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Modelling *Chloris virgata* germination and emergence under different temperature and light quality conditions

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Abstract

Chloris virgata is a problematic weed around the world. Prediction of weed germination rates could be a useful strategy to optimise timing of weed control actions. We studied the germination and emergence of *C. virgata* collected seeds under different after-ripening treatments and different exhumation dates after seed dispersal, to estimate seed dormancy level and predict weed emergence dynamics under field conditions. Three experiments were conducted under controlled conditions to determine base, optimum and maximum germination temperatures (T_b, T_o and T_m respectively) and comprised: (a) exposure of seeds to gradually increasing and decreasing temperatures between 5 and 35°C; (b) exposure of seeds to different constant temperatures; and (c) exposure of seeds to different light quality conditions (red – far red ratio) and temperature regimes (constant and alternating temperatures). To explore genuine environmental conditions, a field experiment was performed to determine weed emergence under different shading levels. Finally, with the data obtained, a thermal time model for dormancy release was used to predict *C. virgata* seedling emergence in the Argentine Pampas region. Seeds after-ripened in cold and wet conditions and constant 25°C showed the highest germination percentages. The values of T_b (7°C), T_o (28°C) and T_m (40°C) remained constant at all exhumation dates. Neither light quality nor thermal regime modified the final germination percentages. However, shading delayed seedling emergence under field conditions, even when it was adjusted by thermal time. These results may allow predicting *C. virgata* emergence in temperate regions and help to improve weed control in integrated weed management strategies.

KEYWORDS

after-ripening, dormancy, feather finger grass, integrated weed management, Pampas region, prediction, thermal time model

1 | INTRODUCTION

Chloris virgata Sw. (feather finger grass) is a summer annual C_4 grass found around the world (Anderson, 1974). Due to its adaptability to different environments, *C. virgata* has become a threatening weed in many parts of the world (Zelaya, 1997; Osten, 2012; Ngo *et al.*, 2017), and numerous herbicide-resistant biotypes of this species have been reported (Heap, 2007). In Argentina, *C. virgata* has increased its abundance in the agricultural systems of the Pampas region and has become a problematic weed in soyabean (*Glycine max* (L.) Merr.) crops (Metzler *et al.*, 2014).

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Recently, the failure of conventional herbicide-based weed control has prompted a change towards long-term management strategies (Satorre, 2011). Mathematical models based on knowledge of plant ecophysiology are suitable to predict timing and magnitude of weed growth and to implement sustainable management strategies that allow farmers to maintain low weed infestation levels in the long term (Martinez-Ghersa *et al.*, 2000). In general, the susceptibility to herbicide in annual weeds decreases with age (Hammerton, 1967). Thus, many models have been proposed to predict the timing of seedling emergence based on the analysis of functional relationships between the germination rate and environmental factors like temperature and water potential (Benech-Arnold *et al.*, 2000). In temperate zones of the world, the main factor that determines the germination of most weed species is temperature (Baskin and Baskin, 1988). Therefore, knowledge of the dynamics of weed establishment in response to temperature could be useful to improve time of farming practices to control weeds (Martinez-Ghersa *et al.*, 2000).

During the season preceding the period favourable for seedling establishment, dormancy of spring-summer species is reduced. Consequently, the number of weed plants established is strongly related to the proportion of seeds that have been released from dormancy (Benech-Arnold *et al.*, 2000). The low temperatures of winter are responsible for reducing the level of dormancy in spring-summer seeds while the high temperatures of late spring and early summer induce increases in the level of seed dormancy (Bouwmeester and Karssen, 1992). However, responses may be more complex and temperature may not be the only factor involved in dormancy release in summer weed species (Ustarroz *et al.*, 2016). The level of seed dormancy can also be modulated by soil moisture (Kruk and Benech-Arnold, 1998), and once seeds have reached a low dormancy level, most weed seed populations require different light conditions and/or alternating temperatures to completely lose dormancy (Thompson *et al.*, 1977; Kruk *et al.*, 2006).

To predict the emergence of weed seedlings, some authors have developed thermal time models based on the estimation of the base temperature (T_b), optimum temperature (T_o), maximum temperature (T_m) and the thermal time required for germination (TT_g) of a determined fraction of the seed population (Washitani, 1987; Steinmaus *et al.*, 2000; Batlla and Benech-Arnold, 2003). Although these parameters have been reported in *C. virgata* populations (Zhang *et al.*, 2015; Lin *et al.*, 2016; Ngo *et al.*, 2017), the influence of after-ripening conditions have not been studied. Therefore, the aim of this work was to study the dynamic of germination and emergence of *C. virgata* seeds under different after-ripening treatments and non-limiting water conditions as a way to accurately predict emergence.

2 | MATERIALS AND METHODS

2.1 | Collection of seeds and viability test

On 25 April 2016, mature panicles of *C. virgata* plants were collected from three different populations (10–15 plants per sample), in three nearby soyabean fields in the Argentine Pampas region (34°51′S, 62°46′W). The panicles collected were manually processed for seed extraction, and the seeds were mixed in a seed pool and stored in paper bags at room temperature (*c.* 20°C) for 2 days until they were used for the experiments on 27 April 2016. Before the experiments, a tetrazolium test was conducted on a random sample of seeds to characterise the viability of the seed lot and adjust the maximum potential germination accordingly. Four replicates of 25 seeds were placed in a 90-mm diameter Petri dish with three layers of filter paper. After exposing them to a period of 18 hr of imbibition with distilled water at 30°C in a germination chamber, seeds were sliced longitudinally, avoiding embryo damage, and incubated in a 1% tetrazolium chloride solution for 24 hr at 30°C in darkness (ISTA, 1996). After that, seeds were observed with a magnifying glass to determine viability percentages. Uniformly red-stained embryos were considered viable.

2.2 | Experiments under controlled conditions

To evaluate the level of seed dormancy, two experiments were conducted under controlled conditions: one with gradually increasing and the other with gradually decreasing temperatures.

2.3 | Germination test using gradual changes in temperature

The germination test was conducted according to the method of Washitani (1987) and modified by Kruk and Benech-Arnold (1998), and consisted in exposing one batch of imbibed seeds to gradually increasing temperatures from 5 to 35°C in 5°C increments (IT regime) and exposing a second batch of imbibed seeds to gradually decreasing temperatures from 35 to 5°C (DT regime). Since below the T_o (physiological range) the germination rate increases with temperature, the duration of each period of exposure to different temperatures decreased. Seeds were exposed for 8 days at 5°C, 6 days at 10°C, 5 days at 15°C, 4 days at 25°C, 3 days at 30°C and 2 days at 35°C (modified from Kruk and Benech-Arnold, 1998). The number of germinated seeds was recorded immediately before each temperature change. Germinated seeds were removed after counting, and the criterion considered was the radicle protrusion (Ustarroz *et al.*, 2016). Each thermal regime (IT and DT) had four replicates of 25 seeds. The seeds were placed in 90-mm-diameter Petri dishes with three layers of filter paper and 5 ml of distilled water, without light restrictions. After IT and DT regimes, the remaining ungerminated seeds were exposed to 25°C and daily alternating temperatures of 10°C [12 hr]/24°C [12 hr], respectively, for 7 days to eliminate secondary dormancy that could have been induced by high temperatures towards the end of the test (Kruk and Benech-Arnold, 1998). This methodology was used to obtain germination curves for each after-ripening treatment as a function of the dormancy level and temperature.

2.4 | After-ripening treatments

Different treatments were applied to harvested seeds: (a) dry storage at 5°C in paper bags; (b) saturated moist chilling at 5°C on filter paper in Petri dishes; (c) dry storage at 25°C in paper bags; and (d) burial at 3 cm depth in a crop production field with a silty clay loam soil with pH 5.6 and organic matter content of 3.8%, (34°40.8′S, 60°02.1′W), where the microenvironment was similar to the environment of the natural soil ('in situ'). For this last treatment, approximately 5,000 seeds were placed inside transparent polyester 5 × 5 cm mesh envelopes (one for each exhumation date) with 0.5 × 0.5 mm openings (adapted from Washitani and Masuda, 1990). Use of the bags prevented seeds from being eaten by the soil fauna. The soil temperature was recorded hourly using two data logger sensors (HOBO pendant; Onset Computer Corporation) located next to the buried seeds. Rainfall was determined from a meteorological station 200 m from to the experiment. Seeds of all treatments were stored under the above-mentioned conditions for 98 and 173 days, starting on 27 April 2016. Also, at the beginning of the experiment the germination test was performed with fresh seeds ('initial test').

2.5 | Development of thermal time model

The germination dynamics of each seed population fraction was quantified as a function of time and temperature by using the model proposed by Washitani (1987). To apply this model, besides using the germination curves of the 'in situ' treatment from the experiment performed in 2016, the same treatment was applied to another collection of *C. virgata* seeds in 2017. The methodology for seed collection was similar to that used in 2016 in the same field lots and seed collection dates. In this experiment, seeds were exhumed from the same crop production field as in 2016 after 41 and 125 days. The above-mentioned model allows estimating two kinds of population thermal parameters in relation to the germination observed. On one hand, are those describing the dormancy status of the seed population: the lower limit temperature ($T_{l(50)}$) and higher limit temperature ($T_{h(50)}$) of the thermal range within which 50% of the seed population germinates at different after-ripening dates; and the thermal time required for germination (TT_{g50}). On the other hand, are those describing the relationship between the germination rate of individual seeds and temperature (T_b, T_o and T_m). The model predicts the germination dynamics of a seed population as a function of temperature during the course of the year. To run the model, the values of $T_{l(50)}$, $T_{h(50)}$, T_b, T_o, T_m and TT_{g50} were tested a priori relating the equations of the germination model previously mentioned (Washitani, 1987). Optimal thermal parameters for the germination model were obtained by a non-linear curve-fitting method by using Microsoft Excel Solver optimisation programme (Solver for Non-linear Programming, Frontline Systems, 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 the optimisation of thermal parameters was minimum root mean square error (RMSE). The value of RMSE used for optimisation was the average of the RMSE resulting from the fit of IT and DT germination regime curves.

Once thermal parameters were calculated for the seeds exhumed at different dates, the stratification thermal time model developed by Batlla and Benech-Arnold (2003) was used. This is a simple dormancy loss model to predict progressive changes in seed population dormancy parameters: lower limit temperature in which 50% of seed population germinates ($T_{l(50)}$) and standard deviation (*SD*), as a function of stratification temperature. To measure the effect of temperature on the dormancy status of the seed population, changes in $T_{l(50)}$ were predicted as a function of the accumulation of stratification thermal time units (S_{tt}) under a 'ceiling' threshold temperature for dormancy release to occur, according to the following equation:

$$S_{tt} = \sum \left(T_c - T_s\right) \quad (1)$$

where T_c is the dormancy release 'ceiling' temperature (the temperature at, or over, which dormancy release does not occur) and T_s is the daily mean soil temperature. Optimal T_c was obtained using different values of this parameter until the best fit of the linear regression between $T_{l(50)}$ and S_{tt} was attained (Batlla and Benech-Arnold, 2003). The initial $T_{l(50)}$ of the population was obtained by extrapolation of the linear function. Therefore, the accumulated S_{tt} and $T_{l(50)}$ were calculated for each day since seed dispersal date, which coincided with the beginning of the initial test. Based on the results obtained and previous results reported by other authors, and for practical modelling reasons, the present model assumes that $T_{h(50)}$ does not change during seed burial (Batlla and Benech-Arnold, 2003).

The performance of the model was evaluated using the thermal parameters obtained for buried seeds. Changes in $T_{l(50)}$ were simulated as a function of daily mean soil temperature by using Equation (4) of the dormancy loss model. Accumulation of S_{tt} began when the daily mean temperature recorded was below T_c. If the prevailing germination test temperature entered the permissive range for germination of a certain fraction of the seed population, which depends on the predicted value of $T_{l(50)}$, the accumulation of TT for that fraction above T_b was assumed to start simulating the germination dynamics at each incubation regime (Batlla and Benech-Arnold, 2003).

2.6 | Germination test using regimes of constant temperature

To complement the information generated by the methodology previously described, the seeds collected in April 2016 and exhumed after 173 days of after-ripening were incubated at constant temperatures. Fifty seeds were placed in 90-mm-diameter Petri dishes with three layers of filter paper and 5 ml of distilled water and were incubated at constant temperatures of 10, 15, 25 and 30°C. A completely randomised design with four replications was used. Daily counts and subsequent removal of germinated seeds

were conducted for 30 days. The time (days) at which 20%, 30%, 40% and 50% of germination occurred was estimated for each temperature by non-linear regression. The germination rate of each of these fractions was plotted as a function of temperature and T_b was determined by the intersection of the regression line with the *x*-axis (Steinmaus *et al.*, 2000).

2.7 | Germination in response to light quality and temperature

To evaluate the effect of light quality on dormancy release under controlled condition, a modified methodology of Deregibus *et al.* (1994) was used. Seeds were exposed to different light quality (R: red light; FR: far red light) and temperature regimes. The experiment was conducted with buried seeds exhumed at different after-ripening periods (0, 124 and 180 days). The storage conditions were the same as the 'in situ' treatment. Exhumed seeds were kept in darkness until experiment was performed (*c.* 6 hr). The light sources used to provide light pulses were (a) saturated red light (i.e. R) and (b) phytochrome photoequilibrium Pfr/Pr = 0.03 (i.e. FR) 42 μmol m^{-2} s^{-1}, provided by a 250 W internal reflector incandescent lamp, in combination with a RG9 filter.

Seeds were incubated in 90-mm-diameter Petri dishes (25 seeds per dish) with three layers of filter paper. Then, 5 ml of distilled water was added under dim green light and the dishes were immediately wrapped with aluminium foil to keep the seeds in darkness. Seeds were incubated for 48 hr at 25°C, and after that, five groups of six dishes were formed and each of them was assigned to one of the following treatments: (a) darkness (*D*); (b) 20 min of red light (20R); (c) 20 min of red light, followed by 15 min of far red light (20R/15FR); (d) 2 min of red light (2R); and (e) 2 min of red light followed by 15 min of far red light (2R/15FR). Treatments were applied once a day for the three consecutive first days, and then, the seeds were maintained in darkness.

From the beginning of the experiment, the groups of dishes corresponding to each treatment were divided into two sub-groups of three dishes. One sub-group remained at 25°C and the other at alternating temperatures of 10°C [12 hr/ 24°C [12 hr] for 15 days. The germinated seeds were counted and removed daily under dim green light, and then, the dishes were immediately wrapped with aluminium foil. The criterion to consider germinated seeds was radicle protrusion. The results were subjected to analysis of variance (ANOVA), and means were compared using Tukey's test by InfoStat software (Di Rienzo *et al.*, 2008). At the end of the experiment, a tetrazolium test was performed to a sample of 50 ungerminated seeds from each treatment to estimate their viability.

2.8 | Emergence under different shading levels in the field

This experiment was conducted at the experimental field of the Department of Plant Production, University of Buenos Aires, Argentina (34°35.6′S, 58°29.1′W). Areas with high previous *C. virgata* infestations were allowed to produce and shed seeds from April 2017 until the end of the experiments, so mature seeds that fell on the soil were exposed to local environmental conditions during the autumn and winter seasons. Different soil thermal amplitudes were generated by shading with black plastic mesh that did not change incident light quality (Ustarroz *et al.*, 2016). The treatments were (a) bare soil (control, with no plastic mesh) and (b) 25% of incident solar radiation reaching the soil surface ('shaded treatment').

Tunnels of metal structure (2.5 m long × 0.5 m wide × 1 m high) oriented north–south and covered by a black plastic mesh were installed on 17 July 2017. Radiation was measured at midday both above and below the black plastic mesh in each experimental unit with a radiometer (RAD Cavadevices BAR-100) to determine the incident radiation in the shaded treatment (Ustarroz *et al.*, 2016). A randomised complete block design with three replicates was used. The emerged seedlings of *C. virgata* were counted weekly during the first 30 days and then every 14 days from a 1,600-cm^2 sampling area (40 × 40 cm) in the centre of each plot, taking as a guide a 2 × 2 cm plastic grid. The soil temperature at 3 cm depth was measured daily at 1-hr intervals, using two data logger sensors (HOBO pendant) in both treatments, and monthly mean temperatures were subjected to ANOVA test and means were compared by Tukey's test using InfoStat software (Di Rienzo *et al.*, 2008).

The cumulative relative emergence (CRE, proportion of total plants emerged in each period) was quantified and modelled as a function of the number of days from the beginning of the experiment and as a function of the TT (°C days) accumulated as a predictor. For this, TT was calculated as the sum of the difference between the daily mean temperature of the soil (average of the hourly records of the temperature data loggers) and T_b:

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

where *i* is the initial day after which TT accumulates, *n* is the number of total days that accumulate TT, and T_s is the soil mean temperature in each treatment. The relationship between TT or days and CRE was adequately described by Gompertz function:

$$CRE = 100 \exp\left(-a \exp\left(-b\,TT\right)\right) \quad (3)$$

where *a* and *b* are parameters. This model was used to estimate the TT required for the emergence of *C. virgata* in each treatment.

3 | RESULTS

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

Seed viability at the beginning of the germination tests was 94% in 2016 and 96% in 2017. During the 'initial' germination test in

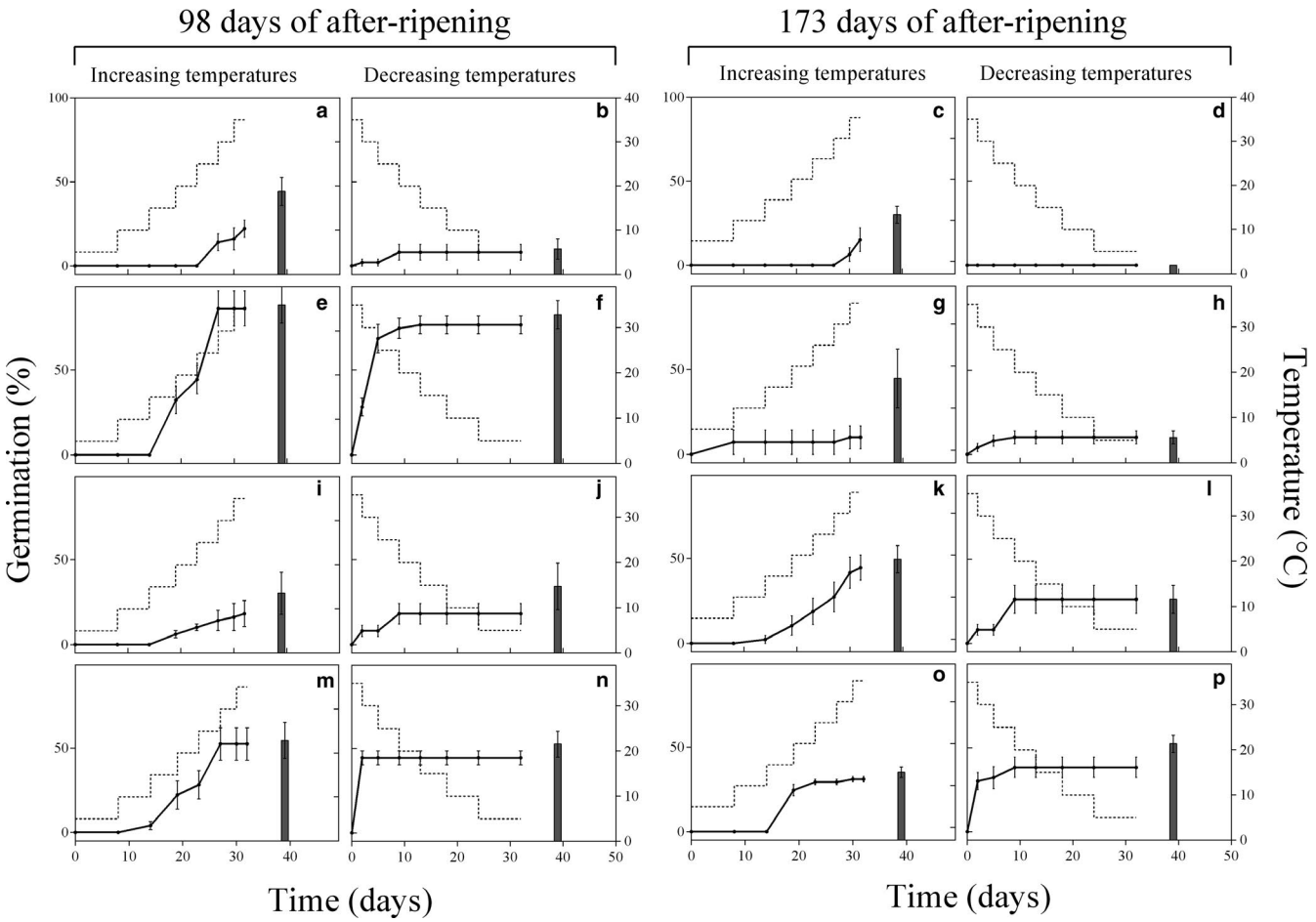

FIGURE 1 Germination behaviour of *Chloris virgata* seeds during the 2016 germination experiment using gradual changes in temperature regimes after 98 days (a, b, e, f, i, j, m, n) and 173 days (c, d, g, h, k, l, o, p) of ripening. The after-ripening treatments were dry storage at 5°C (a–d); moist chilling at 5°C (e–h); dry storage at 25°C (i–l); and seed burial (m–p). The dotted lines show the course of temperature change. In the germination curve, the mean cumulative germination percentage of four replications of 25 seeds is plotted (●), with the vertical lines indicating the standard error of the mean. The vertical black bars on the right show the maximum germination percentage after seeds were subjected to daily alternating temperatures of 10°C [12 hr]/ 24°C [12 hr] or to 25°C for 7 days in the IT regime and DT regime respectively

both years, dormancy was high as germination was lower than 16%.

After 98 days of ripening, the dormancy level of seeds varied according to the treatment conditions (Figure 1). Seeds exposed to 5°C and wet conditions (Figure 1E,F) and buried seeds (Figure 1M,N) showed the highest levels of germination in all treatments. In the IT regime, the former reached 86.3% germination whereas the latter reached 52.4% germination. In contrast, seeds stored at 5 and 25°C in dry conditions showed germination percentages of 18.2% and 22.2% respectively (Figure 1A,B and I,J). In both IT and DT regimes, the final germination percentages were similar, although, in the DT regime, germination was concentrated during the first days, whereas, in the IT regime, germination increased throughout the experiment.

After 173 days of ripening, the seeds stored at 25°C in dry conditions and the seeds buried in the soil were the treatments with the highest germination percentages (Figure 1K,L and O,P). In the IT regime, seeds stored at 25°C in dry conditions began to germinate at 10°C and reached 44.6% germination at the end of the test, while buried seeds began to germinate at 15°C and reached 31% germination (Figure 1K,O). Seeds stored under the other two storage conditions did not exceed 15% germination (Figure 1C,G). In the DT regime, buried seeds and those stored at 25°C and dry conditions also showed the highest germination percentages (38.4% and 26.2% respectively) (Figure 1L–P).

3.2 | Quantification of thermal parameters of dormancy level and germination

There was a high correlation coefficient between $T_{l(50)}$ and S_{tt} using a T_c of 24.3°C (Figure 2) for 2016 and 2017 germination curves, according to the following function:

$$T_{l(50)} = -0.0062.S_{tt} + 23.56 \quad (4)$$

The estimated values of T_b (7°C), T_o (28°C) and T_m (40°C) remained constant at all exhumation dates in both years. T_b and

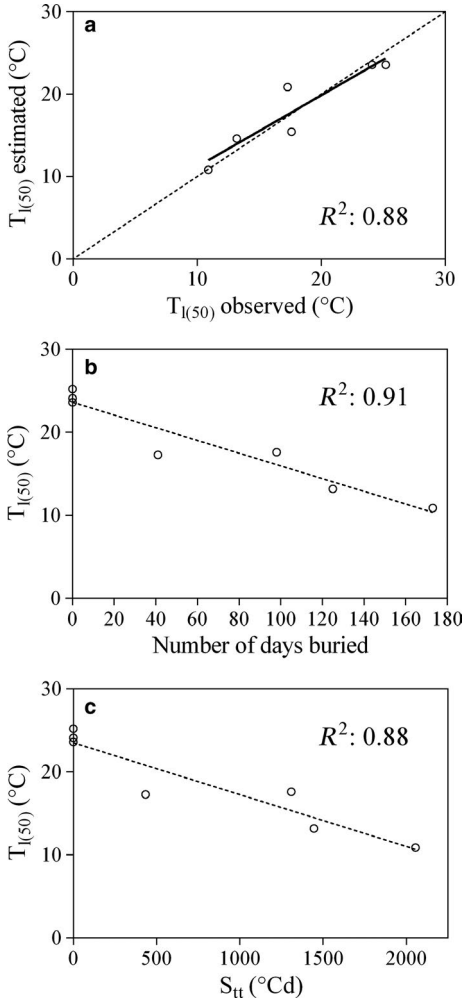

FIGURE 2 Values of the mean lower limit temperature ($T_{l(50)}$) for *Chloris virgata* seeds buried under field conditions estimated by the model of Batlla and Benech-Arnold (2003), as a function of observed values of $T_{l(50)}$ obtained by germination tests using the method of Washitani (1987) (a); and observed $T_{l(50)}$ values plotted against number of days during which seeds were buried (b), and against stratification thermal time (S_{tt}) (c). The dotted line in (a) shows a 1:1 relation; and the dotted line in (b) and (c) is the result of repeated regression analysis to obtain the threshold 'ceiling' temperature (T_c) with the best fit according to Equation (1). The values of parameters corresponding to Equation (4) are slope ($T_{l(50)}$ decrease rate) = −0.0062 ± 0.001°C per °C days and *y*-axis intercept (initial $T_{l(50)}$ of the seed population) = 23.56 ± 1.1°C

T_o were similar to those found by Zhang *et al.* (2015) and Osten (2012). The estimated thermal time required for 50% germination ($TT_{g(50)}$) was 50 and 75°C d for the initial test in 2016 and 2017, respectively, and 10°C days for exhumations at other times in both years (Table 1).

Buried seeds were exposed to the following environmental conditions: in 2016, the soil average temperature after seed buried were higher than in 2017 and months with higher rainfall were October (164 mm) and September (136 mm) in 2016 and 2017 respectively (Figure 3). As seeds were exposed to low winter temperatures under field moisture conditions, the dormancy level of *C. virgata* seeds decreased, allowing the widening of the permissive temperature germination range. The linear regression coefficient of the observed $T_{l(50)}$ and that estimated by the model was 0.88 (Figure 2). In this work, the mean soil temperature reached the $T_{l(50)}$ estimated by the model on August 25 and 50% seed germination of *C. virgata* was expected for the first days of September in both years (Figure 3).

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

The germination rate increased with temperature (Figure 4). The T_b obtained by the germination test using constant temperatures regimes was 7.2°C ± 0.86 (R^2: 0.66). The highest germination percentages were observed at constant temperatures of 25°C (78.1%) and 30°C (65.2%).

3.4 | Germination in response to light quality and temperature

The final germination of *C. virgata* seeds showed no differential responses in the treatments applied, both for light quality (p = .48) and thermal regimes (p = .51). However, important germination differences were observed according to the exhumation date (p < .01) (Table 2). As expected, fresh seeds had low germination percentages (possibly due to high primary dormancy level immediately after seeds were dispersed) and high viability percentages (over 94%). After 124 days of after-ripening, the germination percentages were close to 100%, regardless of the treatment applied. Finally, on the last exhumation date (180 days of after-ripening), the fraction of germinated seeds was below 20%, the viability of ungerminated seeds was very low (<12%), and many seeds were rotten. These results could explain the low level of *C. virgata* seed persistence in the soil under natural field conditions.

3.5 | Emergence under different shading levels in the field

The reduction of incident solar radiation significantly reduced monthly mean temperature (p < .05) from August, 2017 to January, 2018. Shaded treatment had approximately 5°C lower monthly mean temperature and less thermal amplitude than the bare soil (Figure 5).

The shaded treatment delayed seedling emergence, but the final number of established plants was similar in shaded and bare soil treatments. When the seeds were on bare soil, they reached 50% of CRE 69 days before those in the shaded treatment. Moreover, 50% CRE was attained with 147 and 891°C days in the bare soil and shaded treatment respectively (Figure 6). Therefore, alternating temperatures allowed seeds to lose dormancy more quickly. A first emergence cohort was observed during mid-September (on bare soil) and mid-October (on shaded soil), and a second cohort was observed

TABLE 1 Parameters obtained by Washitani (1987) model to quantify dormancy release. Lower ($T_{l(50)}$) and higher ($T_{h(50)}$) limit temperature (°C) of the thermal range within which 50% of the *Chloris virgata* seed population germinates and thermal time required for 50% of germination ($TT_{g(50)}$; °C days) after different number of days buried

Year	Days buried	$T_{l(50)}$	$SD_{Tl(50)}$	$T_{h(50)}$	$SD_{Th(50)}$	$TT_{g(50)}$	$SD_{TTg(50)}$	*RMSE*	R^2
2016	0	23.6	5.0	40.0	5.0	50.0	1.0	0.9744	0.97
	98	17.6	5.0	40.0	1.0	10.0	1.0	2.1584	0.98
	173	10.9	5.0	39.3	5.0	10.0	1.0	1.4998	0.99
2017	0	25.2	5.0	40.0	1.0	75.0	1.0	1.6454	0.51
	41	17.3	5.0	39.8	10.0	10.0	1.0	1.2754	0.98
	125	13.2	1.0	39.7	3.0	10.0	1.0	0.8443	0.99

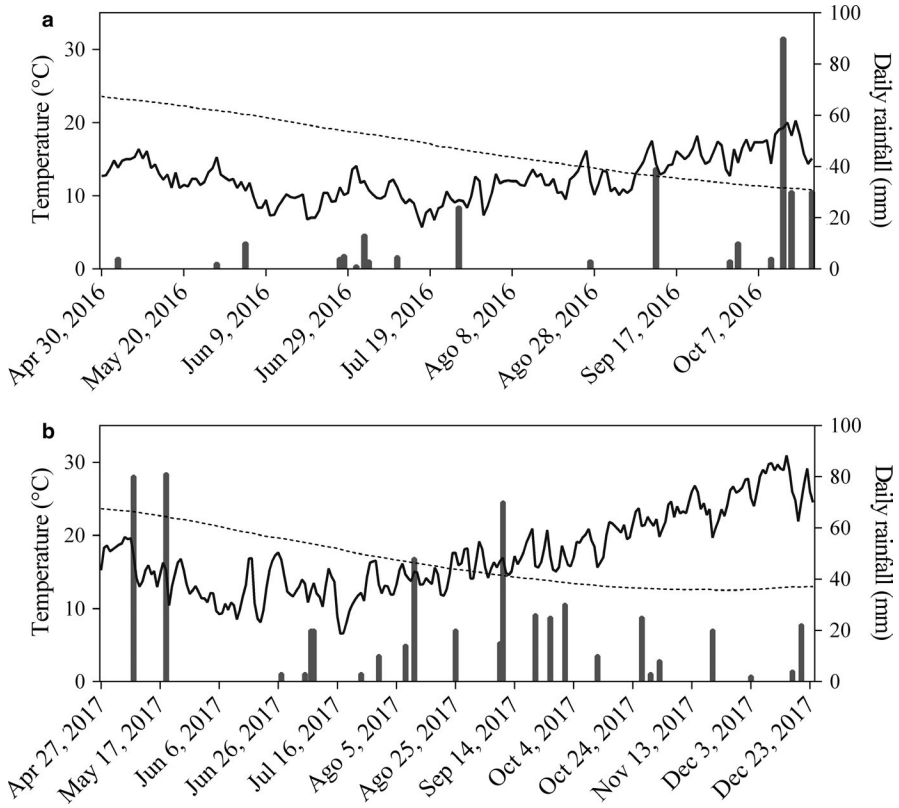

FIGURE 3 After-ripening conditions of buried *Chloris virgata* seeds in Pampas region on field plots (34°40′S, 60°02′W) in the experiments performed in 2016 (a) and 2017 (b). The solid line shows the evolution of the daily average soil temperature (°C), the dotted line the evolution of the values of $T_{l(50)}$ (°C) estimated by the model of Batlla and Benech-Arnold (2003), and the columns represent daily rainfall (mm)

from the end of the first cohort to December (Figure 6). Furthermore, the total duration of the emergence period was 105 days on the bare soil treatment and 84 days on the shaded treatment.

4 | DISCUSSION

The dormancy level of *C. virgata* seeds varied in response to the temperature and water conditions over the course of the year: low temperatures and wet conditions accelerated dormancy release (Figure 1). However, wet storage at 5°C accelerated dormancy release allowing high germination percentages at 98 days of after-ripening but a low germination percentage after 173 days of after-ripening (Figure 1). Some studies have shown that *C. virgata* seeds require an after-ripening period of 6–10 weeks and that the germination response to time fits well to a logistic function (Osten, 2012; Ngo *et al.*, 2017). However, other authors have found fresh seed populations of *C. virgata* that could germinate more than 39% (Zelaya, 1997; Li *et al.*, 2006). In our experiment, a small fraction of the seed population seemed not to have dormancy requirements, because fresh seeds showed less than 16% germination (data not shown). According to Loch *et al.* (2004), the level of dormancy and the current dormancy mechanisms involved in C_4 grasses can vary in species distributed over a wide geographic and climatic range. Thus, the contrasting levels of dormancy observed among studies may be due to the wide geographic and climatic adaptation of this species (Ngo *et al.*, 2017).

Similar to the results found by Ustarroz *et al.* (2016) and Kruk and Benech-Arnold (1998) for summer annual weed seeds, constant temperatures of 25 and 30°C showed the highest germination levels and did not induce secondary dormancy in *C. virgata* seeds. These results suggest that the decreasing level of dormancy of *C. virgata* appeared as independent of thermal fluctuation or dry conditions. However,

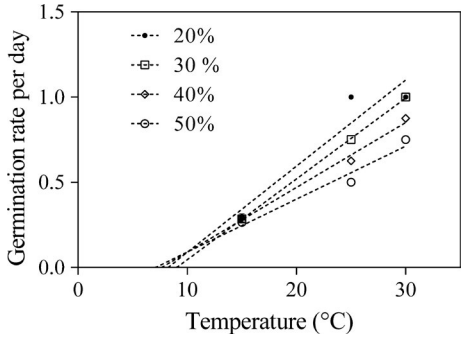

FIGURE 4 Relationship between seed incubation temperature and germination rate of *Chloris virgata* to the 20, 30, 40 and 50 germination percentiles

dry storage at 25°C showed the lowest germination percentage after 98 days of after-ripening, thus being the least effective after-ripening treatment to reduce the dormancy level. This response could be attributed to the fact that the low temperatures of winter are a main factor reducing the level of dormancy in spring-summer seeds (Bouwmeester and Karssen, 1992). Moreover, after 173 days of after-ripening, final germination percentages were lower or similar to those observed after 98 days of ripening, which could be showing an ageing of the seeds.

The emergence pattern of *C. virgata*, which occurred in two emergence cohorts from the first days of October, coincides with that observed by Metzler *et al.* (2014) in the Pampas region. The $TT_{g(50)}$ (50°C days) was similar to that estimated for other summer annual grass weeds (Steinmaus *et al.*, 2000; Ustarroz *et al.*, 2016), whereas the value of T_b (7 and 7.2°C) estimated by both germination tests using gradual changes in temperature and constant temperatures are similar to those found by Zhang *et al.* (2015) and is higher than that found by Ngo *et al.* (2014) (2.1–3°C). In the Pampas region, *C. virgata* can rapidly germinate and emerge under field conditions after spring rainfall events due to its low T_b.

According to the model of Batlla and Benech-Arnold (2003), germination under field conditions occurs when the soil temperature enters the germination permissive range. In our study, the permissive temperature range for germination of *C. virgata* widened as seed dormancy was lost. This response was observed through the decline of the $T_{l(50)}$ over the course of both years experiments (2016 and 2017) (Figure 3). On August 25 of both years, soil temperature reached $T_{l(50)}$, and 50% cumulative germination was expected by 2 September 2016 and 3 September 2017. In fact, the results of the 'in situ' experiment showed that the cumulative emergence of 50% *C. virgata* seedlings was observed during the first days of September on the bare soil treatment. Moreover, the population dynamics observed was congruent to that obtained by Metzler *et al.* (2014). Therefore, it appears that this model could be useful to predict the establishment of this weed in the Pampas region.

For most weed seed populations, dormancy must be terminated by the effect of light, nitrate or fluctuating temperatures, to allow germination to proceed (Benech-Arnold *et al.*, 2000). However, in spite of having small seeds, *C. virgata* seems not to be demanding of any specific light quality requirements to break dormancy. Furthermore, the fluctuating temperature did not modify the final germination percentage of *C. virgata* seeds, but modified the germination rate. According to Pezzani and Montaña (2006), this species is adapted to both open (bare soil) and closed (dense vegetation cover) habitats, but grows preferentially in open ones.

In our experiment, the plastic mesh simulated the effect of alternating temperatures generated by a crop canopy. The final number of weed seeds emerged was similar in both shaded and bare soil treatments while the dynamic of emergence as a function of thermal time differed between treatments (Figure 6). Despite the fact that neither light quality nor alternating temperatures affected seed germination, seedling emergence in the field could be delayed because some species need certain amplitude of soil moisture fluctuations to promote the dormancy release (Baskin & Baskin, 1988; Egley, 1995), and the shaded treatment could have attenuated this effect. In addition, *C. virgata* germination delay until conditions were suitable for seedling emergence could also be conditioned by the seed persistence in the soil. Some authors have found that the viability of *C. virgata* seeds decreases as time progresses under field conditions and that they lose their viability completely after 8–12 months (Osten, 2012; Ngo *et al.*, 2014).

The results of this study may allow prediction of the dormancy loss of *C. virgata* seeds and seed germination dynamics in temperate regions, which could be an important tool to improve weed control

TABLE 2 Final germination percentages of *Chloris virgata* seeds (FG) under different light quality conditions: darkness; 20 min of red light for three consecutive days 20R; 20 min of red light, followed by 15 min of far red light, for three consecutive days 20R/15FR; 2 min of red light, for three consecutive days 2R; 2 min of red light followed by 15 min of far red light, for three consecutive days 2R/15FR; and different temperature regimes: constant 25°C; and alternating temperatures (10°C [12 hr]/24°C [12 hr])

		Constant 25°C		Alternating temperatures	
Days buried	Treatment	FG	*SEM*	FG	*SEM*
0 days	Darkness	11.2[b]	0.28	12.4[b]	0.74
	20R	14.0[b]	1.56	10.4[b]	1.40
	20R/15FR	10.7[b]	2.45	12.6[b]	0.49
	2R	12.9[b]	1.22	10.4[b]	0.74
	2R/15FR	12.6[b]	0.97	12.6[b]	0.49
124 days	Darkness	100.0[a]	0.00	98.7[a]	1.33
	20R	100.0[a]	0.00	98.7[a]	1.33
	20R/15FR	100.0[a]	0.00	100.0[a]	0.00
	2R	100.0[a]	0.00	100.0[a]	0.00
	2R/15FR	100.0[a]	0.00	100.0[a]	0.00
180 days	Darkness	13.3[b]	8.33	6.7[b]	6.67
	20R	6.7[b]	4.81	8.0[b]	2.31
	20R/15FR	13.3[b]	1.33	17.3[b]	3.53
	2R	6.7[b]	4.81	12.0[b]	2.31
	2R/15FR	12.0[b]	6.93	4.0[b]	0.00

Values accompanied with the same letter have no significant difference ($p < .05$).

Abbreviation: *SEM*, Standard error of the mean.

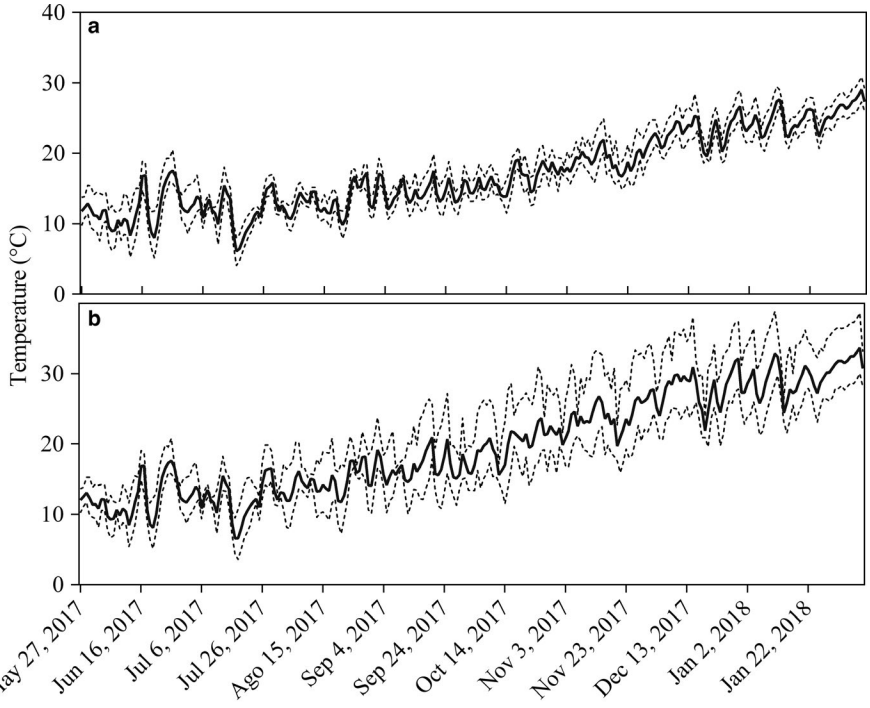

FIGURE 5 Average daily temperature (solid line), maximum and minimum daily soil temperature (dashed lines) in the shaded, receiving 25% incident radiation (a) and bare soil (b) treatments in the field experiment performed in 2017

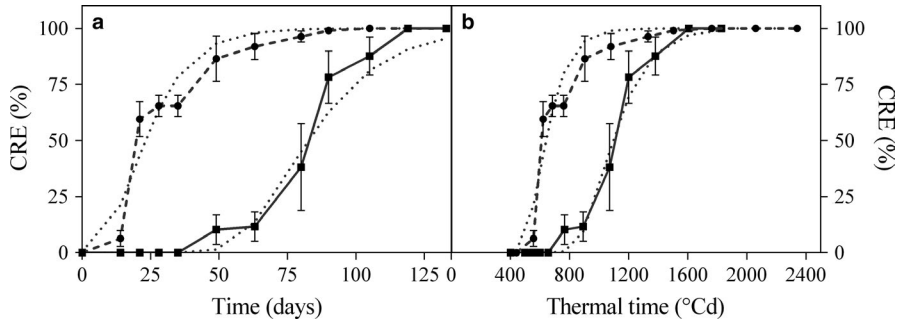

FIGURE 6 Cumulative relative emergence (CRE) of *Chloris virgata* as a function of time (days) (a) and accumulated thermal time (b) of seeds under bare soil (●) and shaded (■) treatments. Vertical lines indicate standard error, and dotted lines show the fit by Gompertz model. The model is $y = 100 \exp(-5.3762 \exp(-0.0888x))$ (a-circles), $y = 100 \exp(-59.4679 \exp(-0.0539x))$ (a-squares), and $y = 100 \exp(-307.3377 \exp(-0.0095x))$ (b-circles), $y = 100 \exp(-549.5046 \exp(-0.0061x))$ (b-squares)

using effective herbicides during this crucial period. This tactic could be complemented with changes in the crop production systems (i.e., crop sowing date, introduction of winter cover crops) to generate an integrated weed management approach (Martinez-Ghersa *et al.*, 2000; Kruk *et al.*, 2006; Swanton *et al.*, 2008). However, it should be considered that the precise adaptive mechanisms may vary in *C. virgata* populations growing in different habitats and that may differ among locations, even within the same region. More research is needed to understand the adaptation of this weed to different environmental conditions and to identify whether other dormancy breaking mechanisms are present or may be developed within the species.

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REFERENCES

Anderson, D.E. (1974) Taxonomy of the genus *Chloris* (Gramineae). Brigham Young University Science Bulletin. *Biological Series*, 19(2), 1.

Baskin, C.C. and Baskin, J.M. (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany*, 75(2), 286–305.

Batlla, D. and Benech-Arnold, R.L. (2003) A quantitative analysis of dormancy loss dynamics in *Polygonum aviculare* L. seeds: development of a thermal time model based on changes in seed population thermal parameters. *Seed Science Research*, 13(1), 55–68.

Benech-Arnold, R.L., Sánchez, R.A., Forcella, F., Kruk, B.C. and Ghersa, C.M. (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Research*, 67(2), 105–122.

Bouwmeester, H.J. and Karssen, C.M. (1992) The dual role of temperature in the regulation of the seasonal changes in dormancy and germination of seeds of *Polygonum persicaria* L. *Oecologia*, 90(1), 88–94.

Deregibus, V.A., Casal, J.J., Jacobo, E.J., Gibson, D., Kauffman, M. and Rodriguez, A.M. (1994) Evidence that heavy grazing may promote the germination of *Lolium multiflorum* seeds via phytochrome-mediated perception of high red/far-red ratios. *Functional Ecology*, 8(4), 536–542.

Di Rienzo, J., Casanoves, F., Balzarini, M., Gonzalez, L., Tablada, M. and Robledo, C.I. (2008) *Infostat*. Córdoba (Argentina): Grupo InfoStat, FCA, Universidad Nacional de Córdoba.

Egley, G.H. (1995) Seed germination in soil: dormancy cycles. In: Kijel, J. and Galili, G. (Ed.) *Seed development and germination*, vol. 41. New York, NY: CRC Press, pp. 529–543.

Hammerton, J.L. (1967) Environmental factors and susceptibility to herbicides. *Weeds*, 15, 330–336.

Heap, I. (2007) *The international survey of herbicide resistant weeds*. Available at: https://www.weedscience.org/ [Accessed 10 December 2017].

ISTA (1996) Biochemical test for viability: the topographical tetrazolium test. *Seed Science and Technology*, 24, 203–245.

Kruk, B.C. and Benech-Arnold, R.L. (1998) Functional and quantitative analysis of seed thermal responses in prostrate Knotweed (*Polygonum aviculare*) and common purslane (*Portulacca oleracea*). *Weed Science*, 46, 83–90.

Kruk, B.C., Insausti, P., Razul, A. and Benech-Arnold, R. (2006) Light and thermal environments as modified by a wheat crop: effects on weed seed germination. *Journal of Applied Ecology*, 43(2), 227–236.

Li, X., Li, X., Jiang, D. and Liu, Z. (2006) Germination strategies and patterns of annual species in the temperate semiarid region of China. *Arid Land Research and Management*, 20(3), 195–207.

Lin, J., Shao, S., Wang, Y., Qi, M., Lin, L., Wang, Y. and *et al* (2016) Germination responses of the halophyte *Chloris virgata* to temperature and reduced water potential caused by salinity, alkalinity and drought stress. *Grass and Forage Science*, 71(3), 507–514.

Loch, D.S., Adkins, S.W., Heslehurst, M.R., Paterson, M.F. and Bellairs, S.M. (2004) Seed formation, development, and germination. In: Moser, L.E., Burson, B.L. and Sollenberger, L.E. (Eds.), *Warm-season (C4) grasses*, 45. pp. 95–143. Madison, WI: American Society of Agronomy.

Martinez-Ghersa, M.A., Ghersa, C.M. and Satorre, E.H. (2000) Coevolution of agricultural systems and their weed companions: implications for research. *Field Crops Research*, 67(2), 181–190.

Metzler, M., Papa, J.C. and Tuesca, D. (2014) *Chloris* spp. Un problema en franca expansión. *Para Producir Mejor*, 51, 139–146.

Ngo, T.D., Boutsalis, P. and Preston, C. and Gill, G. (2014). *Seed biology of* Chloris truncata *(windmill grass) and* Chloris virgata *(feathertop Rhodes grass)*. Tasmanian Weed Society, 75–78.

Ngo, T.D., Boutsalis, P., Preston, C. and Gill, G. (2017) Growth, development, and seed biology of feather fingergrass (*Chloris virgata*) in Southern Australia. *Weed Science*, 65(3), 413–425.

Osten, V. (2012) *Feathertop Rhodes Grass: A Best Weed Management Guide*. Department of Agriculture, Fisheries and Forestry Queensland, Australia.

Pezzani, F. and Montaña, C. (2006) Inter-and intraspecific variation in the germination response to light quality and scarification in grasses growing in two-phase mosaics of the Chihuahuan Desert. *Annals of Botany*, 97(6), 1063–1071.

Satorre, E.H. (2011) Recent changes in pampean agriculture: possible new avenues in coping with global change challenges. In: Araus, J.L. and Slafer, G.A. (Eds.), *Crop Stress Management and Global Climate Change*. Wallingford, UK: CABI, pp. 47–57.

Steinmaus, S.J., Prather, T.S. and Holt, J.S. (2000) Estimation of base temperatures for nine weed species. *Journal of Experimental Botany*, 51(343), 275–286.

Swanton, C.J., Mahoney, K.J., Chandler, K. and Gulden, R.H. (2008) Integrated weed management: knowledge-based weed management systems. *Weed Science*, 56(1), 168–172.

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

Ustarroz, D., Kruk, B.C., Satorre, E.H. and Ghersa, C.M. (2016) Dormancy, germination and emergence of *Urochloa panicoides* regulated by temperature. *Weed Research*, 56(1), 59–68.

Washitani, I. (1987) A convenient screening test system and a model for thermal germination responses of wild plant seeds: behaviour of model and real seeds in the system. *Plant, Cell & Environment*, 10(7), 587–598.

Washitani, I. and Masuda, M. (1990) A comparative study of the germination characteristics of seeds from a moist tall grassland community. *Functional Ecology*, 4, 543–557.

Zelaya, I.A. (1997) Germination characteristics of eight weed species from the dry tropics. *Ceiba*, 38, 137–149.

Zhang, H., Tian, Y. and Zhou, D. (2015) A modified thermal time model quantifying germination response to temperature for C3 and C4 species in temperate grassland. *Agriculture*, 5(3), 412–426.

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