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Soil nitrogen fertilisation as a maternal effect on *Buglossoides arvensis* seed germinability

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Summary

Different ecological strategies are developed by weed species to improve their fitness under unpredictable environmental conditions. Maternal effects are a way to enhance the performance of progeny. The external ecological environment of mother plants influences phenotypic traits of the progeny, such as seed germinability. *Buglossoides arvensis* is a facultative winter annual weed species present in cereal crops of the semiarid temperate region of Argentina. Recently, the intensification of agricultural systems has led to a significant increment of external inputs, such as nitrogen fertilisers. In this work, we aimed to determine the effect of different maternal nitrogen fertiliser levels on the germinability of two successive progenies (F_1–F_2). A population-based model was used to estimate thermal time parameters. Our results indicated that under field conditions, nitrogen fertilisation produced an increment on the germinability of the progeny. Nitrogen supply promoted a widening of the permissive germination thermal range through an increment in the mean maximum germination temperature. However, different maternal fertilisation levels did not influence germination thermal time requirements either in F_1 or F_2 progenies. It might be inferred that a significant increment of nitrogen fertiliser supply could increase the probability of occurrence of very early emergence fluxes of *B. arvensis*. From a weed control perspective, the occurrence of early cohorts during summer may demand a redesign of control tactics, to minimise the potential economic and environmental impact of chemical interventions.

Keywords: *Lithospermum arvense*, corn gromwell, thermal time model, seed dormancy, after-ripening, weed management, seed progeny, germination temperature.

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Introduction

Different ecological strategies are developed by weed species to improve their fitness under unpredictable environmental conditions. Maternal effects are a way to enhance the performance of progeny. The environmental conditions experienced by the mother plants, particularly during seed development, serve as cues to predict the likely environment that offspring will encounter (Galloway, 2005). The external ecological environment of mother plants influences phenotypic traits of the progeny, such as seed germinability (Gutterman, 2000). This occurs, mainly, because all the tissues surrounding the embryo and most of the endosperm are of maternal origin, as the mother plant is the main source of nutrients and hormones for the developing seed (Roach & Wulff, 1987; Donohue & Schmitt, 1998; Donohue, 2009).

Seed dormancy is a crucial adaptive ecological trait of the life cycle of weeds. According to Benech-

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Arnold *et al*. (2000), dormancy is an internal condition of the seed characterised by its inability to germinate under otherwise optimal hydric, thermal and gaseous conditions. Primary dormancy is determined during seed development and maturation on the mother plants, thus being influenced by both environmental and management conditions, such as soil nitrogen content. Several studies have shown that maternal environmental factors (i.e. temperature, light quality and intensity, mineral nutrition and water supply) influence seed germinability (Roach & Wulff, 1987; Fenner, 1991; Baskin & Baskin, 1998; Gutterman, 2000). Gutterman (2000) mentioned as a general rule that nutrient addition to the parent plants (chiefly nitrogen fertilisers) reduces seed dormancy levels, increasing seed germinability. In fact, the addition of nitrogen fertilisers to maternal plants has proven to increase seed germinability in several species, such as *Beta vulgaris* L. (Inoe & Yamamoto, 1977), *Chenopodium album* L. (Fawcett & Slife, 1978), *Nicotiana tabacum* L. (Thomas & Raper, 1979), *Arabidopsis thaliana* L. (Alboresi *et al*., 2005) and *Amaranthus retroflexus* L. (Karimmojeni *et al*., 2014). Conversely, higher dormancy levels were obtained with additional nitrogen supply in *Sinapis arvensis* L. (Luzuriaga *et al*., 2006).

Population-based thermal time models are useful tools for describing the dormancy status of a given seed population (Alvarado & Bradford, 2002). Thermal time (i.e. expressed as a sum of day degrees (d°C)) provides a measure of the biological time required for the completion of a given process (Trudgill *et al*., 2005); thus, the magnitude of a given process (e.g. dormancy release) can be described by means of the calculation of specific population-based thermal parameters. Many weed species, both summer- (*Polygonum aviculare* L., *Helianthus annuus* L.) and winter (*Buglossoides arvensis* (L.) I.M. Johnston) and annual or perennial species (*Aesculus hippocastanum* L., *Vitis vinifera* L. subsp. *sylvestris*, *Rhamnus persicifolia* Moris., *Carex diandra* W.D.J. Koch, *Eurotia lanata* (Pursh) Moq.) have been evaluated to assess seed germinability with various population-based modelling approaches (Batlla & Benech-Arnold, 2003; Steadman & Pritchard, 2003; Wang *et al*., 2004; Chantre *et al*., 2009a; Bazin *et al*., 2011; Orrù *et al*., 2012; Porceddu *et al*., 2013; Fernández-Pascual *et al*., 2015). For the specific case of *B. arvensis*, Chantre *et al*. (2009a) proposed an after-ripening model, in which the level of primary dormancy of the seed population was described as a function of after-ripening thermal time accumulation. As indicated by Chantre *et al*. (2009a), the rate of dormancy release in *B. arvensis* is positively correlated with seed storage temperature, increasing seed germinability through a widening of the permissive thermal range for germination.

Buglossoides arvensis (L.) I.M. Johnston [syn. *Lithospermum arvense* (L.)] (corn gromwell) is a facultative winter annual weed species present in cereal crops (wheat, barley and flax) in the South-west area of Buenos Aires province, Argentina. At seed maturity, *B. arvensis* seeds show physiological dormancy, thus requiring a period of dry after-ripening for primary dormancy loss to occur (Baskin & Baskin, 1998). After natural seed dispersal, *B. arvensis* seeds are exposed to high field temperatures during late spring and early summer (Chantre *et al*., 2009b). Seedling emergence occurs mainly in autumn and early spring; thus, late-emerging cohorts behave as a short-lived summer annual species.

According to a study performed by Bischoff and Mahn (2000), on the regeneration of weed communities after cessation of fertilisation on arable fields of the central German Chernozem region, *B. arvensis* appearance is frequently associated with soils with low nitrogen availability. Despite this fact, *B. arvensis* vegetation coverage and seed production *per* plant tend to increase in nitrogen-enriched plots in long-term field experiments (Bischoff & Mahn, 2000).

In the semiarid temperate region of Argentina, specifically in the south-west area of Buenos Aires province, the intensification of extensive agriculture associated with the expansion of non-tillage systems has led to a significant increase in external inputs, such as nitrogen fertilisers. The potential impact of nitrogen supply on *B. arvensis* demographic behaviour is largely unknown. Thus, species-specific data should be generated in order to provide information that might help to develop better weed intervention strategies. As suggested by Mahn (1988), in order to understand the response of the plant community to different supplies of nitrogen, we need to deepen our knowledge of the ability of a single population to use different nitrogen levels. Such investigations would help to elucidate the interrelations between direct and indirect effects of changes in nitrogen supply in long-term field studies (Mahn, 1988).

Based on the hypothesis that nitrogen fertilisation of the mother plants of *B. arvensis* influences seed germinability of the progeny, we aimed to determine the effect of different nitrogen fertiliser levels, as a maternal environmental effect, on the germinability of two successive seed progenies (F_1 and F_2). The modelling approach proposed by Chantre *et al*. (2009a) was used to estimate population-based thermal parameters.

Materials and methods

Seed source material

Mature seeds of *B. arvensis* were hand-collected in December 2010 from oat fields (*Avena sativa* L.) at the Experimental Station of INTA Bordenave (37°50′55″S, 63°01′20″W), Buenos Aires, Argentina. After harvest, obtained seeds were dry-stored at room temperature for 180 days until the initiation of the experiments, when field environmental conditions were adequate for seedling establishment.

Field experiments

Maternal effects were evaluated on two successive generations (F_1 and F_2). Field experiments were conducted during 2011 and 2012, to quantify the effect of nitrogen fertiliser level on offspring germinability (F_1 and F_2 respectively). The experiments were performed at the experimental field of the CCT-CONICET Bahia Blanca (38°39′54″S, 62°13′58″W). The soil type was sandy loam (typic haplustoll) with organic matter of 2%, 4.6 mg kg^{-1} of NO_3-N and alkaline reaction (pH = 7.5).

In a selected area of the experimental field, source seeds (collected in 2010) of *B. arvensis* were sown at 2 cm of burial depth (Chantre *et al.*, 2009b) in 24 plots of 1 m^2 each. An average stand of 90 plants m^{-2} was obtained 45 days after sowing in 2011 and 2012. Maternal treatments consisted of three levels of nitrogen fertiliser (Urea, 46% N) (Control = 0 kg N ha^{-1}; N^+ = 75 kg N ha^{-1} and N^{++} = 150 kg N ha^{-1}) applied at 14/22 (four – true leaves, two – side shoots) stage following the BBCH scale (Hess *et al.*, 1997). A completely randomised factorial design with eight replicates was used. A drip irrigation system provided additional water supply to avoid drought conditions. Plots were hand weeded on a weekly basis.

At harvest time (January 2012), F_1 seeds were collected in three main groups corresponding to each of the applied maternal fertiliser levels. Seeds were further divided into two subgroups in order to: (i) perform germinability tests after 90 days (partially dormant seeds, PD) and 380 days (non-dormant seeds, ND) of dry storage in a growth chamber at 22 (±1°C) (see Germinability test section) and (ii) generate the mother plants to obtain the following seed progeny (F_2). F_2 seeds were harvested in January 2013 and further after-ripened under the same conditions (i.e. time and temperature) described for F_1 until the onset of germinability tests.

Germinability test

Offspring germinability (F_1 and F_2) was assessed on an aluminium temperature gradient bar (Chatterton & Kadish, 1986) at six constant temperatures (5, 8, 12, 16, 20 and 23°C) for 21 days. Four replicates of 30 seeds *per* each maternal treatment and after-ripening time combination were used. Viability of the remaining seeds (ungerminated) was evaluated by a crush test following Borza *et al.* (2007).

Estimation of population thermal parameters

A thermal germination model was used to compare seed germinability behaviour under different maternal environments. Following Chantre *et al.* (2009a), a normal distribution of both base temperature (T_b) and ceiling temperature (T_c) were assumed within the seed population, while suboptimal (θ_1) (1) and supra-optimal (θ_2) (2) thermal time parameters were considered constant among seed fractions (g) as follows:

$$\theta_1 = (T - T_b)t_g \quad (1)$$

$$\theta_2 = (T_c - T)t_g \quad (2)$$

where T is the incubation temperature and t_g is the germination time of a given g seed fraction. An optimal germination temperature of 15°C was assumed to define both thermal ranges (Chantre *et al.*, 2009a). The proportion of germinated seeds for the suboptimal (3) and supra-optimal thermal (4) range was calculated as follows

$$p(T_{b(g)}) = \Phi[(T_{b(g)} - T_{b(50)})/\sigma_{Tb}] \quad (3)$$

$$p(T_{c(g)}) = 1 - [\Phi[(T_{c(g)} - T_{c(50)})/\sigma_{Tc}] \quad (4)$$

where p is the proportion of germinating seeds at a given T_b of a g fraction of the seed population, Φ is the normal probability integral, $T_{b(50)}$ and σ_{Tb} are the mean and standard deviation of the normal distribution respectively. In eqn (4), $T_{c(50)}$ and σ_{Tc} are the mean and the standard deviation of the normal distribution. Optimal thermal parameters were obtained by a non-linear least-squares curve-fitting method using the Levenberg–Marquardt optimisation algorithm (Excel Solver Platform 7.0; Frontline Systems, Inc.).

Statistical analyses

Seed germinability was assessed through the estimation of the thermal parameters of the seed population as described above. A three-way ANOVA was performed to analyse the effect of the maternal fertiliser level (0, 75 and 150 kg N ha^{-1}), after-ripening period under controlled laboratory conditions (90 and 380 days of dry storage) and seed progeny (F_1 and F_2) on *B. arvensis* seed germinability. Tukey's multiple range test was used ($P < 0.05$).

Results

Maximum, minimum and average air daily temperatures from the onset of seed formation in the field until harvest time are shown for 2011 and 2012 (Fig. 1). Collected seeds of both progenies (F_1 and F_2) were assumed to reach full seed maturity (brownish coloured seeds) on 25 December. Seeds were collected on 6 January being exposed to a 12-day after-ripening period in the field previous to seed harvest. Registered mean air daily temperature values during seed formation and field after ripening were on average 0.3 and 8.2°C day^{-1} higher in 2011 compared with 2012 (Fig. 1).

Estimated population thermal parameters for both seed generations (F_1 and F_2) subjected to increasing maternal nitrogen fertilisation levels are shown in Table 1. The mean maximum germination temperature ($T_{c(50)}$) and germination thermal time requirements at suboptimal temperatures (θ_1) were influenced by the after-ripening time and the maternal nitrogen fertiliser levels in both seed progenies (Table 1). Conversely, the rest of the population's thermal parameters (i.e. $T_{b(50)}$, σ_{Tb}, θ_2 and σ_{Tc}) were not influenced either by the fertiliser level or the after-ripening period ($P > 0.10$) (data not shown).

As observed in Table 2, $T_{c(50)}$ values were highly influenced by the level of nitrogen fertiliser applied to the mother plants and the after-ripening time period ($P < 0.01$). As indicated in Fig. 2A, higher $T_{c(50)}$ values were obtained as nitrogen fertiliser supply increased. As after-ripening time progressed, $T_{c(50)}$ values increased (Fig. 2B), irrespective of the maternal nitrogen environment or the seed progeny. Observed differences in $T_{c(50)}$ among seed generations for the different after-ripening periods and maternal N fertiliser levels (Table 2) averaged 0.2°C.

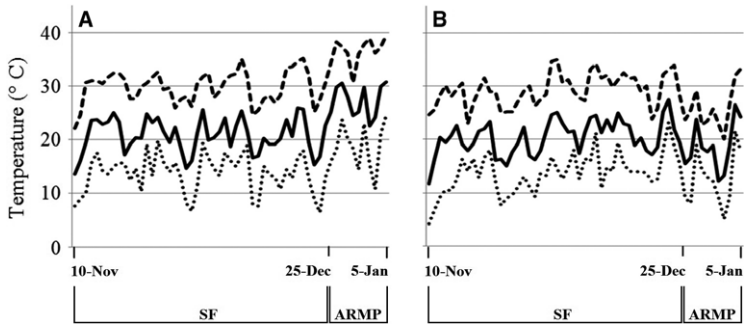

Fig. 1 Maximum (–), mean (—) and minimum (··) air daily temperatures in the field during seed formation (SF) (from 10th November to 25th December) and after ripening on the mother plants (ARMP) (from 25th December to 5th January) for (A) 2011 and (B) 2012.

Table 1 Estimated thermal parameters for two successive generations of *Buglossoides arvensis* seeds (F_1 and F_2) subjected to different levels of maternal nitrogen fertilisation (Control; 75 kg N ha^{-1}:N$^+$; 150 kg N ha^{-1}:N^{++})

Maternal treatment	Days of storage	$T_{b(50)}$ (°C)	θ_1 (°Cd)	σ_{Tb}	RMSE	$T_{c(50)}$ (°C)	θ_2 (°Cd)	σ_{Tc}	RMSE
F_1 (2011)									
Control	90	7.6	72.4	4.43	7.1	18.7	12.7	3.37	13.2
Control	380	7.6	38.4	4.87	8.7	22.4	28.1	9.0	9.6
N$^+$	90	7.0	56.9	4.50	17.9	20.3	22.4	5.39	10.3
N$^+$	380	7.6	25.6	3.31	7.8	21.9	25	7.0	13.5
N^{++}	90	4.9	59.1	3.43	12.3	21.3	29.1	5.11	25.4
N^{++}	380	6.1	50.9	4.13	12.0	25.0	29	7.0	10.2
F_2 (2012)									
Control	90	7.6	139.8	4.38	4.9	18.7	28.3	3.83	11.8
Control	380	4.9	19.6	1.0	24.7	22.4	22.9	4.03	12.9
N$^+$	90	7.6	191.1	5.41	3.9	18.6	33.7	4.47	11.8
N$^+$	380	4.9	20.5	1.11	19.1	24.0	26.1	4.08	13.6
N^{++}	90	7.6	160.0	4.24	5.3	19.1	21.5	2.70	23.1
N^{++}	380	4.9	17.1	1.0	20.0	26.0	27.5	5.60	12.2

RMSE, root-mean-square error (goodness of fit).

Seeds corresponding to the first and second progeny (F_1 and F_2) were harvested in 2011 and 2012, respectively, and further incubated at 5, 8, 12, 16, 20 and 23°C, after 90 and 380 days of dry storage. Parameters were obtained following Chantre *et al.* (2009a) by simulation of the germination time-course curves assuming a normal distribution of both T_b and T_c in the seed population. $T_{b(50)}$ and σ_{Tb} are the mean and standard deviation of the normal distribution of the base germination temperature respectively. $T_{c(50)}$ and σ_{Tc} are the mean and the standard deviation of the normal distribution of the maximum germination temperature. θ_1 and θ_2 are the sub- and supra-optimal thermal time parameters among seed fractions.

Table 2 Three-way ANOVA for the mean maximum germination temperature ($T_{c(50)}$) and the suboptimal germination thermal time (θ_1) as a function of the seed progeny (F_1 or F_2), after-ripening time under dry storage (PD, partially dormant and ND, non-dormant) and maternal nitrogen fertiliser level (0, 75 or 150 kg N ha^{-1})

Dependent variable	Source of variation	SS	df	MS	*F*	*P*
$T_{c(50)}$	Seed progeny (F)	16.46	1	16.46	6.5	0.0152
	After-ripening time (AT)	290.23	1	290.23	114.63	<0.0001
	Maternal nitrogen level (N)	51.74	2	25.87	10.22	0.0003
	F * AT	0.57	1	0.57	0.22	0.6392
	F * N	5.47	2	2.73	1.08	0.3505
	AT * N	5.13	2	2.56	1.01	0.3732
	F * AT * N	1.83	2	0.91	0.36	0.6994
θ_1	Seed progeny (F)	0.28	1	0.28	21.62	<0.0001
	After-ripening time (AT)	2.24	1	2.24	173.79	<0.0001
	Maternal nitrogen level (N)	$6.3^{-0.3}$	2	$1.8^{-0.3}$	0.14	0.8701
	F * AT	0.71	1	0.71	55.35	<0.0001
	F * N	0.17	2	0.09	6.7	0.0034
	AT * N	0.07	2	0.03	2.6	0.0881
	F * AT * N	0.02	2	0.02	1.66	0.2047

SS, sum of squares; df, degrees of freedom, MS, mean square.
F = f-ratio (*F*-statistic); *P* = probability.

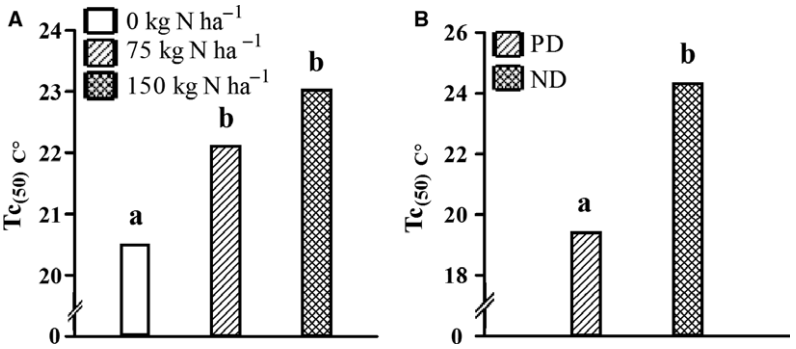

Fig. 2 Mean maximum germination temperature ($T_{c(50)}$) obtained for: (A) different maternal nitrogen fertiliser levels. and (B) for both storage periods in the laboratory. PD, partially dormant (partially after-ripened, 90 days); ND, non-dormant (fully after-ripened seeds, 380 days). Bars with the same letter are not significantly different at $P = 0.05$ by Tukey's multiple range test.

A first-order interaction between *seed progeny *after-ripening time* ($P < 0.001$) was registered for germination thermal time requirements at suboptimal temperatures (θ_1; Table 2). As after-ripening time progressed, lower θ_1 values were obtained for both seed progenies, with the highest germination thermal time requirements associated with partially after-ripened seeds of the F_2 progeny (Fig. 3A; Table 1). Although the interaction *seed progeny *maternal nitrogen level* was statistically significant (Fig. 3B; Table 2), no influence of the maternal nitrogen environment was observed ($P = 0.87$). Thus, differences in θ_1 values could be attributed solely to different germination thermal time requirements between seed progenies (Fig. 3B).

Discussion

By implementing a population-based model, we were able to quantify the effect of the maternal nitrogen fertiliser level on the germinability of two successive generations of *B. arvensis* as a function of after-ripening time. Our results indicate that under field conditions, nitrogen fertilisation of the mother plants of *B. arvensis* produced an increment on the germinability of the seed progeny. Nitrogen supply promoted a widening of the permissive germination thermal range by increasing the mean maximum temperature ($T_{c(50)}$) (Fig. 2A). Higher $T_{c(50)}$ was also obtained as after-ripening progressed under dry storage conditions (Fig. 2B). Our results match those obtained by Chantre *et al.* (2009a) that showed that *B. arvensis* seeds were able to germinate at higher incubation temperatures with after-ripening thermal time accumulation.

Lower suboptimal thermal time requirements for germination were obtained for non-dormant seeds compared with partially after-ripened seeds for both F_1 and F_2 generations (Fig. 3A). These results also coincide with those published by Chantre *et al.* (2009a) that described changes in θ_1 values as a polynomial function of storage temperature and after-ripening

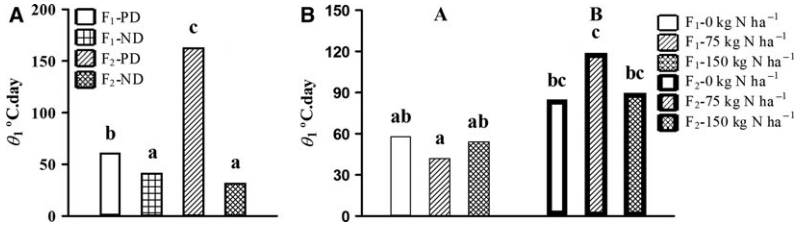

Fig. 3 Germination suboptimal thermal time requirements (θ_1) for the first (F_1) and second (F_2) seed generation: (A) on partially dormant (PD) (90 days of after-ripening) and non-dormant (ND) (380 days of after-ripening) seeds; and (B) for different maternal nitrogen fertiliser levels. Bars with the same letter are not significantly different at $P = 0.05$ by Tukey's multiple range test. Capital letters indicate differences between seed progenies (B). Small letters indicate differences among the evaluated treatments (A and B).

thermal time accumulation. As observed in Fig. 3B, maternal nitrogen fertiliser levels did not influence thermal time requirements either in F_1 or F_2. However, θ_1 figures were clearly higher in F_2 compared with F_1 (Fig. 3B), mainly due to partially after-ripened seeds of the F_2 progeny, which showed the highest thermal time requirements (Fig. 3A).

Although a higher germinability of the F_2 progeny might have been expected due to a higher fertiliser pressure compared with F_1, other environmental variables such as field temperature could have influenced obtained results. As observed in Fig. 1, F_1 seeds experienced an after-ripening period on the mother plants characterised by higher mean and maximum air daily temperatures compared with F_2 (mean air daily temperature was 8.2°C day^{-1} higher in 2011 compared with 2012). Thus, F_1 seeds were able to accumulate more after-ripening thermal time than F_2 prior to seed harvest. Other winter annual species also showed higher germinability when seeds experienced warmer temperatures during pre- and post-dispersal, such as *Lolium rigidum* (Steadman *et al*., 2003a,b) and *Arabidopsis thaliana* (Schmuths *et al*., 2006).

We confirm our working hypothesis that nitrogen fertilisation of the mother plants of *B. arvensis* influences seed germinability within each seed progeny. Nitrogen fertiliser addition as a maternal environmental effect also reduced seed dormancy levels in other weed species (Fawcett & Slife, 1978; Gutterman, 2000; Alboresi *et al*., 2005). It was suggested that nitrogen may act as a signal involved in abscisic acid or gibberellin pathways during seed dormancy release (Alboresi *et al*., 2005). However, more studies are required to elucidate whether nitrogen is associated with the synthesis or the sensitivity of the embryo to the above-mentioned hormones.

Based on our results, it might be expected that a significant increment of nitrogen fertiliser supply due to the intensification of extensive agricultural areas in the semiarid temperate region of Argentina could increase the probability of occurrence of very early emergence fluxes of *B. arvensis* during late summer after natural seed dispersal. It might be expected that nitrogen fertilisation of adult plants in cereal crops would generate offspring with higher germinability compared to unfertilised crop fields. In the semiarid region under study (Bordenave region), historic air mean temperature values during late summer average 18.8 ± 1.5°C (March: 1960–2015; http://inta.gob.ar/documentos/informacion-agrometeorologica-1). On average, mean maximum germination temperature values of both progenies of nitrogen-fertilised mother plants reached 19.8°C after 90 days of dry storage. Thus, it might be expected that *B. arvensis* could generate not only typical autumn and early spring cohorts, but also an earlier cohort during late summer, soon after dispersal, given that rainfall allows for adequate soil moisture conditions for seedlings establishment. Experimental evidence of *B. arvensis* seedlings recruitment during late summer under semiarid conditions was provided by G.R. Chantre (unpubl. obs).

From a weed control perspective, the occurrence of early emergence cohorts associated with nitrogen fertilisation practices, mainly under non-tillage systems, might demand a redesign of weed control tactics to reduce the economic and environmental impact of chemical weed interventions. Early treatments (i.e. prior to crop seeding) could increase operation costs and also generate a higher selection pressure on weed-resistant biotypes. In fact, in 2009, *B. arvensis* -resistant biotypes to tribenuron-methyl were detected in wheat fields of China (Heap, 2016). This is a very concerning issue in Argentina because of the high reliance on ALS inhibitor herbicides for *B. arvensis* control and the possibility of cross-resistance to other group B/2 (ALS inhibitors) herbicides (e.g. metsulfuron- and iodosulfuron-methyl).

To our knowledge, mathematical models have not been previously used to analyse the effect of nitrogen fertiliser as a maternal factor on seed germinability. Considering maternal effects on the development of population-based models would allow us to quantify

seed population's germination behaviour and to better predict seed germinability changes associated with the dormancy status of weed species and their ecological implications. From a weed management perspective, the information provided by such models might help to design better and more precise intervention tools, such as adequate weed emergence predictive models (Chantre *et al.*, 2012, 2014; Blanco *et al.*, 2014) and operational-based planning models for optimal time of intervention (Lodovichi *et al.*, 2013).

As previously mentioned, no evidence of nitrogen fertilisation pressure was observed across progenies. Evidently, field temperature variation between years during seed formation and seed after ripening on the mother plants could have masked a potential cumulative effect of nitrogen on seed germinability of the F_2 progeny. Thus, further studies should be performed under controlled environmental conditions during various successive generations to evaluate nitrogen pressure on *B. arvensis* seed germinability.

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