



Seed dormancy and longevity in *Stipa tenacissima* L. (Poaceae)

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Abstract

In the present paper we studied the life history traits related to seed germination of *Stipa tenacissima*, a key species in semiarid environments of western Mediterranean areas. *S. tenacissima* is a perennial tussock grass, which has traditionally been considered to expand mainly by vegetative propagation with little or no sexual reproduction. We analysed seed longevity as well as the type of seed dormancy and the role of the seed covers from seeds collected from different populations in SE Spain. We also studied the variation in seed germinability among populations, individuals, and years and the ability of seeds of *S. tenacissima* to form soil seed banks. There was significant variation in seed germination among individuals, populations and years. Lemma and palea were the main factor controlling these differences since their removal promoted higher and faster germination and eliminated the differences in germination parameters among populations. However, the control of dormancy by lemma and palea was independent of their weight, suggesting that their chemical nature plays a more important role than does size in controlling seed germination. Mechanical scarification treatments (via abrasion with sand) did not affect seed germination. The decay in seed germinability two years after seed collection and the low density of viable seeds in soils one year after seed dispersal indicated that *S. tenacissima* forms transient soil seed banks.

Introduction

Soil erosion is the main determinant of land degradation in the arid and semiarid regions, which are widespread in the Mediterranean Basin. One of the foremost causes of soil erosion and desertification is human activity (agricultural practices, overstocking, abandonment of fields, forest fires), which leads to the degradation or destruction of the natural plant cover (Mensching 1986; López Bermúdez and Albaladejo 1990; Pérez-Trejo 1994; Albaladejo et al. 1996).

One way to regenerate degraded soils, reduce soil erosion and prevent the spread of desert-like conditions is by means of revegetation (Mensching 1986; Correal et al. 1989; Francis and Thornes 1990). Therefore, there is a need for ecological knowledge to better manage natural vegetation. The identification and characterization of factors influencing the growth, development, and persistence of key plant species is needed (Call and Roundy 1991).

The first step in any programme of rehabilitation of soils degraded by erosion is to select the most suitable species. This will be based on the capacity of these species to germinate and establish themselves in the given environmental conditions, leading to improved vegetation and soil properties (Morgan et al. 1990; Albaladejo et al. 1996).

In many cases, the use of shrubs in revegetation is very advisable, as they grow quickly to provide an adequate canopy and ground-litter cover, bind the surface soil with their root, and provide a ready source of green manure when they die. Some grasses, for example *Stipa tenacissima*, are already widely used (Francis and Thornes 1990). Certain characteristics of *S. tenacissima*, such as the protection of soil against erosion (Sánchez and Puigdefábregas 1994; Bochet et al. 1998), its resistance to long drought periods (Pugnaire and Haase 1996; Pugnaire et al. 1996), its resprouting ability (Martínez-Sánchez et al. 1997), and its ecological amplitude (soils, climates, slopes) (Le

Houérou 1969), make it a very valuable species with a view to using it in revegetation programmes. More information about its life cycle is needed in order to efficiently use and manage this plant for resource conservation. One of the main aspects unknown about its life cycle is the life history traits related to germination, provided that germination means the transition from a state tolerant to drought and extreme temperatures (the seed) to a more vulnerable state (the seedling) (Esler and Phillips 1994; Kigel 1995).

The Esparto Service in Spain reported that germination of the seeds of *S. tenacissima* is not synchronous and that seeds stored in a dry and ventilated place can maintain germinability for two or three years (Servicio del Esparto 1953). These traits could indicate a seed dormancy in this species, which would be in accord with germination features of other plants of the genus *Stipa* (Ellis et al. 1985; Kigel 1995; White and Van Auken 1996).

Seed dormancy in the Poaceae often disappears following a period of after-ripening (Simpson 1990). In species from dry regions, high soil temperatures during the summer may increase seed coat permeability to water and to oxygen (Baskin and Baskin 1989; Probert 1992; Kigel 1995) and as a result, innate dormancy is broken (Ellis et al. 1985; Probert 1992; Gutterman 1993). The rate of loss of dormancy increases with temperature. Temperatures from 40 °C to 100 °C are the most effective (Ellis et al. 1985; Baskin and Baskin 1989). In the case of Poaceae, the longer and warmer the storage environment, the greater the loss of dormancy (Murdoch and Ellis 1992).

Where seed covering structures act as a physical barrier to germination, the obvious dormancy-breaking mechanism involves damage of the seed coverings (Baskin and Baskin 1998). Natural scarification is brought by mechanical abrasion, microbial attack or passage through the digestive tract of animals, which causes the seed coat to crack (Mayer and Poljakoff-Mayber (1989) and Mohamed-Yasseen et al. (1994), but see Baskin and Baskin (2000)). As reported in some other species of grasses (Peart 1979, 1981), and in other plants of the genus *Stipa* (Ghermandi 1995), the caryopses of *S. tenacissima* have an awn that, after dispersal, aids the seed to drill into the soil by means of hygroscopic movement. We hypothesised that these movements aid to scarify the seed coat and promote seed germination.

Seed germinability is subject to genotypic variability and also can be affected by the parental environment (Baskin and Baskin 1998). Day length, temper-

ature, position of the seed in the inflorescence, age of the mother plant, and water stress affect the germinability of seeds through changes in the development of the seed coat and its surface structure, which modify seed coat thickness and resistance against fungus and therefore affect seed dormancy and seed longevity (Gutterman 1980/81, 1992; Fenner 1985, 1991). As plants experience variations in the environment among sites and years, seed dormancy may vary among and within populations from year to year in a given location (Roach and Wulff 1989; Fenner 1991; Gutterman 1992; Murdoch and Ellis 1992; Mousseau and Fox 1998). This phenomenon (asynchronous germination) is particularly well developed in certain families such as the Poaceae (Fenner 1985), and it insures that, even under the most suitable conditions for germination, only a portion of the total seed population of a certain plant species will be ready to germinate at one time (Gutterman 1992). Therefore these species are capable of forming at least a transient seed bank.

Features as asynchronous germination (Servicio del Esparto 1953), seed morphology, and post-dispersal drilling behaviour permit us to hypothesize that seeds of *S. tenacissima* have dormancy and that scarification, as well as exposure to high temperatures at the soil surface, may improve seed germination. Also, because seed and fruit coat traits are determined via the effect of environment interacting with genotypes, seed dormancy in *S. tenacissima* may vary within and among populations and years. If *S. tenacissima* achieves all of these premises, then we hypothesize that this species may form a soil seed bank.

The objectives of this paper are:

1. To assess seed longevity by observing seed germinability through time.
2. To verify the existence of seed dormancy.
3. To analyze the role of the glumes on dormancy.
4. To analyze the variation in seed germinability among different populations and among different individuals within a population.
5. To investigate the ability of *S. tenacissima* to form a soil seed bank.

Study species

Stipa tenacissima L. (Poaceae) (alfa or esparto grass) is a perennial tussock grass widely distributed in arid and semiarid ecosystems of the south and western

Mediterranean Basin (Suárez et al. 1991). Most of the steppes in the Maghreb and semiarid regions of Spain are dominated by alfa grass or plant communities associated with it (Le Houérou 1969; White 1983; Djebaili 1988; Puigdefábregas and Mendizábal 1998). The steppes of *S. tenacissima* in Spain are widespread in the southeast, where alfa occupies about 600,000 ha (Servicio del Esparto 1950).

This is a suitable species for the reclamation and rehabilitation of degraded soils, as it forms a dense clump which can trap sediments and seeds, provides shelter for other species to grow in, and can grow in nutrient deficient soils (Francis and Thornes 1990; Maestre et al. 2001; García-Fayos and Gasque 2002). Moreover, in alfa steppes, tussocks tend to adopt spatial structures that minimize runoff lengths and sediment movement along slopes (Puigdefábregas and Mendizábal 1998).

S. tenacissima regenerates by vegetative spread and also reproduces by seeds, being a reputed mast-species (Haase et al. 1995). Flowering of *S. tenacissima* in our study areas occur along March and April and dispersal do during May and June. Hereafter, we used the term "seed" to refers to the dispersal unit, that is, the lemma and palea plus the caryopsis containing the true seed.

The germination season in natural populations occurs from autumn to early spring, always depending on the amount of precipitation (M. Gasque pers. obs.).

Materials and methods

Seed harvest areas

Seeds were collected in several localities covering most of the natural distribution of *S. tenacissima* in southeastern Spain (Figure 1). In all of the sampling sites the vegetation is similar, dominated by esparto grass and some woody shrubs like *Rosmarinus officinalis* L., and diverse species of *Teucrium*, *Helianthemum*, *Fumana* and *Thymus*. The climate is typically Mediterranean semiarid, with hot summers, mild winters, and a dry season that lasts for over three months. Mean annual temperature ranges from 15° to 20 °C and annual precipitation amounts to 250–375 mm.

Germination tests

The experiments were carried out with seeds that were selected previously for germination tests, so that

only those that were filled and firm were used. Seeds were kept in paper bags under laboratory conditions (darkness, 21 ± 1 °C) until they were used.

A total of 200 seeds per treatment were used. The seeds were placed in petri dishes on a filter paper sheet moistened with 3.5 ml of distilled water and covered with polyethylene sheets to prevent evaporation. A total of four petri dishes were arranged per treatment with 50 seeds each. The seeds were placed in a germination chamber (Model Economic, A.S.L., Madrid) and maintained in day/night environment of 12 h at 20 °C under light ($27.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 12 h at 10 °C in darkness (environmental conditions during the germination season in natural populations). Dishes were monitored daily for 28 days and germinated seeds were removed. A seed was considered to be germinated when the radicle had emerged. The procedure followed in the selection of the seeds, the conditions under which seeds were stored whenever a storage time was required, the arrangement of the dishes, the control of germination, the temperature and light conditions in the germination chamber, and the test duration were the same in all the laboratory experiments performed in this paper. Additionally, in the experiments on seed longevity, the seeds were disinfected in 0.5% sodium hypochloride solution for 1 minute and then washed three times (1 minute each) with distilled water before germination tests.

Germination percentages as well as the number of days until the first seed germinated (the time to the onset of germination) were the variables used for comparison. All statistical analyses in this study were performed with the SPSS package v. 8.0.

Seed longevity

Seed longevity under laboratory conditions was studied using seeds collected in 1996 in Finestrat. Germination tests were carried out 8, 11, 20, 24 and 28 months after harvest.

The influence of the time of storage on germination parameters was analyzed with a one-way analysis of variance (ANOVA).

Seed dormancy

In order to differentiate between seed dormancy and the need of particular environmental conditions for seed germination, the comparative analysis of seed germination during the early months after dispersion of seeds was performed. With this aim, we compared



Figure 1. Sampling sites from north to south: Porta-Coeli (PC), Albal-CIDE (AL-C) and Finestrat (F) (Comunidad Valenciana), Hellín (H) and Cancarix (CX) in the Albacete province (Castilla-La Mancha), Caravaca (CV), Zarzilla de Ramos (ZR), Zaradilla de Totana (ZT) and La Parroquia (PQ) (Murcia), and Rambla Honda (RH) and Carboneras (C) in the Almería province (Andalucía).

germination of seeds immediately after harvest (spring to early summer), two months after harvest, and four months after harvest in outdoor conditions. We also compared germination of seeds two and four months after harvest in controlled environmental conditions at the laboratory (simulating that of the germination season). Seeds were collected in May 1997 in Rambla Honda. In the outdoor experiment seeds were placed in flowerpots in the garden of the Research Center and watered by sprinklers every 2–3 days. A total of 4 flowerpots per treatment with 50 seeds each were used. Flowerpots were checked for emerged seedlings daily for 50 days. In the laboratory experiment only the treatments representing seed stored for two and four months after harvest were performed. Data from the experiments carried out in the flowerpots were analyzed with a one-way ANOVA and those of the germination chamber with a t-test.

Effect of the lemma and palea on germination

In order to assess whether the seed covering structures have a negative effect on germination, an experiment was performed in July 1997 with seeds collected the same year in four different populations (Rambla Honda, Finestrat, Hellín, and Porta-Coeli). A total of 400 seeds were selected from each population and in 200 of them the lemma and palea were manually removed with the help of a scalpel. The 400 seeds from each population were arranged in 8 petri dishes with 50 seeds in each – 4 petri dishes contained the intact seeds and the other 4 dishes contained the treated seeds – and placed in the germination chamber. A two-way analysis of variance was used to test for effect of population (geographical influence) and seed morphology (intact or treated seeds) on germination percentages and the time to onset of germination.

Another set of germination tests with seeds subjected to mechanical scarification were performed to analyze the role of scarification in breaking the dor-

mancy of *S. tenacissima* seeds. To carry out this experiment, seeds from Rambla Honda and Porta-Coeli populations were used. Seeds were mixed with 0.5–2 mm diameter quartz abrasive particles in closed 32 cm³ pipes, which were half filled with the quartz particles. These pipes were placed in a shaker at 750 rph for either 3 or 15 h. There was also a control group of seeds which were not subjected to this scarification treatment. The tests were performed in April 1998. Data were analyzed with a one-way ANOVA and with a Kruskal-Wallis test when the data did not fit the assumptions of the parametric tests.

Besides the mechanical treatments aforementioned, an experiment was carried out to assess the influence of high temperatures on germination. Four lots of 50 seeds each collected in June 1997 in the Porta-Coeli population were subjected to 50 °C in an oven for either 3 or 6 days. There was also a control group of seeds collected from the same population and year that were not subjected to 50 °C. After this treatment was applied, the seeds were put in flowerpots in the garden of the Research Center and watered by sprinklers every 2–3 days. The experiment lasted for 50 days in the autumn of 1997. A laboratory experiment was also performed that consisted of comparing germination of seeds previously subjected to 50 °C in an oven for either 5 or 10 days with that of a control group. These seeds were collected in June 1999 in Zarcilla de Ramos and the test was performed in August 1999.

In both experiments, the emergence (flowerpots) or germination (petri dish) of seeds was monitored daily and the time to the onset of the emergence/germination, as well as the emergence/germination percentages were analyzed with one-way ANOVA.

Variation among populations and individuals

With the aim of verifying the existence of differences in germination and dormancy among different populations and years, as well as among different individuals of the same population, we performed four experiments.

In the first experiment we compared germination of seeds collected in 1997 in eight populations (Rambla Honda, Finestrat, Carboneras, Hellín, Porta-Coeli, La Parroquia, Zarcilla de Ramos, and Zarzadilla de Totana) four months after harvest and coinciding with the germination period in the field. Eight replicates per population were used (8 petri dishes with 50 seeds in each). Germination percentages were analyzed

with one-way ANOVA whereas the onset of germination was analyzed with a Kruskal-Wallis test since this data did not satisfy the assumptions of parametric tests.

The second experiment consisted of comparing germination of seeds from several populations in two different years. The populations studied were Rambla Honda, Finestrat, Hellín, and Porta-Coeli, and the tests were carried out in July 1997 and June 1998 with fresh seeds. Germination parameters between years were compared within each population with t-tests. The influence of the population where the seeds were collected was not analyzed because it had already been analyzed in the preceding experiment.

As the mother plant controls the development of seed covering structures, then the variations detected in seed germinability among different populations and years (see results) could have a maternal origin. Because seeds differed greatly in their size and the size of their lemma and palea, we weighed separately the intact seeds and their lemma and palea of 200 seeds arranged in 4 groups of 50 seeds in each one. The seeds were collected from the same eight populations used in the first experiment. Then the average lemma and palea dry weight and the ratio of lemma and palea-dry weight to seed-dry weight of each population were related to their germination percentage and to their time to onset of germination (Pearson correlation coefficient).

In the fourth experiment we compared the germinability of seeds from 5 individuals growing on the same slope in the La Parroquia study area in 1997. Individuals were separated by at least five to ten meters and seeds were collected only from west-facing spikes. As a reference group, we collected another set of seeds from spikes of 80 individuals growing on the same slope. Germination was assessed in October 1997 with eight replicates per individual. Germination parameters of the different individuals and of a reference group were compared with one-way ANOVA and with a Kruskal-Wallis test when the data did not fit the assumptions of the parametric tests.

Soil seed bank

In order to verify if *S. tenacissima* forms a seed bank, ten soil samples 50 × 50 cm and 2 cm deep were collected in March 1997 in an alfa grass steppe located at Cancarix, after the main period of seed germination and before the dispersal of the next seed generation.

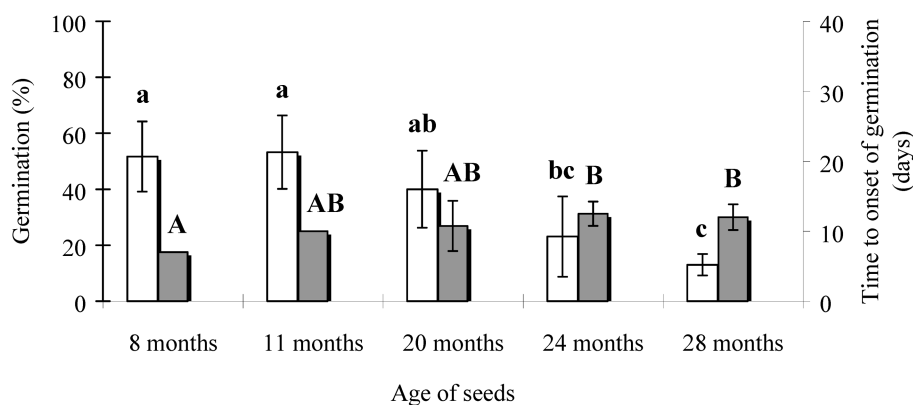


Figure 2. Seed germination in relation to the age of the seeds. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean \pm 1 SD. Different letters over the bars indicate significant differences among treatments (Tukey, 95%).

Soil samples were sifted through a 1-mm sieve to separate the seeds of *S. tenacissima*. We extracted the seeds that had no visible damage and carried out a germination test. At the end of the experiment, the ungerminated seeds were assessed for viability with a tetrazolium test (1% solution). This test is not entirely accurate when applied to *S. tenacissima* seeds, since the embryo of some of the viable seeds do not stain red (M. Gasque pers. obs.). Nonetheless we applied this test because the presence of some stained embryos would at least indicate the existence of some viable seeds.

Results

Seed longevity

Seeds of *S. tenacissima* were still able to germinate 28 months after harvest when stored under laboratory conditions but their germination percentage decreased substantially and significantly from 50% to less than 15% after 28 months ($F_{4,15} = 8.5$, $p < 0.0001$). Also the onset of germination was significantly affected by the time passed since harvest ($F_{4,15} = 4.9$, $p = 0.010$), showing delays of more than 5 days after 24 months relative to fresh seeds (Figure 2).

Seed dormancy

Seedling emergence in outdoor conditions in the flowerpot experiment took place slowly and was particularly scarce among the seeds recently collected ($2.0\% \pm 2.3$) (mean \pm 1 SD) and those stored for two months ($2.5\% \pm 3.8$), but was greater in seeds stored

for four months after harvest and seeded in autumn ($31.8\% \pm 2.6$). These differences were statistically significant ($F_{2,4} = 99.5$, $p < 0.0001$). Seeds that were either recently collected or stored two months exhibited a greater number of days to the onset of germination (35.0 ± 19.3 and 29.5 ± 29.0 respectively) than seeds stored for four months after harvest (8.5 ± 0.6), but the differences were not significant ($F_{2,4} = 2.5$, $p = 0.158$).

In the tests carried out in the germination chamber no significant differences were observed in the germination percentage ($t = 1.074$; $df = 3.826$, $p = 0.346$) or the number of days to the onset of germination ($t = -1.964$; $df = 6$; $p = 0.097$). The germination percentages obtained in these tests were $60.0\% \pm 3.3$ and $55.0\% \pm 8.7$ two and four months after harvest respectively whereas the number of days to the onset of germination were 6.8 ± 0.5 two months after harvest, and 7.5 ± 0.6 four months after harvest.

Effect of the lemma and palea

The germination percentages obtained in the tests with intact seeds and seeds without their lemma and palea of several populations indicate that the lemma and palea interfere with seed imbibition and its subsequent germination, but that the extent of it depends on the population where seeds were collected, as the interaction term denotes ($F_{3,24} = 6.2$, $p = 0.003$). Germination percentage of the seeds without lemma and palea was high and homogenous among populations, and varied between $89.9\% \pm 2.2$ (seeds from Hellín) and $97.5\% \pm 1.0$ (seeds from Porta-Coeli). On the contrary, the germination percentages of the intact seeds varied greatly among populations, fluctuating

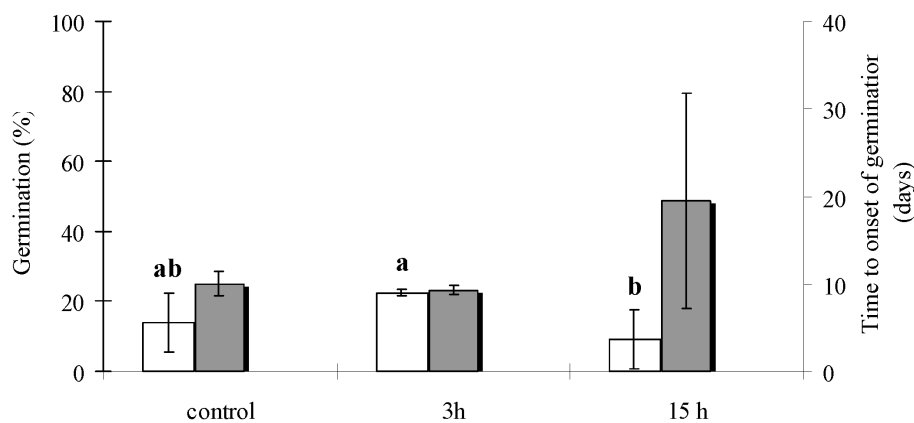


Figure 3. Effects of mechanical scarification on germination of seeds from Porta-Coeli population. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean \pm 1 SD. Different letters over the bars indicate significant differences among treatments (Tukey, 95%). There was not significant effect of treatment on the onset of germination ($F_{2, 9} = 2.5$, $p = 0.134$).

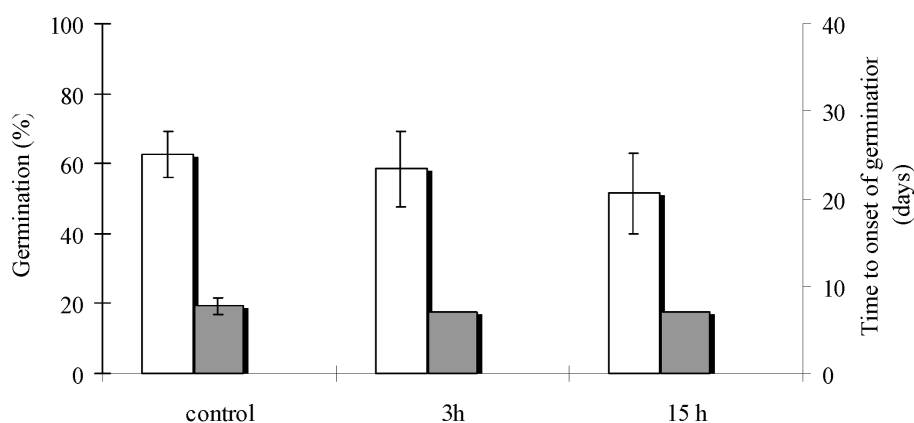


Figure 4. Effects of mechanical scarification on germination of seeds from Rambla Honda population. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean \pm 1 SD. There was not significant effect of treatment on germination percentage ($F_{2, 9} = 1.7$, $p = 0.244$) nor on the onset of germination (Kruskal-Wallis test, $p = 0.113$).

between $20.0\% \pm 4.3$ (seeds from Hellín) and $60.0\% \pm 3.3$ (seeds from Rambla Honda). In any case, the germination percentage of the intact seeds was always lower than that of the seeds without lemma and palea. The differences between the two treatments were also significant in all populations with regard to the number of days to the onset of germination, which was always longer and less uniform in intact seeds, (ranging between 6.8 ± 0.5 in the seeds from Rambla Honda and 9.0 ± 1.4 in the seeds from Finestrat), than in seeds without lemma and palea (4.0 ± 0.0 in all populations). The extent of the time to germination also depends on the population where the seeds were collected ($F_{3,24} = 4.3$, $p = 0.015$, interaction term).

Germination percentage from the Porta-Coeli seeds was affected by mechanical scarification ($F_{2, 9} = 5.2$, $p = 0.032$). However, post hoc comparisons

with the Tukey test showed that seeds suffered a reduction in the germination percentage in the 15 h scarification treatment relative to the 3 h treatment, but that there was no differences between either the 3 h or 15 h treatment and the control. Time to the onset of germination remained unaffected (Kruskal-Wallis test, $p = 0.134$) (Figure 3). There were no effects of the different mechanical scarification treatments on either of the germination parameters in seeds from Rambla Honda ($F_{2,9} = 1.7$, $p = 0.244$ for germination percentage and Kruskal-Wallis test, $p = 0.134$ for the onset of germination; Figure 4).

The afterripening treatments increased both the emergence of seedlings in flowerpots ($F_{2, 9} = 8.9$, $p = 0.007$) and the germination percentage in the laboratory ($F_{2, 9} = 5.6$, $p = 0.026$). The emergence percentage of the seeds subjected to 50°C for 6 days (26.5%

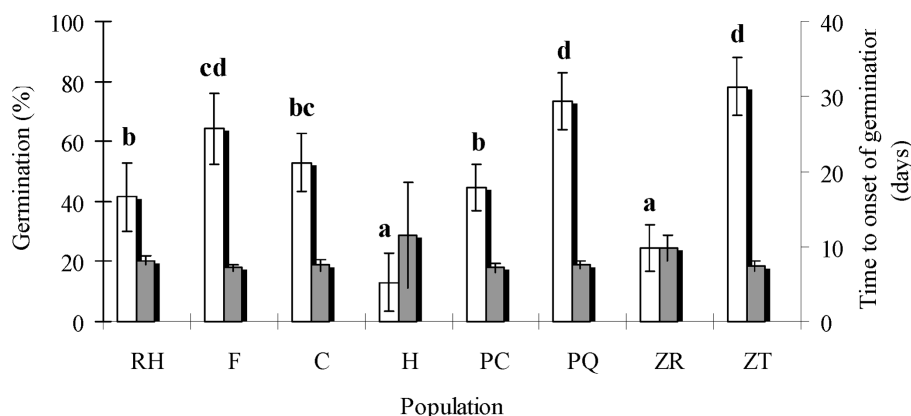


Figure 5. Variation of seed germinability among populations. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean \pm 1 SD. Different letters over the bars indicate significant differences (Tukey 95%). There was a significant effect of treatment on the onset of germination (Kruskal-Wallis test, $p = 0.001$).

± 11.1) was significantly higher than the 3-days treatment ($5.5\% \pm 5.5$) and the control ($7.5\% \pm 5.3$). Likewise, seeds subjected to $50\text{ }^{\circ}\text{C}$ for 10 days in the laboratory experiment showed the highest percentage of germination ($72.2\% \pm 5.3$), and differed significantly from 5-days treatment ($64.9\% \pm 2.9$) and the control ($55.7\% \pm 10.5$). Surprisingly, the onset of germination did not differ among treatments ($F_{2, 9} = 0.3$, $p = 0.748$), and varied between 6.3 ± 0.5 (seeds from control as well as seeds subjected to $50\text{ }^{\circ}\text{C}$ during 5 days), and 6.5 ± 0.6 (seeds subjected to $50\text{ }^{\circ}\text{C}$ during 10 days).

Variation among populations and individuals

The percentages of germination of the different populations studied ranged between $13.1\% \pm 9.5$ in Hellín and $78.2\% \pm 9.7$ in Zarzadilla de Totana, and showed significant differences among populations ($F_{7, 56} = 44.5$, $p = 0.0001$). The number of days to the onset of germination, which fluctuated between 7.1 ± 0.4 (seeds from Finestrat) and 11.5 ± 7.1 (seeds from Hellín), also was significantly affected by population (Kruskal-Wallis test, $p = 0.001$) (Figure 5).

The results of the experiment, in which germination of seeds from several populations in two different years was compared, show that germination percentage varied between years (Figure 6a). Separate t-tests within each population indicated that there were significant differences in seed germinability between years in all but the Porta-Coeli populations. The time to the onset of germination also varied significantly between years (Figure 6b) and it would appear that the differences in this parameter are not al-

ways consistent with seed germinability, since the seeds that germinated quickly did not always show the greatest germination percentages: in the Finestrat population, the year with the highest germination percentage also had the highest time to the onset of germination.

The germination behaviour of the seeds collected the same year in the same population and slope, from different individuals and from spikes facing identical direction, showed significant differences among the individuals ($F_{5, 22} = 25.1$, $p = 0.0001$), fluctuating between $19.6\% \pm 9.0$ (individual number 1) and $61.0\% \pm 5.3$ (individual number 5), whereas the germination percentage of the set of seeds from several individuals was $73.5\% \pm 9.5$. In relation to the onset of germination, the different individuals showed significant effects (Kruskal-Wallis test, $p = 0.008$). This parameter varied between 7.5 ± 0.6 (individual number 4) and 10.3 ± 0.5 (individual number 2), whereas the mean value for the set of seeds from several individuals was 7.6 ± 0.5 (Figure 7).

Table 1 shows the mean values of the germination percentage and the onset of germination, as well as the lemma and palea dry weight and the lemma and palea-dry weight to seed-dry weight ratios. No correlation was found between lemma and palea dry weight and germination percentage ($r = 0.244$, $p = 0.560$), or onset of germination ($r = -0.248$, $p = 0.554$). No correlation was either found between lemma and palea-dry weight: seed-dry weight ratio and germination parameters (germination percentage: $r = -0.269$, $p = 0.519$; onset of germination: $r = -0.062$, $p = 0.884$). These results indicate that the size

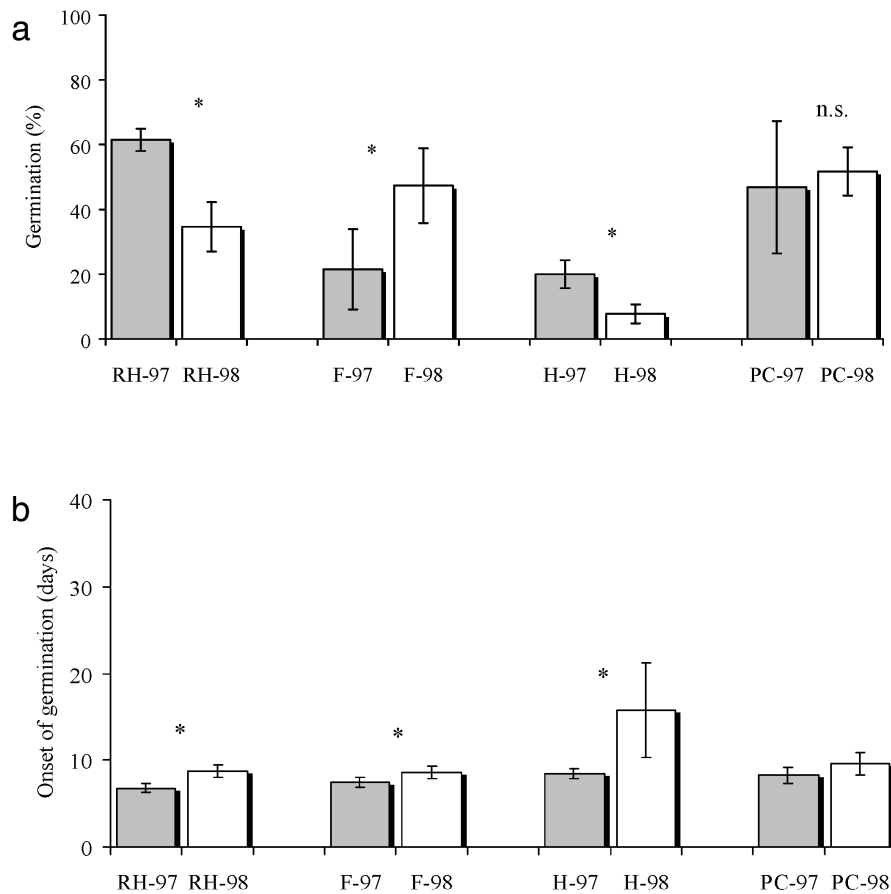


Figure 6. Variation of seed germinability between years (1997 and 1998) for seeds from Rambla Honda (RH), Finestrat (F), Hellín (H), and Porta-Coeli (PC) populations. (a) Germination percentage, (b) Time to the onset of germination. Data are mean \pm 1 SD. Mean comparisons were performed with *t*-tests. (* indicates significant differences at the 0.05 level; n.s. indicates not significant differences).

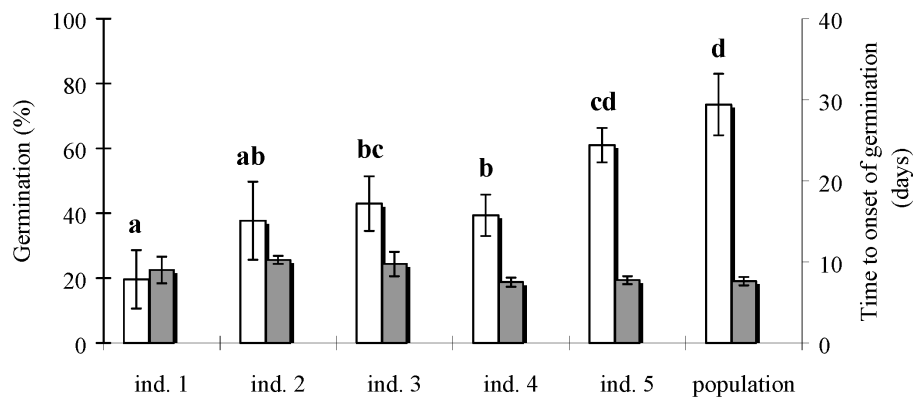


Figure 7. Variation of seed germinability among individuals. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean \pm 1 SD. Seeds were collected only from west-facing spikes from 5 different individuals in the same slope, as well as a set of seeds from several individuals from the population. Different letters over the bars indicate significant differences (Tukey 95%). There was a significant effect of treatment on the onset of germination (Kruskal-Wallis test, $p = 0.008$).

of the lemma and palea has no control on germination of seeds.

Table 1. : Germination percentage, time to the onset of germination, lemma and palea dry weight (mg), as well as the lemma and palea dry-weight:seed-dry-weight ratio, in the 8 populations in which the relationship between lemma and palea and germination parameters was studied.

Population	% Germination	Onset of germination (days)	Lemma and palea dry weight (mg)	Lemma and palea d.w/seed d.w.
ZT	78.24	7.38	49.52	0.7010
PQ	73.52	7.63	53.66	0.6514
F	64.25	7.13	54.02	0.5677
C	53.00	7.50	45.34	0.5696
PC	44.58	7.13	44.14	0.8871
RH	41.50	8.13	53.68	0.9101
ZR	24.34	9.75	54.64	0.7231
H	13.08	14.25	45.10	0.6695

Soil seed bank

We found a mean of 34.1 ± 30.3 seeds m^{-2} in the soil seed bank, ranging from 25 to 460 seeds m^{-2} among samples. After germination and tetrazolium tests were applied, this seed density was reduced to 1.1 ± 0.9 seeds m^{-2} , indicating that a low number of the seeds of *S. tenacissima* remain viable in the soil for 9 months.

Discussion

The comparative analysis of seed germination during the early months after dispersal (summer) and in controlled conditions simulating the average environmental conditions during the emergence period in field verifies the existence of seed dormancy. This seed dormancy is controlled by the impermeability of the seed covering structures (lemma and palea) since the removal of them produce a very important and significant increase of seed germination, which has already been described in other species of the genus *Stipa* (Ellis et al. 1985). However, although it seems likely that the impermeability of lemma and palea is the main cause of seed dormancy, no statistical relationship has been found between germination parameters and the lemma and palea weight (used as an indicator of the size of these covering structures). Perhaps an examination of the lemma and palea chemical variations (kinds of cellulose, presence of wax, inhibitors, etc.) could give insight to the influence of them on germination. This supposition is also supported by the increase in seed germination following a period of afterripening, which is known to cause chemical transformations of membranes and cell

walls and the degradation of chemical inhibitors (Mayer and Poljakoff-Mayber 1989; Baskin and Baskin 1989).

The lack of beneficial effects after mechanical scarification do not fit with the hypothesis that the rotation movement of the seeds during the burial process promotes seed germination through the abrasion of the seed coat or the lemma and palea. It would seem then, that the contribution of the burial process to the increase of the establishment of *S. tenacissima*, if any, comes from other causes. Some studies have established the benefits of the burial process in awned species by the role of the awn in searching for germination sites and from the increase in the surface of contact between the seed and the soil particles (Peart 1979, 1981; Ghermandi 1995). Other causes such as reduction of seed predation by granivorous animals could also be invoked (Westoby et al. 1982; Crawley 1992).

The results of the afterripening experiments also agree with the complete absence of germination of *S. tenacissima* before autumn (M. Gasque pers. obs.), which has also been described for other species, like *S. leucotricha* (Fowler 1986) and *S. capensis* (Kadmon 1993). It would mean that these species, which disperse their seeds at the end of the spring or during early summer, have developed a strategy to avoid germination during the time of the year in which the survival chances of the seedlings are very low due to drought.

Seed germination variables of the seeds of *S. tenacissima* differed among populations and years. This would indicate that genetic and environmental factors have a great influence on seed dormancy. The relative importance of both factors is difficult to separate, given that on the one hand the time to the onset of

germination and the germination percentages of each single population varied from year to year. On the other hand, differences in seed germinability of the seeds collected from five individuals of the same population and slope, support the idea that genotypes of the individuals also have an important influence on seed dormancy. This fact would support the hypothesis of the maternal origin.

Germinability of the seeds of *S. tenacissima* diminishes progressively with age and, at the time that the germination percentages become lower, the onset of germination is delayed. These data agree with the results obtained by the Servicio del Esparto (1953) and indicate that seed longevity, a trait that is an essential condition to form a soil seed bank, is low. This is corroborated by the results of the soil sampling, which indicate that there is a very low viable seed density that remains buried in the soil nearly one year after dispersal. We do not know if these seeds are capable of remaining viable until the favourable period of the second year, but the low density of the surviving seeds and the results of the longevity tests in laboratory conditions allow us to predict that this possibility is not very high. Therefore, the soil seed bank of *S. tenacissima* should be considered a "transient seed bank" (*sensu* Thompson and Grime (1979)), which is in accordance with the conclusions of Kemp (1989) concerning that in hot deserts the perennial species do not form persistent seeds banks.

In conclusion, seed dormancy in *S. tenacissima* is controlled by seed covers, which prevent seeds from germinating during a very unfavourable period (summer). This control seems to be subjected to both genetic and maternal influence. A small fraction of the ungerminated seeds remain viable after a year but their germinability decays afterwards resulting in a transient soil seed bank.

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