 'maximum germination percentage'. With this methodology, germination curves were obtained as a function of seed dormancy level and temperature. At the end of the germination test, ungerminated seeds were evaluated by a tetrazolium test. Seed viability was 85–90%, except for seeds stored at 4°C in wet conditions that showed a significant loss of viability, independently of storage duration.

The thermal parameters were quantified using the mathematical model described in detail by Washitani (1987). The model predicts the germination dynamics of a seed population as a function of time and temperature. Thus, germination time–course curves obtained with the above-mentioned screening system were reproduced by simulating the performance of *dispersed seeds* under the prevailing soil temperature conditions and that of seeds from the *natural seedbank* collected 6 months after the beginning of the after-ripening treatment. To run the model for simulation of the germination curves obtained with the germination test, values for the mean lower limit temperature (T_l) and the mean higher limit temperature (T_h) of the thermal range within which 50% of the seed population germinates, T_b, T_o, T_m and TTg_{50} were given *a priori* to the programme. The programme relating the equations of the germination model previously mentioned (Washitani, 1987) was developed in the Squeak Smalltalk computing environment (Batlla & Benech-Arnold, 2003) and is a modified version of that previously developed in DOS language (Kruk & Benech-Arnold, 1998). This version has an optimization module, which optimizes the values for each of the thermal parameters of the seed population to maximize the fit of simulated curves with experimentally obtained ones. Optimization is achieved by a dynamic hill-climbing global optimization algorithm (Russell & 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.

The model (Washitani, 1987) estimated two kinds of thermal parameters of the seed population in relation to the observed data: (1) the dormancy level of the seed population and (2) the relationship between the germination rate and the temperature of non-dormant seeds. The dormancy level of the seed population can be characterized by (i) the final germination percentage obtained with the different treatments and after-ripening periods and (ii) the temperature range within which 50% germination occurs. This range is determined by T_l and T_h. As it is considered that both temperature limits are normally distributed within the seed population, the mean values of these limits were estimated, together with their standard deviations (σ_{Tl}

and σ_{Th}). Within the range that allowed germination, the parameters that describe the relationship between the temperature and germination rate of individual seeds can be approximated by two linear equations with four parameters: T_b, T_o, T_m and TT_g.

Germination test system using regimes of constant temperature

To complement the information generated with the methodology previously described, the seeds collected from the soil surface in August 2008 (*natural seedbank*) and stored in paper bags at room temperature (between 10 and 25°C) until the beginning of the experiment were incubated at constant temperatures of 9, 15, 25 and 34°C.

In June 2009, four replications of 50 seeds were placed on three disks of Whatman N°3 filter paper, with 5 mL of distilled water in 9-cm-diameter Petri dishes. The number of germinated seeds was counted daily and germinated seeds were subsequently removed until no germination was observed for seven consecutive days. The seeds that had not germinated at any test temperature were exposed to 25°C for a week as the highest percentage of germination was achieved at this temperature. At the end of the germination test, 85% of the ungerminated seeds were viable after the tetrazolium test.

The time (days) at which 30%, 50% and 70% of germination occurred was estimated for each temperature by nonlinear regression. The germination rate was plotted against temperature for each subpopulation. With this information, T_b was estimated by a linear regression model, with the germination rate as a dependent variable and temperature as an independent one, and determined by the intersection with the *x*-axis (Steinmaus *et al.*, 2000).

Emergence of Urochloa panicoides under different levels of shading in the field

The experiment was conducted in a field at INTA Manfredi Experimental Station in 2008, on a silty-loam soil with pH 6.5 and organic matter content of 2.5% in the superficial horizon. The field had shown high infestation of *U. panicoides* the previous year. Black plastic mesh of varying density was applied to reduce the incident solar radiation reaching the soil surface and thus decrease the soil temperature range without causing changes in light quality. The treatments were (i) bare soil (control, with no plastic mesh); (ii) 70% of incident solar radiation on the soil surface and (iii) 20% of incident solar radiation on the soil surface.

Tunnels of metal structure (1.5 m long, 1 m wide and 0.6 m high) oriented north–south, covered by a black plastic mesh, according to the treatments, were installed on 15 September 2008. Radiation was measured at midday above and immediately below the black plastic mesh in each experimental unit with a radiometer (RAD Cavadevices BAR-100, Buenos Aires, Argentina) connected to a data logger. The reduction of radiation due to the effect of the plastic mesh was calculated as follows:

$$\text{Reduction}(\%) = \frac{\text{Radiation above - Radiation below}}{\text{Radiation above}}(100) \quad (1)$$

The design was a randomized complete block with three replications. Emerged seedlings of *U. panicoides* were *counted weekly during the* first 30 days and then every 20 days and removed after each count. The experiment was irrigated weekly so that moisture was not a limiting factor for germination and emergence. The soil temperature at 1 cm depth was recorded daily, in two of the three replicates of each treatment, using sensors connected to a data logger (TEMPLOGGER). All measurements were conducted in an area of 1600 cm^2 (40 × 40 cm) in the centre of the tunnels.

The cumulative relative emergence (CRE, proportion of plants emerged in each period with respect to the total number of plants emerged in each treatment) was quantified and modelled both as a function of the number of days from the beginning of the field experiment and as a function of the TT accumulated for each date as a predictor. For this, TT (d °C) was calculated as the sum of the difference between the daily mean temperature of the soil (average of the hourly records of temperature data loggers) and T_b (Eqn 2) from the beginning of the test (15 September). Because there was no rainfall as late autumn, the accumulation of TT was initiated after the completion of the first irrigation.

$$TT = \sum_{i}^{n}(T_{med} - T_b) \quad (2)$$

where i is the day after which TT accumulates (15 September), n is the number of total days that accumulate TT, and T_{med} is the soil mean temperature in each treatment.

The relationship between TT or days and CRE was adequately described by a Gompertz function:

$$CRE = 100\exp(-a\exp(-bTT)) \quad (3)$$

where a and b are parameters. Using this model, we estimated the TT required for the emergence of *U. panicoides* in each treatment.

The total number of seeds germinated at constant temperature and the number of plants emerged under different levels of shading were subjected to analysis of variance and means compared by Duncan's test (Infostat, 2008).

Results

Seed germination under gradual changes of temperature and different after-ripening conditions

Before the beginning of the after-ripening treatments, the viability of seeds was greater than 90%, and the level of dormancy was high as germination was not observed during the initial germination test (data not shown). Seeds stored *in situ* on the soil surface under the crop residues were exposed to normal environmental conditions for the region (i.e. high rainfall conditions during the first 2 months, and after that, low rainfall). The average temperature was *c*. 25°C during the first 30 days and then 12°C on average in the winter. The level of dormancy of the *dispersed seeds* remained high in all treatments after 3 months of after ripening (Fig. 1), and only a small fraction of *undispersed seeds* germinated at the beginning of the *DT-regime* (Fig. 1H).

After 6 months, the dormancy level of *dispersed seeds* changed according to the storage condition. Seeds stored at 4°C in dry conditions did not germinate at any temperature (Fig. 2A and B), while seeds

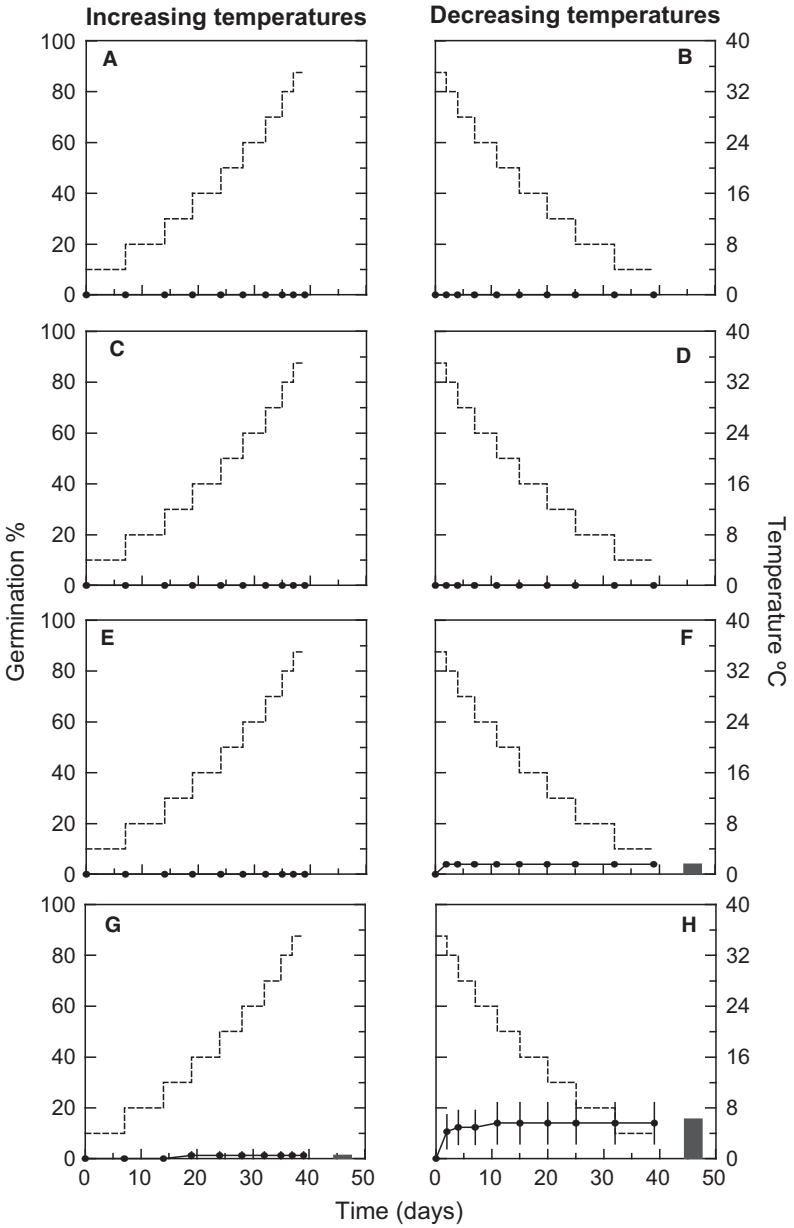

Fig. 1 Germination behaviour of the *Urochloa panicoides*seed during a germination test system using gradual changes in temperature regimes after 3 months of ripening (30 May 2008) in the following conditions: dry storage at 4°C (A, B); dry storage at 25°C (C, D); *in situ*, *dispersed seeds* (E, F) and *undispersed seeds* (G, H). Dotted lines show the courses of temperature change. In the germination curve, the mean cumulative percentage germination of four replications of 25 seeds is plotted (circles) with a vertical bar showing the standard error. The vertical black bar on the right shows the maximum germination percentage after the seeds had been subjected to daily alternating temperatures (20°C[12 h]/30°C[12 h]) or to 25°C for 7 days in the *IT-regime* and *DT-regime* respectively. Left panel: gradually increasing temperatures (*IT-regime*); Right panel: gradually decreasing temperatures (*DT-regime*).

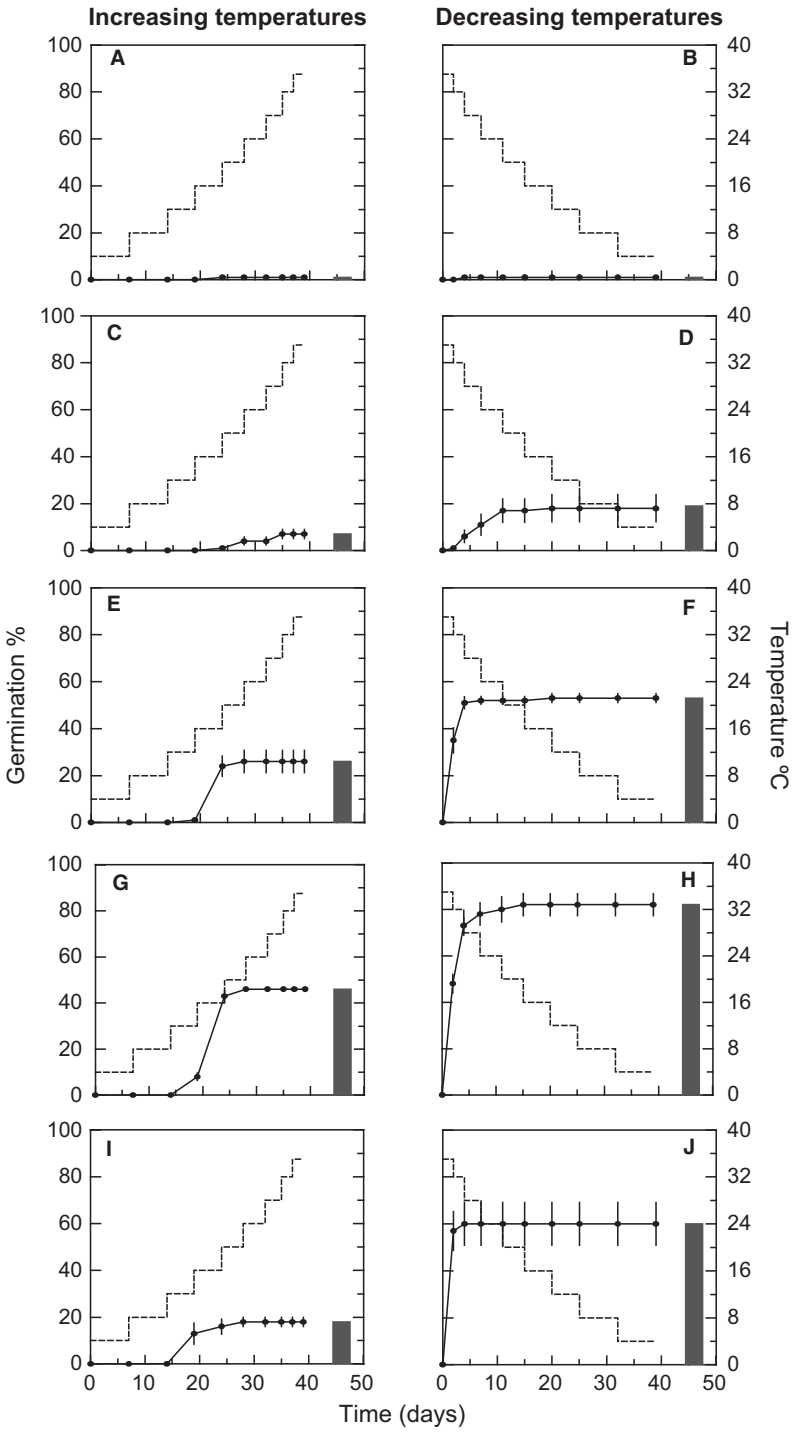

Fig. 2 Germination behaviour of *Urochloa panicoides* seeds during a germination test system using gradual changes in temperature regimes after 6 months of ripening (30 August 2008) in the following conditions: dry storage at 4°C (A, B); dry storage at 25°C (C, D); *in situ*, *dispersed seeds* (E, F); *undispersed seeds* (G, H) and *natural seedbank* (I, J). Dotted lines show the courses of temperature change. In the germination curve, the mean cumulative percentage germination of four replications of 25 seeds is plotted (circles) with a vertical bar showing the standard error. The vertical black bar on the right shows the maximum germination percentage after the seeds had been subjected to daily alternating temperatures (20°C [12 h]/30°C [12 h]) or to 25°C for 7 days in the *IT-regime* and *DT-regime* respectively. Left panel: gradually increasing temperatures (*IT-regime*); Right panel: gradually decreasing temperatures (*DT-regime*).

stored at 25°C in dry conditions and seeds exposed to after-ripening *in situ* germinated *c*. 20% and 60%, respectively, in the *DT-regime* (Fig. 2D–F). In these two treatments, germination was initiated at 16°C in the *IT-regime* and at 36°C in the *DT-regime*. The *natural seedbank* had a behaviour similar to that of *dispersed seeds* when exposed to after ripening in the field, while *undispersed seeds* showed a higher percentage of germination (Fig. 2E–J). Remarkably, the percentage of germination in the *DT*-regime was higher than that in the *IT*-regime, regardless of the seed category (Fig. 2E–J).

Quantification of thermal parameters of dormancy level and germination

The germination dynamics observed in the test of gradual changes in temperature regimes for *dispersed*

seeds stored *in situ* for 6 months and the *natural seedbank* (Fig. 2E–F, I–J) was properly fitted to the model proposed by Washitani (1987). The linear regression coefficients of the recorded and simulated data for germination percentages of *U. panicoides* were close to 0.98 ($P < 0.001$). These two populations of seeds had the same T_b (6°C), T_o (35°C) and T_m (45°C). The permissive temperature range for germination was established from 9 ± 1°C (T_l) to 45 ± 0.5°C (T_h) for both populations. Nevertheless, the estimated thermal time required for germination of 50% of the non-dormant fraction (TT_{50}) (once it had entered the temperature range within which germination can occur) varied for *dispersed seeds* stored *in situ* for 6 months and for those from the *natural seedbank*. The *dispersed seeds* required 55 d °C accumulated above a T_b of 6°C, while the TT_{50} for the *natural seedbank* was lower (27 d °C). The *dispersed seeds* had a D_{50} = 5 d °C, while the *natural seedbank* showed a D_{50} = 2 d °C, thus indicating that germination was synchronic between populations.

Seed behaviour in the germination test system of regimes of constant temperature

The seed germination percentage was similar to that observed in the germination test with 6 months of after ripening (Figs 2J and 3), suggesting that the level of dormancy of the seed population was not modified. The germination of seeds incubated at 9°C was initiated after 7 days of exposure and was completed at 30 days (Fig. 3). Germination at 34°C showed no significant differences with respect to that at 25°C. The germination percentage was higher at 25°C than at 9 and 15°C ($P < 0.05$), but this difference was not large (Fig. 3).

As expected from the results shown in Fig. 3, the germination rate increased with temperature (Fig. 4). When the incubation temperature was 34°C, 90% of non-dormant seeds germinated within 2 days of exposure while the remaining seeds had germinated at 6 days.

The T_b was estimated at 6°C (Fig. 4) and the TT required for 30%, 50% and 70% germination (inverse of the slope) was 25, 30 and 36 d °C respectively. The germination rate for the 30 percentile at 34°C could not be estimated, as at the time of the first count (24 h after starting the test) the germination percentage was already above 30%.

Emergence of Urochloa panicoides under different levels of shading

The reduction of incident solar radiation on the soil modified the soil thermal regime. Treatments with 70% and 20% of incident radiation on the soil showed lower mean temperature and thermal amplitude than bare soil (data not shown). The differences were due to variations in daily maximum temperature, while the minimum temperatures were similar in all treatments. The number of plants emerged was reduced by the shading treatments (Fig. 5). Treatments receiving 70%

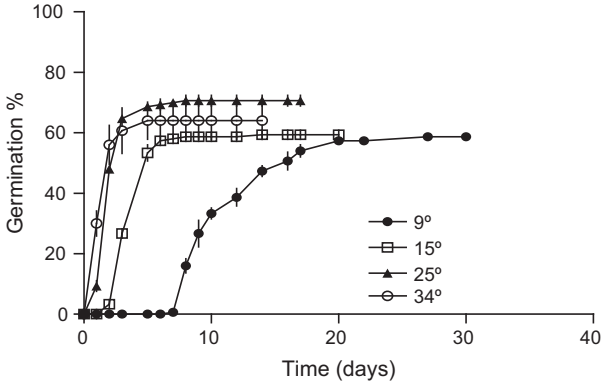

Fig. 3 Cumulative germination percentages of *Urochloa panicoides* incubated at different temperatures (2 June 2009). Vertical lines indicate the standard error.

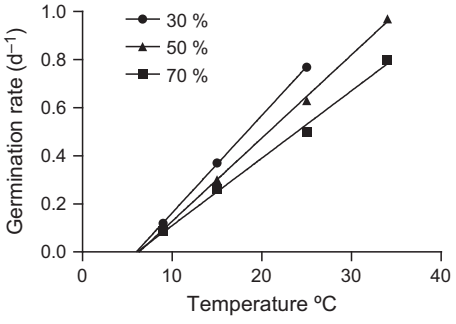

Fig. 4 Relationship between seed incubation temperature and germination rate of *Urochloa panicoides* to the 30, 50 and 70 germination percentiles.

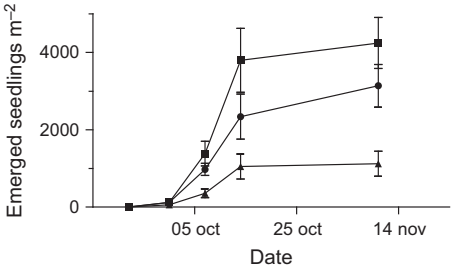

Fig. 5 Cumulative emergence of *Urochloa panicoides* in plots with different levels of incident solar radiation on the soil surface as a function of time (days) from the beginning of the test (15 September 2008). Bare soil (squares), 70% of incident radiation (circles) and 20% of incident radiation (triangles). Vertical lines indicate the standard error.

and 20% of the incident radiation on the soil surface reduced the number of plants emerged by 27% and 74% respectively. However, when the incident radiation was 70%, the number of emerged seedlings did not differ ($P > 0.05$) from that observed in bare soils, possibly due to the natural variability of the seedbank (Fig. 5).

Seedling emergence was recorded from early October to mid-November. However, more than 80% of seedlings emerged during the first 2 weeks of October, with the largest flush towards mid-October (Fig. 5). Although the number of plants recorded on each date was dependent on the treatment, the pattern of emergence remained stable (Fig. 5). Therefore, the cumulative relative emergence (CRE) was not modified by the level of imposed shading (Fig. 6A). In contrast, when the CRE was related to the TT accumulated for each date and shading level, the model parameters differed between treatments ($P < 0.05$, Fig. 6B).

Discussion

Dormancy breaking of *U. panicoides* seeds varied in response to temperature, but the temperature range for germination remained unchanged in all the after-ripening treatments explored (Figs 1 and 2). In this regard, the performance of *U. panicoides* seeds in response to temperature did not follow the patterns usually reported for summer species. The after-ripening treatment at 4°C and below 16°C at the beginning of the *IT-regime* kept high seed dormancy levels (Figs 1 and 2). This physiological condition could not be reversed by exposing seeds to fluctuating temperatures towards the end of the test. In fact, it appeared that low temperatures increased the number of dormant seeds. The proportion of seeds with secondary dormancy induced by low temperatures depended on the time during which they remained at that condition. For example, exposure of seeds to low temperatures at the beginning of the *IT-regime* induced dormancy in only a fraction of the population (Figs 1 and 2), while ripening at 4°C in dry conditions for an extended period induced dormancy in the whole population (Fig. 2a and b). In contrast, high temperatures did not induce secondary dormancy, resulting in the highest germination percentages when seeds were exposed to constant temperatures of 25 and 34°C (Fig. 3). These results suggest that the decreased level of dormancy of a spring–summer species such as *U. panicoides* is not due to low winter temperatures, but to the exposure to moderate mean temperatures, thermal fluctuation and dry conditions. This response to temperature is similar to that reported for *P. oleracea* (Kruk & Benech-Arnold, 1998) and would ensure success in weed seedling establishment. In the study area, the low-level dormancy under drought conditions would be an indispensable ecological requirement in weed seeds with a spring–summer cycle, due to the monsoon-type rainfall with low rainfall during winter and high rainfall in mid-spring to summer period.

Seed dormancy level decreased after a ripening period longer than 3 months (Figs 1 and 2). Teuton *et al.* (2004) observed that germination of *Urochloa subquadripara* (Trin) R.D. also increased after the time from harvest. Therefore, our results suggest that *U. panicoides* seeds require a minimum after-ripening period at which the level of dormancy depends on environmental conditions. If after this period, the seeds are exposed to low constant temperatures (4°C) for prolonged periods, they remain in a state of dormancy (Figs 1 and 2). In contrast, constant temperatures of 25°C favour the exit of dormancy (Fig. 2C and D), resulting in the most effective thermal condition for seeds present in the field towards the winter (Fig. 2E and F). The low effectiveness to reduce the dormancy level when seeds were kept at 25°C could be attributed to the fact that seeds in the field are exposed to fluctuating temperatures. Environments with low-temperature

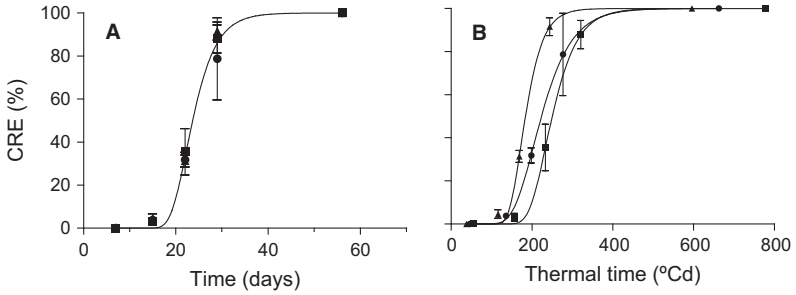

Fig. 6 Cumulative relative emergence of *Urochloa panicoides* in each treatment as a function of time (days) from the beginning of the test (15 September 2008) (A), and accumulated thermal time (B). Bare soil (squares), 70% of incident radiation (circles) and 20% of incident radiation (triangles). Vertical lines indicate the standard error. The model is $y = 100\exp(-590.5\ \exp(-0.28x))$ (A), and $y = 100\exp(-254.1\ \exp(-0.023x))$ (squares), $y = 100\exp(-52.2\ \exp(-0.019x))$ (circles), and $y = 100\ \exp(-344.3\ \exp(-0.033x))$ (triangles) (B).

amplitude were less effective in inducing loss of dormancy. This was evident in the behaviour of seeds exposed to different levels of incident solar radiation on the soil surface (Fig. 5). Also, the lower dormancy level of the seeds before natural dispersal (*undispersed seeds*, Figs 1H and 2G–H) indicates that seed removal from the panicles may result in a seedbank more sensitive to crop management practices.

The emergence pattern of *U. panicoides,* which occurs in a main flush in early spring, coincides with that observed by Walker *et al*. (2010) under non-limiting water conditions. The TT required for 50% germination of seeds was 50 d°C, similar to that estimated for *Digitaria sanguinalis* (L.) Scop. and *Echinochloa crus-galli* (L.) Beauv. (Steinmaus *et al*., 2000). However, the emergence of *U. panicoides* is earlier than the other species. This could reflect the value of T_b (6°C, Fig. 4), which showed no changes within the population and whose value coincided in both approaches used to estimate it. This T_b value is lower than that reported for other grass weeds frequent in the area. Steinmaus *et al*. (2000) estimated a T_b of 13°C for *D. sanguinalis* (L.) Scop. and *Ech. crus-galli* (L.) Beauv.

The number of weed seeds emerged was lower in treatments with high shading, because they had lower soil thermal amplitude (Fig. 5; data not shown), and thus, only the fraction of the population with lower levels of dormancy germinated. The less dormant fraction began to accumulate TT earlier. Therefore, when the cumulative relative emergence of *U. panicoides* was analysed in each treatment as a function of accumulated thermal time, model parameters differed between treatments. However, as final number of weeds varied with shading, a single model described the emergence with time (days). That is to say that the effect of temperature on CRE (%), estimated as percentage of total non-dormant seeds for each shading level, was dependent on soil thermal amplitude and the dormancy level of the seeds (Fig. 6). Theisen *et al*. (2000) reported an exponential reduction in the number of emerged seedlings of *Brachiaria plantaginea*(Link) Hitchc.(syn. *Urochloa plantaginea* (Link) R. Webster) when the soil surface was covered with a plant residue of *Avena strigosa* Schreb. and suggested that this reduction could be due to the lower soil thermal amplitude. Responses similar to those obtained in these experiments have been observed in other species (Faccini & Vitta, 2007). Therefore, the inclusion of cover crops and plant residues through various crop rotations may provide a tool to reduce the number of emerged plants of *U. panicoides*.

In the central region of Córdoba, Argentina, the thermal requirements of *U. panicoides* seeds to reduce the dormancy level are satisfied in late winter–early spring. In this region, maize is commonly sown after the first rainfall in early spring (October), coinciding with the main flushes of weed emergence (Fig. 5). In general, weed control is achieved with pre-emergent herbicides (atrazine mixed with amides). However, it has been determined that a percentage of the seedling population of *U. panicoides* is not controlled, thus adding to the seedbank of this species (Ustarroz, 2011). These escapes are essential for the perpetuation of the species, as the seeds have a short persistence in soil (Walker *et al*., 2010).

The dormancy-breaking mechanism of this weed appears to trigger a high germination rate, producing a concentrated flush of seedlings in the field. The results of the present study allowed not only the prediction of dormancy breaking, which would improve weed control using effective herbicides in this crucial period, but also the evaluation of the possible benefit of changes in the crop production systems (late sowing of maize crops, introduction of winter cover crops, etc.). However, it may be considered that the precise adaptive mechanisms may vary in *U. panicoides* populations growing in other parts of the world. More research is needed both to evaluate whether this weed is particularly successful in regions where the prevailing conditions trigger this mechanism and to identify whether other different dormancy breaking, germination and seedling establishment mechanisms are present within the species.

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