Short communication

A plurality of causal mechanisms explains the persistence or transience of soil seed banks

C.E. Sartor [a,*], L. Marone [a,b,c]

[a] Desert Community Ecology Research Team (Ecodes), IADIZA Institute (CONICET), Casilla de Correo 507, 5500 Mendoza, Argentina
[b] Center for Advanced Studies in Ecology & Biodiversity (CASEB), Santiago, Chile
[c] Instituto de Ciencias Básicas, Universidad Nacional de Cuyo, Centro Universitario, M5502JMA Mendoza, Argentina

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ABSTRACT

Annual forbs form short-term persistent soil seed banks whereas perennial grasses form mostly transient ones in the central Monte desert. A conceptual framework predicts that annual forb seeds will have primary dormancy, whereas perennial grasses will have low dormancy levels. We assessed whether the dormancy traits of four annual forb species and five perennial grass species can account for their soil seed bank dynamics. To overcome dormancy, we treated perennial grasses and autumn annual forbs with high temperatures, and spring annual forbs with low temperatures. To force seeds into secondary dormancy we exposed non-dormant perennial grasses to low temperatures. Most of the annual forbs and two perennial grasses (*Setaria leucopila* and *Sporobolus cryptandrus*) showed low germination rates. The remaining perennial grasses presented moderate (*Pappophorum caespitosum* and *Digitaria californica*) or high germination levels (*Trichloris crinita*). Low temperatures increased germination in spring forbs (*Chenopodium papulosum* and *Parthenium hysterophorus*), but high temperatures did not break dormancy in autumn forbs (*Sphaeralcea miniata* and *Phacelia artemisioides*). Germination of perennial grasses increased after they had been exposed to high temperatures, but only two species reentered into dormancy under low temperature. Given that in the central Monte desert winter–autumn granivores eat mainly grass seeds, we conclude that high seed dormancy and low consumption may contribute to the persistent soil seed bank of most forbs, and that seed dormancy itself does not explain the transience of grass seed banks.

1. Introduction

Mechanisms such as seed dormancy, germination, predation, pathogen attack, deep burial and physiological death affect seed persistence in the soil bank (Simpson et al., 1989).

Dormancy is a mechanism that delays germination until the proper season for plant recruitment. Former works on soil seed banks suggested that seed dormancy is a necessary condition to form a persistent seed bank and that non-dormant seeds usually form transient seed banks (Grime, 1981). Recently, several authors have pointed out that dormancy is related to short-term persistence (from several months to one or two years) and the lack of proper environmental clues for germination relates to long-term persistence (more than five years) (Thompson, 2000; Thompson et al., 2003; Walck et al., 2005).

In the central Monte desert of Argentina, annual forbs and perennial grasses disperse their seeds in late summer (Marone et al., 1998a) but they exhibit different persistence in the soil seed bank. Annual forb seeds remain in the soil bank until the next growing season, forming a short-term persistent seed bank, but perennial grass seeds are mostly depleted from the soil bank at the beginning of the next growing season (i.e. they form a transient soil bank, Marone et al., 1998b). Plants also show different emergence patterns. Emergence of annual forbs is markedly seasonal; some species germinate in early autumn and other species in spring. In contrast, perennial grasses germinate during autumn, spring and summer months (Marone et al., 2000). These patterns suggest that annual forbs could have dormant seeds from dispersal until germination season, and that perennial grasses have non-dormant seeds until the beginning of the growing season.

Our first goal is to corroborate whether dormancy of annual forbs and perennial grasses in the central Monte desert are compatible with their short-term persistent and transient soil seed

* Corresponding author. Present address: Cátedra de Fisiología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Alte Brown 500, M5528AHB, Chacras de Coria, Luján de Cuyo, Mendoza, Argentina. Tel.: +54 2614135010; fax: +54 2614960469.
E-mail address: csartor@fca.uncu.edu.ar (C.E. Sartor).

banks. Since temperature is the main environmental signal governing dormancy (Bewley and Black, 1994; Gutterman, 1994; Probert, 2000; Baskin and Baskin, 2001), our second goal is to survey whether the effect of temperature on seed dormancy can explain the emergence patterns of both groups of species.

Despite the attractive conceptual framework that explains seed bank dynamics based only on factors controlling dormancy and germination, in the central Monte desert losses due to germination are low for both groups of species (Marone et al., 2000), and seed predation has been suggested to be an important mechanism governing the transience of the perennial grass seed bank and the persistence of the annual forb seed bank (Marone et al., 1998b, 2008). Our final goal is to assess all available evidence to identify those mechanisms most likely determining seed bank dynamics in the central Monte desert.

2. Materials and methods

For all germination and dormancy trials we collected seeds from the Biosphere Reserve of Ñacuñán (34° 02′ S, 67° 58′ W), an area with 25–50% grass cover, mostly perennial C4 poaceae species (Cavagnaro, 1988). Annual forb cover is usually lower than grass cover, although highly variable from year to year (Marone et al., 1998a). Ñacuñán's climate is dry and temperate with cold winters. Over 75% of the annual rainfall occurs in spring–summer (October–March average = 250 mm, $n = 25$ years; Marone et al., 1998b).

We collected seeds of the five most abundant perennial grasses in the soil seed bank, Digitaria californica (Benth) Henrard, Pappophorum caespitosum R. Fries, Setaria leucopila (Scribner et Merrill), Sporobolus cryptandrus (Torr) A. Gray, and Trichloris crinita (Lag) Parodi. We also collected seeds of two of the most abundant spring-germinating annual forbs, Chenopodium papulosum Moq (Chenopodiaceae), Parthenium hysterophorus L. (Compositae), and seeds of two of the most abundant autumn-germinating annual forbs Phacelia artemisioides Gris (Hydrophylaceae) and Sphaeralcea miniata (Cav) Spach (Malvaceae) (Marone et al., 2004). Seeds were collected in May 1999 from the mother plant, and kept in paper bags under laboratory conditions for 5 months before the beginning of every trial. We use the term "seed" to refer to the unit of dispersal and germination.

2.1. Germination

For each species, we incubated five replicates of 40 seeds each in 9-cm diameter plastic Petri dishes prepared with a layer of cotton and a paper filter disk. We moistened the substratum with distilled water and remoistened it when necessary. We carried out germination tests in temperature-controlled incubators (Precision Scientific model 818) at 30 °C for perennial grass species and 20 °C for annual forb species. Preliminary experiments in our laboratory indicated that these temperatures were appropriate for germination of each group of species (L. Marone, unpublished results). We kept Petri dishes in darkness by wrapping them with black plastic sheet. Radicle emergence was the criterion for germination. Those seeds that did not germinate after 15 days were checked for viability by using Tetrazolium test (I.S.T.A., 1985). Final germination percentages were corrected by the number of viable seeds.

2.2. Seed dormancy release

As temperature of the season before the germination season usually breaks seed dormancy (Baskin and Baskin, 2001) we exposed autumn forbs and perennial grasses to warm temperatures similar to those of summer (warm stratification).

For warm stratification (Baskin and Baskin, 2001), we placed three groups of 300 seeds of each species in fine-mesh poly organza bags. Seeds were superficially buried inside 350 cc plastic boxes filled with sandy soil. We placed the plastic boxes in temperature-controlled incubators at an alternating temperature of 45°/15 °C for 8 and 16 h respectively, and watered them daily with 50 ml of tap water. On the 15th, 21st, and 45th day after warm stratification, we exhumed one bag of each species and placed the stratified seeds for germination following the same experimental design described in Section 2.1.

We exposed spring forbs to winter temperatures (cold stratification). For cold stratification (Bewley and Black, 1994), we put seeds of each species between moist cotton layers in 9-cm Petri dishes and placed them in a refrigerator at a temperature ranging from 2° to 4 °C. On the eighth, 15th, and 44th day we removed one group of seeds from the refrigerator and placed the stratified seeds for germination following the same experimental design described in Section 2.1.

2.3. Secondary dormancy induction

Some seeds can enter into secondary dormancy when exposed to temperatures of the season following the germination season (Baskin and Baskin, 2001) and are thus able to persist in the soil seed bank until the next growing season (Walck et al., 2005). Due to this, we exposed seeds of the perennial grasses D. californica, P. caespitosum, S. leucopila, and S. cryptandrus to low temperatures to find out whether winter temperatures could induce them into secondary dormancy.

We warm stratified (in the same way as described in Section 2.2.) three groups of 300 seeds each, for 15 days. After this period, we exhumed all groups of seeds. Two groups were cold stratified (in the same way as described in Section 2.2) to induce secondary dormancy and the remaining one was placed for germination to see whether seed dormancy was broken. At the same time, we put a group of non-stratified seeds of each species for germination in order to find out the germination percentage of dispersed seeds. On the 8th and 15th day we removed one bag from the refrigerator and placed the seeds for germination following the same experimental design described in Section 2.1.

2.4. Statistical analysis

Data were square-root transformed and then we tested for differences among means in temperature trials using ANOVA and a posteriori Tukey tests. When transformed data did not comply with the assumptions of normality and homogeneity of variances, we used the Kruskal–Wallis test, and a Tukey-type test (Zar, 1996).

3. Results

3.1. Germination

Perennial grass seeds could be separated into three groups (Table 1). S. cryptandrus and S. leucopila germinated <10%, D. californica and P. caespitosum germinated 60–80%, and T. crinita had a high germination rate (almost 100%). Most annual forb seeds tested had, in turn, low levels of germination (<15%; Table 1), except for P. hysterophorus (>63%).

3.2. Seed dormancy release

Warm stratification caused a significant increase in germination of P. caespitosum ($H = 15.1$; d.f. = 3; $p = 0.001$), D. californica ($H = 14.3$; d.f. = 3; $p < 0.01$), S. leucopila ($F = 32.9$; d.f. = 3;

Table 1
Germination percentages (±SE) of perennial grasses at 30 °C, and annual forbs at 20 °C.

	Germination (%)
Perennial grasses	
Sporobolus cryptandrus	1.6 ± 1.5
Setaria leucopila	7.5 ± 5.2
Digitaria californica	62 ± 16.9
Pappophorum caespitosum	76.4 ± 1.7
Trichloris crinita	99.4 ± 1.4
Annual forbs	
Phacelia artemisioides	0
Chenopodium papulosum	7.9 ± 5.7
Sphaeralcea miniata	12.5 ± 4.2
Parthenium hysterophorus	62.8 ± 11.5

$p < 0.0001$), and *S. cryptandrus* ($F = 29.2$; d.f. $= 3$; $p < 0.0001$), whereas the high germination level of non-stratified *T. crinita* seeds did not modify under the warm treatment (Table 2). Germination of the autumn forbs did not change after warm stratification (Table 2).

Cold stratification caused a significant increase in germination percentages of *C. papulosum* ($F = 34.4$; d.f. $= 3$; $p < 0.0001$), and it could have had a more restricted although also positive effect on the germination of *P. hysterophorus* ($F = 13.7$; d.f. $= 3$; $p < 0.001$. Table 2).

3.3. Secondary dormancy induction in perennial grasses seeds

Germination did not change when warm stratified seeds (i.e. the highest proportion of non-dormant seeds for all species) of *P. caespitosum* and *D. californica* were exposed to cold stratification. By contrast, germination of *S. leucopila* ($F = 19.9$; d.f. $= 3$; $p < 0.0001$) and *S. cryptandrus* ($F = 23.9$; d.f. $= 3$; $p < 0.001$) seeds did decrease under this treatment (Table 3).

4. Discussion

Seeds of the annual forbs *C. papulosum*, *S. miniata* and *P. artemisioides* remained dormant when dispersed, as it was expected for seeds with short-term persistent soil bank. Since in our study site 90–95% of forb soil seed bank comes from these species (Marone et al., 1998a), their dormancy may satisfactorily explain the overall forb seed bank dynamics, despite *P. hysterophorus* seeds reached the soil with only moderate levels of dormancy.

Table 2
Influence of stratification on the germination percentages (±SE) of perennial grasses and annual forbs. Different letters represent significant differences between control and stratification treatments ($p \leq 0.05$).

	Control	Warm stratification		
		15 days	21 days	45 days
Perennial grasses				
T. crinita	99.4 ± 1.4	100 ± 0	92.4 ± 6.4	100 ± 0
P. caespitosum	76.4 ± 1.7^a	98.4 ± 3.6^b	90.9 ± 7.5^a	99.2 ± 1.7^b
D. californica	62 ± 16.9^a	94.5 ± 5.6^a	99.2 ± 1.9^b	84.1 ± 12.1^a
S. leucopila	7.5 ± 5.2^a	30.2 ± 9.2^b	30.4 ± 7.4^b	25 ± 7^b
S. cryptandrus	1.6 ± 1.5^a	17.3 ± 2.8^b	2.6 ± 1.8^a	9.8 ± 3.3^b
Annual forbs				
S. miniata	12.5 ± 6.4	18.5 ± 8.5	9.3 ± 1.7	12.4 ± 10.1
P. artemisioides	0	0	0	0
	Control	Cold stratification		
		8 days	15 days	44 days
P. hysterophorus	62.8 ± 11.5^a	74.3 ± 4.8^a	84.7 ± 10.1^b	48.5 ± 9.7^a
C. papulosum	7.9 ± 5.7^a	41 ± 8.7^b	69 ± 8.6^b	35.4 ± 10.3^b

Table 3
Influence of cold stratification on germination percentages (±SE) of warm stratified seeds of perennial grasses. Different letters represent significant differences between treatments.

	Control	Warm stratification (dormancy release)	Cold stratification (dormancy induction)	
			8 days	15 days
D. californica	94.7 ± 3.2	100 ± 0	99.2 ± 1.6	100 ± 0
P. caespitosum	59.6 ± 13.8^a	88.8 ± 1.6^{ab}	93.7 ± 5.7^b	98.2 ± 1.6^b
S. leucopila	1.5 ± 3.3^a	21.4 ± 8.4^b	7.8 ± 1.5^c	9.6 ± 3.4^c
S. cryptandrus	0^a	31.5 ± 5.5^b	8 ± 8.9^c	6 ± 4.9^c

As it was expected for annual plants with seed dormancy controlled by temperature (Baskin and Baskin, 2001), summer annual forbs (*C. papulosum* and *P. hysterophorus*) increased their germination percentage with the cold stratification treatment, suggesting that these seeds can overcome dormancy during the winter (Fig. 1). However, we need additional information to determine the causes of low field emergence in the summer. High temperatures might induce secondary dormancy in forb seeds (Baskin et al., 1993), or low germination may be simply a response to unfavorable environmental conditions during the summer (i.e. drought; enforced dormancy sensu Harper, 1957). Both strategies are found in annual species living in unpredictable habitats (Freas and Kemp, 1983; Baskin et al., 1993; but see Adondakis and Venable, 2004).

Conversely, warm stratification did not increase germination percentage of the autumn forbs *S. miniata* and *P. artemisioides*, implying that other mechanisms should contribute to break seed dormancy (Fig. 1). *S. miniata* seeds are covered by a hard coat that could impose physical dormancy as has been indicated for many
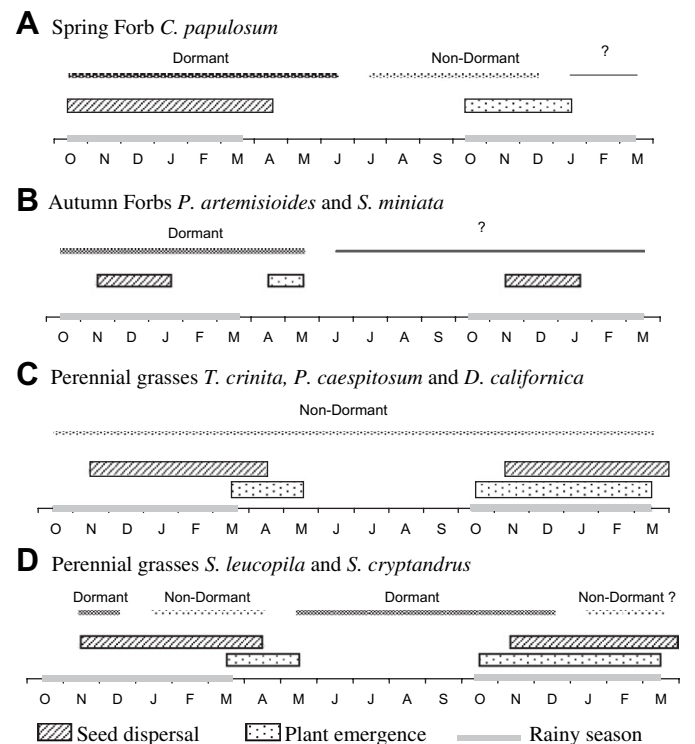

Fig. 1. Seed dispersal (Marone et al., 1998a), Plant emergence (Marone et al., 2000) and dormancy status (this study) of A) Spring forb *Chenopodium papulosum*; B) autumn forbs *Phacelia artemisioides* and *Sphaeralcea miniata*; C) Perenial grasses *Trichloris crinita*, *Pappophorum caespitosum* and *Digitaria californica* and D) Perennial grasses *Setaria leucopila* and *Sporobolus cryptandrus*.

other species of the Malvaceae family (Baskin and Baskin, 2001). On the other hand, several annual winter species of *Phacelia* require light for germination (Baskin and Baskin, 2001), and it is possible that *P. artemisioides* was not exposed to enough light during our experiments.

A model of the mechanisms affecting soil seed bank dynamics of annual forbs in the central Monte desert indicates (1) that forb seeds have primary dormancy when dispersed, (2) that the number of emerging seedlings in the field is usually <1% of seed reserves (Marone et al., 2000), and, (3) that forb seeds represent a very low percentage of the granivorous diet of both birds (Marone et al., 1998b, 2008), and ants (Pirk and Lopez de Casenave, 2006; Pirk, 2007). High seed dormancy as well as low vulnerability to granivorous animals are consistent with the mostly persistent forb soil seed bank at Ñacuñán.

In summer, *T. crinita* dispersed non-dormant seeds, whereas *P. caespitosum* and *D. californica* dispersed a high proportion of non-dormant seeds. In the last two species, warm stratification had a widely positive effect on germination capacity and subsequent cold stratification did not induce seeds into secondary dormancy (Fig. 1). In agreement with all such features, the three grasses form transient soil seed banks at Ñacuñán (Marone et al., 1998a). However, they also show low levels of seedling emergence at field conditions (0–5% of seed reserves; Marone et al., 2000). This evidence suggests that germination is limited by some environmental restrictions like the lack of significant rainfall during most of the summer, and that seed consumption may be a major mechanism contributing to the seasonal variability of soil seed bank. Accordingly, the seeds of the three grasses are heavily consumed by both ants (Pirk and Lopez de Casenave, 2006; Pirk, 2007) and birds (Marone et al., 2008) at Ñacuñán.

S. leucopila and *S. cryptandrus*, on the other hand, dispersed a very high proportion of dormant seeds, a fraction of which would be non-dormant in autumn, and enter into secondary dormancy in winter (Fig. 1). Despite their dormancy traits and low levels of emergence in field conditions, both species have transient seed banks in the central Monte desert (Marone et al., 1998b). Granivory may be the main mechanism governing the dynamics of these seed species in the soil: *S. leucopila* (0.6 mg in mass), which is the largest grass seed at our study site, is heavily consumed by birds (Marone et al., 2008), and is preferred by all the most common seed-eating bird species (Cueto et al., 2006); on the other hand, *S. cryptandrus* (0.06 mg) is the smallest but most abundant grass seed in the soil bank, and the seed item most frequently consumed by granivorous birds (Marone et al., 2008).

Our results suggest that a plurality of mechanisms determines whether a plant species forms a persistent or transient soil seed bank in the central Monte desert (Fenner, 1995; Marone and Horno, 1997).

Acknowledgments

References

Adondakis, S., Venable, D.L., 2004. Dormancy and germination in a guild of Sonora desert annuals. Ecology 85, 2582–2590.

Baskin, C.C., Chesson, P.L., Baskin, J.M., 1993. Annual seed dormancy cycles in two desert winter annuals. Journal of Ecology 81, 551–556.

Baskin, C.C., Baskin, J.M., 2001. Seeds, Ecology, Biogeography and Evolution of Dormancy and Germination. Academic Press, San Diego.

Bewley, J.D., Black, M., 1994. Seeds, Physiology of Development, and Germination. Plenum Press, New York.

Cavagnaro, J.B., 1988. Distribution of C3 and C4 grasses in a temperate arid region of Argentina. Oecologia 76, 273–277.

Cueto, V.R., Marone, L., Lopez de Casenave, J., 2006. Seed preferences in sparrow species of the Monte desert: implications for seed–granivore interactions. Auk 123, 358–367.

Fenner, M., 1995. Ecology of seed banks. In: Kigel, J., Galili, G. (Eds.), Seed Development and Germination. Marcel Dekker, New York, pp. 507–543.

Freas, K.E., Kemp, P.R., 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. Journal of Ecology 71, 211–217.

Grime, J.P., 1981. The role of seed dormancy in vegetation dynamics. Annals of Applied Biology 98, 555–558.

Gutterman, Y., 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. Botanical Review 60, 373–425.

Harper, J.L., 1957. The ecological significance of dormancy and its importance in weed control. Proceedings of the International Congress for Crop Protection 4, 415–420.

International Seed Testing Association, 1985. International rules for seed testing. Seed Science and Technology 13, 299–355.

Marone, L., Horno, M.E., 1997. Seed reserves in the central Monte Desert, Argentina: implications for granivory. Journal of Arid Environments 36, 661–670.

Marone, L., Rossi, B.E., Horno, M.E., 1998a. Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert. Plant Ecology 137, 143–150.

Marone, L., Rossi, B.E., Lopez de Casenave, J., 1998b. Granivore impact on soil-seed reserves in the central Monte desert, Argentina. Functional Ecology 12, 640–645.

Marone, L., Horno, M.E., González del Solar, R., 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. Journal of Ecology 88, 940–949.

Marone, L., Cueto, V.R., Milesi, F.A., Lopez de Casenave, L., 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Canadian Journal of Botany 82, 1809–1816.

Marone, L., Lopez de Casenave, J., Milesi, F.A., Cueto, V.R., 2008. Can seed-eating birds exert top-down effects on grasses of the Monte desert? Oikos 117, 611–619.

Pirk, G.I., 2007. Granivoría por hormigas del género Pogonomyrmex en el Monte central: consumo de semillas e impacto sobre el banco de suelo. Tesis doctoral. Universidad de Buenos Aires, Buenos Aires, Argentina.

Pirk, G.I., Lopez de Casenave, J., 2006. Diet and seed removal rates by harvester ants *Pogonomirmex rastratus* and *Pogonomyrmex pronotalis* in the central Monte desert, Argentina. Insectes Sociaux 53, 119–125.

Probert, R., 2000. The role of temperature in the regulation of seed dormancy and germination. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International, London, pp. 261–292.

Simpson, R.L., Allessio-Leck, M., Parker, T., 1989. Seed banks: general concepts and methodological issues. In: Allessio-Leck, M., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, pp. 3–8.

Thompson, K., 2000. The functional ecology of seed banks. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International, London, pp. 215–235.

Thompson, K., Ceriani, R.M., Bakker, J.P., Bekker, R.M., 2003. Are seed dormancy and persistence in soil related? Seed Science Research 13, 97–100.

Walck, J.L., Baskin, J.M., Baskin, C.C., Hidayati, S.N., 2005. Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. Seed Science Research 15, 189–196.

Zar, J.H., 1996. Biostatistical Analysis, third ed. Prentice-Hall, Englewood Clifs, New Jersey.