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

María Gasque & Patricio García-Fayos*

Centro de Investigaciones sobre Desertificación -CIDE- (CSIC-UV-GV)
Apartado Oficial
46470 VALENCIA (SPAIN)

* Author for correspondence. Phone: +34961220540; Fax: +34961270967.
E-mail <patricio@uv.es>

Text file: germinacion06-3.doc;
Figure files: Figure 1.doc; Figures 2 to 7.doc
All are in Word 97 SR-1

Key Words: afterripening, lemma and palea, seed dormancy, seed longevity, seed scarification, semiarid steppes.

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 of seeds 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 & 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 & 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 & 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 & Thornes, 1990). Certain characteristics of *S. tenacissima*, such as the protection of soil against erosion (Sánchez & Puigdefábregas, 1994; Bochet *et al.* 1998), its resistance to long drought periods (Pugnaire & 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 & 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 & 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 & 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 40ºC to 100ºC are the most effective (Ellis *et al.* 1985; Baskin & Baskin, 1989). In the case of Poaceae, the longer and warmer the storage environment, the greater the loss of dormancy (Murdoch & 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 & 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 & Poljakoff-Mayber, 1989; Mohamed-Yasseen *et al.* 1994, but see Baskin & 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 & Baskin, 1998). Day length, temperature, 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 & Wulff, 1989; Fenner, 1991; Gutterman, 1992; Murdoch & Ellis, 1992; Mousseau & 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 & Mendizabal, 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 & Thornes, 1990; Maestre *et al.* 2001; Garcia-Fayos & Gasque, in press). Morevoer, in alfa steppes, tussocks tend to adopt spatial structures that minimize runoff lengths and sediment movement along slopes (Puigdefábregas & Mendizabal, 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* generally starts in May and finishes at the end of June or the beginning of July, even though the spikes are already visible from January (Servicio del Esparto, 1950). However, if precipitation is favourable during the autumn and the winter is mild, flowering can be in advance and occur at the beginning of April (Djebaili, 1988).

Seeds usually ripen during May or June. Florets (caryopsis lemma and palea, with the caryopsis containing the seed) are dispersed by wind. The germination season in natural populations occurs from autumn to early spring, always depending on the amount of precipitation (M. Gasque, pers. obs.). Henceforth, when the term "seed" is used throughout this paper, it refers to what is dispersed from the plant, that is to say, the floret.

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 15º to 20ºC and annual precipitation amounts to 250-375mm.

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 ± 1ºC) 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 20ºC under light (27.6 μmol m^{-2}

s^{-1}) and 12 h at 10ºC 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 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 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 dormancy 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 cm^3 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 50ºC 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 50ºC. 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 50ºC 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 x 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.

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% ± 2.3) (mean ± 1 SD) and those stored for two months (2.5% ± 3.8), but was greater in seeds stored for four months after harvest and seeded in autumn (31.8% ± 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% ± 3.3 and 55.0% ± 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% ± 2.2 (seeds from Hellín) and 97.5% ± 1.0 (seeds from Porta-Coeli). On the contrary, the germination percentages of the intact seeds varied greatly among populations, fluctuating between 20.0% ± 4.3 (seeds from Hellín) and 60.0% ± 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 15h scarification treatment relative to the 3h treatment, but that there was no differences between either the 3h 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 50ºC for 6 days (26.5% ± 11.1) was significantly higher than the 3-days treatment (5.5% ± 5.5) and the control (7.5% ± 5.3). Likewise, seeds subjected to 50ºC for 10 days in the laboratory experiment showed the highest percentage of germination (72.2% ± 5.3), and differed significantly from 5-days treatment (64.9% ± 2.9) and the control (55.7% ± 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 50ºC during 5 days), and 6.5 ± 0.6 (seeds subjected to 50ºC during 10 days).

Variation among populations and individuals

The percentages of germination of the different populations studied ranged between 13.1% ± 9.5 in Hellín and 78.2% ± 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 always 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% ± 9.0 (individual number 1) and 61.0% ± 5.3 (individual number 5), whereas the germination percentage of the set of seeds from several individuals was 73.5% ± 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 of the lemma and palea has no control on germination of seeds.

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 & Poljakoff-Mayber, 1989; Baskin & 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 & 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.

Acknowledgments

This study has been funded by the Plan Valenciano de Ciencia y Tecnología, (project GV-2311/94) and by a doctoral grant of the Consejo Superior de Investigaciones Científicas to María Gasque. Two anonymous referees provided critical comments on an earlier version of the manuscript.

References

Albaladejo, J., Castillo, V. & Roldán, A. 1996. Rehabilitation of degraded soils by water erosion in semiarid environments. pp 265-278. In: Rubio, J.L. & Calvo, A. (eds), Soil degradation and desertification in mediterranean environments. Geoforma Ediciones, S.L.

Baskin, C.C. & Baskin, J.M. 1998. Seeds. Ecology, biogeography, and evolution of dormancy and germination. Academic Press. San Diego.

Baskin, J.M. & Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. pp. 53-66. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds), Ecology of Soil Seed Banks. Academic Press Inc., San Diego.

Baskin, J.M. & Baskin, C.C. 2000. Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles. Seed Science Research, 10: 409-413.

Bochet, E., Rubio, J.L. & Poesen, J. 1998. Relative efficiency of three representative matorral species in reducing water erosion at the microscale in a semi-arid climate (Valencia, Spain). Geomorphology 23:139-150.

Call, C.A. & Roundy, B.A. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. Journal of Range Management 44:543-549.

Correal, E., Sánchez-Gómez, P. & Alcaraz, F. 1989. Woody species (trees and shrubs) of multiple value for the arid and semi-arid zones of northern mediterranean EEC countries. pp 1-39. In: Morandini, R. (ed), Agriculture. Programme de recherche Agrimed. Les espèces ligneuses à usages multiples des zones arides méditerranéennes. Recueil des communications, Saragosse, Espagne, 25-26 septembre 1987. Commission des Communautés Européennes.

Crawley, M.J. 1992. Seed predators and plant population dynamics. pp: 157-191. In: Fenner, M. (ed), Seeds. The ecology of regeneration in plant communities. C.A.B. International, Melksham.

Djebaili, S. 1988. Connaissances actuelles sur l'alfa (*Stipa tenacissima*, L.): auto-écologie, phénologie, productivité et valeur nutritive. Biocénoses 3(1/2): 43-53.Alger.

Ellis, R.H., Hong, T.D. & Roberts, E.H. 1985. Handbook of seed technology for genebanks, Vol. I y II, IBPGR (International Board for Plant Genetic Resources) Rome.

Esler, K.J. & Phillips, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. Journal of Arid Environments 26:325-337.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, London.

Fenner, M. 1991. The effects of the parent environment on seed germinability. Seed Science and Research 1:75-84.

Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115:131-145.

Francis, C.F. & Thornes, J.B. 1990. Matorral: erosion and reclamation. pp 87-116. In: Albaladejo, J., Stocking, M.A. & Díaz, E. (eds), Soil degradation and rehabilitation in mediterranean environmental conditions. Consejo Superior de Investigaciones Científicas. Murcia.

García-Fayos, P. & Gasque, M. (in press). Consequences of a severe drought on spatial patterns of woody plants in a two-phase mosaic steppe of *Stipa tenacissima* L. Journal of Arid Environments.

Ghermandi, L. 1995. The effect of the awn on the burial and germination of *Stipa speciosa* (Poaceae). Acta Oecologica 16:719-728.

Gutterman, Y. 1980/81. Influences on seed germinability: phenotypic maternal effects during seed maturation. Israel Journal of Botany 29:105-117.

Gutterman, Y. 1992. Maternal effects on seeds during development. pp. 27-59. In: Fenner, M. (ed), Seeds. The ecology of regeneration in plant communities. C.A.B. International, Melskham.

Gutterman, Y. 1993. Seed germination in desert plants. Springer-Verlag, Berlin.

Haase, P., Pugnaire, F. I. & Incoll, L. D. 1995. Seed production and dispersal in the semi-arid tussock grass *Stipa tenacissima* L. during masting. Journal of Arid Environments 31:55-65.

Kadmon, R. 1993. Population dynamic consequences of habitat heterogeneity: An experimental study. Ecology 74:816-825

Kemp, P.R. 1989. Seed banks and vegetation processes in deserts. pp. 257-281. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds), Ecology of Soil Seed Banks. Academic Press Inc., San Diego.

Kigel, J. 1995. Seed germination in arid and semiarid regions. pp. 645-699. In: Kigel, J.; & Galili, G. (eds), Seed development and germination Marcel Dekker Inc., New York.

Le Houérou, H. N. 1969. La végétation de la Tunisie steppique. Annales de l'Institut National de la Recherche Agronomique de Tunisie 42:1-624.

López Bermúdez, F. & Albaladejo, J. 1990. Factores ambientales de la degradación del suelo en el área mediterránea. pp 15-45. In: Albaladejo, J., Stocking, M.A. & Díaz, E. (eds), Soil degradation and rehabilitation in mediterranean environmental conditions. Consejo Superior de Investigaciones Científicas. Murcia.

Maestre, F.T., Bautista, S., Cortina, J. & Bellot, J. 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecological Applications, 11: 1641-1655.

Martínez-Sánchez, J. J., Herranz, J. M., Guerra, J. & Trabaud, L. 1997. Influence of fire on plant regeneration in a *Stipa tenacissima* L. community in the Sierra Larga Mountain Range (SE Spain). Israel Journal of Plant Science 45:309-316.

Mayer, A. M. & Poljakoff-Mayber, A. 1989. The germination of seeds. (4th edition). Pergamon Press, Oxford.

Mensching, H.G. 1986. Desertification in Europe?. A critical comment with examples from Mediterranean Europe. pp 3-8. In: Fantechi, R. & Margaris, N.S. (eds), Desertification in Europe. Proceedings of the Information Symposium in the EEC Programme on Climatology, Mytilene, Greece, 15-18 April 1984. Commission of the European Communities, D. Reidel Publishing Company, Dordrecht, Holland.

Mohamed-Yasseen, Y., Barringer, S.A., Splittstoesser, W.E. & Costanza, S. 1994. The role of seed coats in seed viability. The Botanical Review 60:426-439.

Morgan, R.P.C., Rickson, R.J. & Wright, E. 1990. Regeneration of degraded soils. pp 69-85. In: Albaladejo, J., Stocking, M.A. & Díaz, E. (eds), Soil degradation and rehabilitation in mediterranean environmental conditions. Consejo Superior de Investigaciones Científicas. Murcia.

Mousseau, T.A. & Fox, C. W. 1998. The adaptative significance of maternal effects. Trends in Ecology and Evolution 13:403-407.

Murdoch, A.J. & Ellis, R.H. 1992. Longevity, viability and dormancy. pp. 193-229. In: Fenner, M. (ed), Seeds. The ecology of regeneration in plant communities. C.A.B. International, Melksham.

Peart, M.H. 1979. Experiments on the biological significance of the morphology of seed dispersal units in grasses. Journal of Ecology 67:843-863.

Peart, M.H. 1981. Further experiments on the biological significance of the morphology of seed dispersal units in grasses. Journal of Ecology 69:425-436.

Pérez-Trejo, F. 1994. Desertification and land degradation in the European Mediterranean. EEC. Luxembourg. 63 pp.

Probert, R.J. 1992. The role of temperature in germination ecophysiology. pp. 285-325. In: Fenner, M. (ed), Seeds. The ecology of regeneration in plant communities. C.A.B. International, Melksham.

Pugnaire, F.I. & Haase, P. 1996. Comparative physiology and growth of two perennial tussock grass species in a semi-arid environment. Annals of Botany 77:81-86.

Pugnaire, F.I., Haase, P., Incoll, L.D. & Clark, S.C. 1996. Response of the tussock grass *Stipa tenacissima* to watering in a semi-arid environment. Functional Ecology 10:265-274.

Puigdefábregas, J. & Mendizábal, T. 1998. Perspectives on desertification: Western Mediterranean. Journal of Arid Environments 39: 209-224.

Roach, D. A. & Wulff, R. D. 1989. Maternal effects in plants. Annual Review in Ecology and Systematics 18:209-235.

Sánchez, G. & Puigdefábregas, J. 1994. Interaction of plant growth and sediment movement on slopes in a semi-arid environment. Geomorphology 9:243-260.

Servicio del Esparto. 1950. El Esparto y su Economía. Ministerios de Industria y Comercio y de Agricultura. Madrid. 303 pp.

Servicio del Esparto. 1953. Estudios y experiencias sobre el esparto. (2nd vol.). Ministerios de Industria y Comercio y de Agricultura. Madrid.

Simpson, G. M. 1990. Seed dormancy in grasses. Cambridge University Press, New York.

Suárez, F., Sainz, H., Santos, T. & González-Bernáldez, F. 1991 Las estepas ibéricas. Ministerio de Obras Públicas y Transporte, Madrid.

Thompson, K. & Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:893-921.

Westoby, M., Cousins, J.M. & Grice, A.C. 1982. Rate of decline of some seed populations during drought in western New South Wales. pp. 7-10. In: Buckley, R.C. (ed) Ant-plant interactions in Australia. The Hague: W. Junk.

White, F. 1983. The vegetation of Africa. Natural Resources Research XX, UNESCO, Paris.

White, J.J. & Van Auken, O.W. 1996. Germination, light requirements, and competitive interactions of *Stipa leucotricha* (Gramineae). The Southwestern Naturalist 41:27-34.

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

Figure captions

Fig. 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), Zarzadilla de Totana (ZT) and La Parroquia (PQ) (Murcia), and Rambla Honda (RH) and Carboneras (C) in the Almería province (Andalucía).

Fig. 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 ± 1 SD. Different letters over the bars indicate significant differences among treatments (Tukey, 95%).

Fig. 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 ± 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 ($F_{2, 9} = 2.5$, $p = 0.134$).

Fig. 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 ± 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, $p = 0.113$).

Fig. 5: Variation of seed germinability among populations. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean ± 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, $p = 0.001$).

Fig 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 ± 1 SD. Mean comparisons were performed with *t*- tests. (* indicates significant differences at the 0.05 level; n.s. indicates not significant differences).

Fig. 7: Variation of seed germinability among individuals. Open bars: Germination percentage, shaded bars: Time to the onset of germination. Data are mean ± 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, $p = 0.008$).

Figure 1

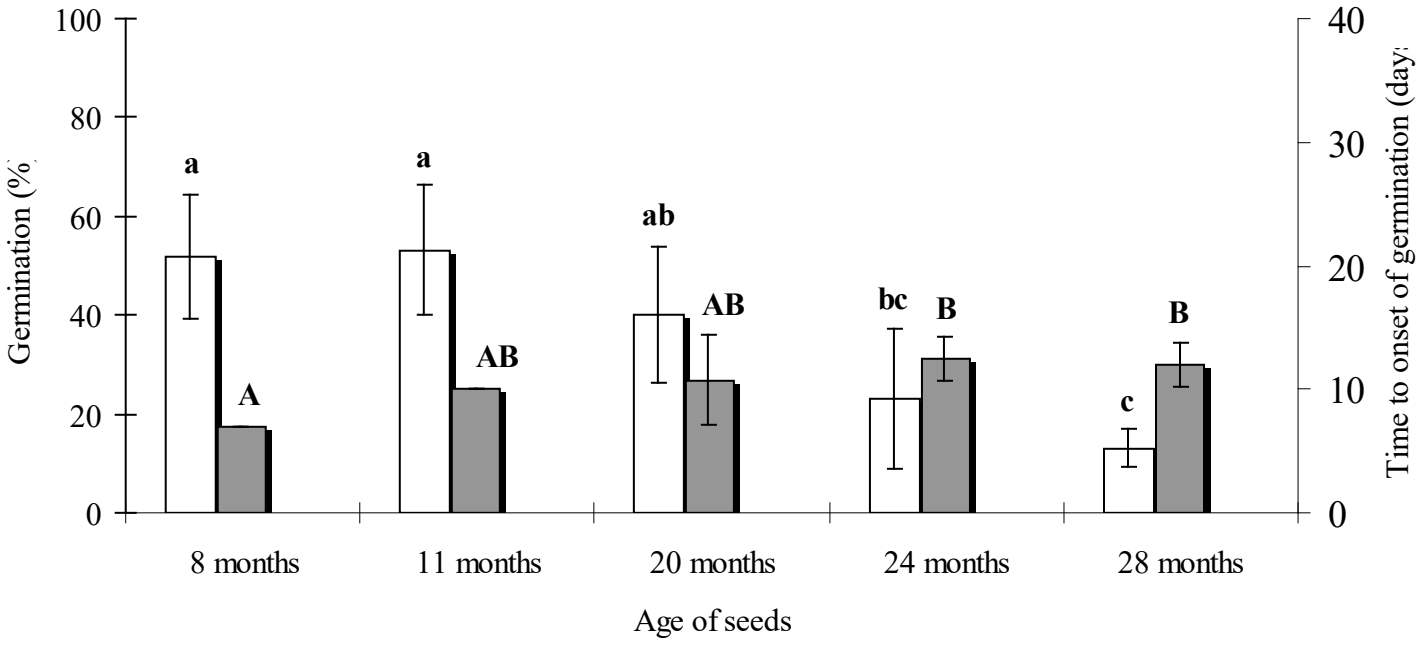
100
80
60
40
20
0
Germination (%
40
30
20
10
0
Time to onset of germination (day
a
A
a
AB
ab
AB
bc
B
c
B
8 months
11 months
20 months
24 months
28 months
Age of seeds

Figure 2

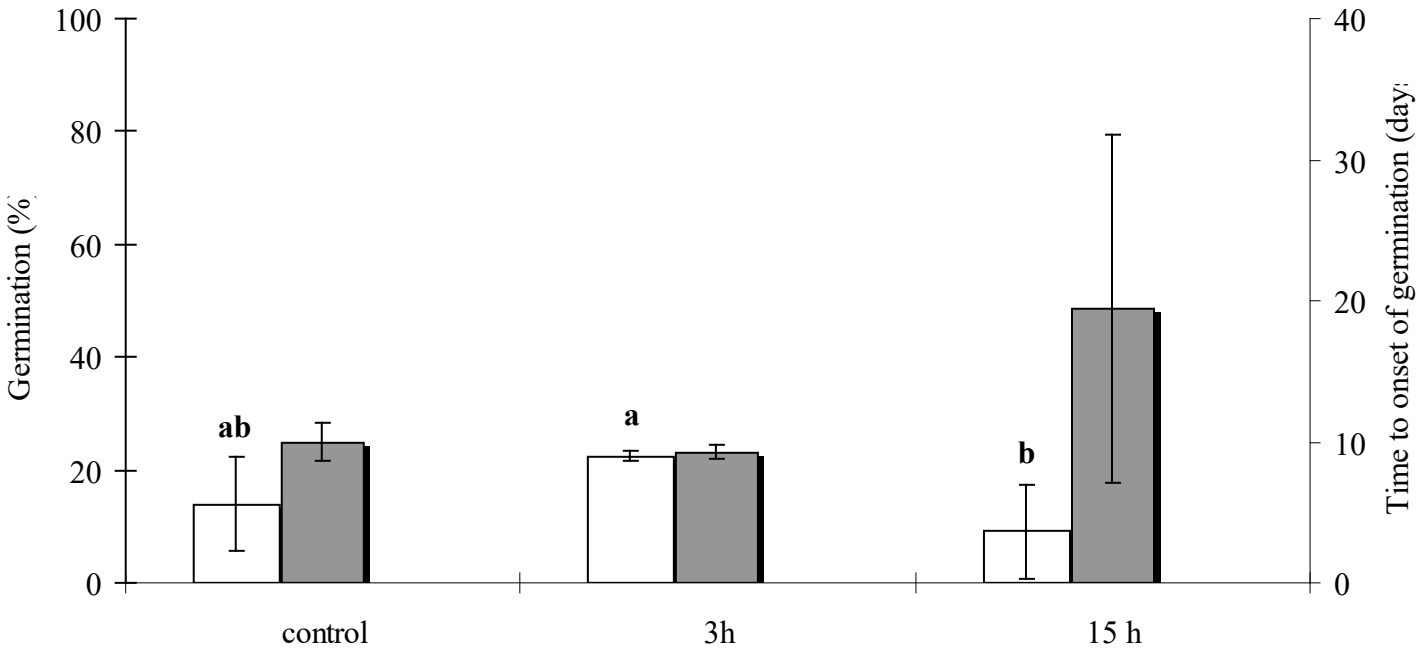
100
80
60
40
20
0
Germination (%
40
30
20
10
0
Time to onset of germination (day
ab
a
b
control
3h
15 h

Figure 3

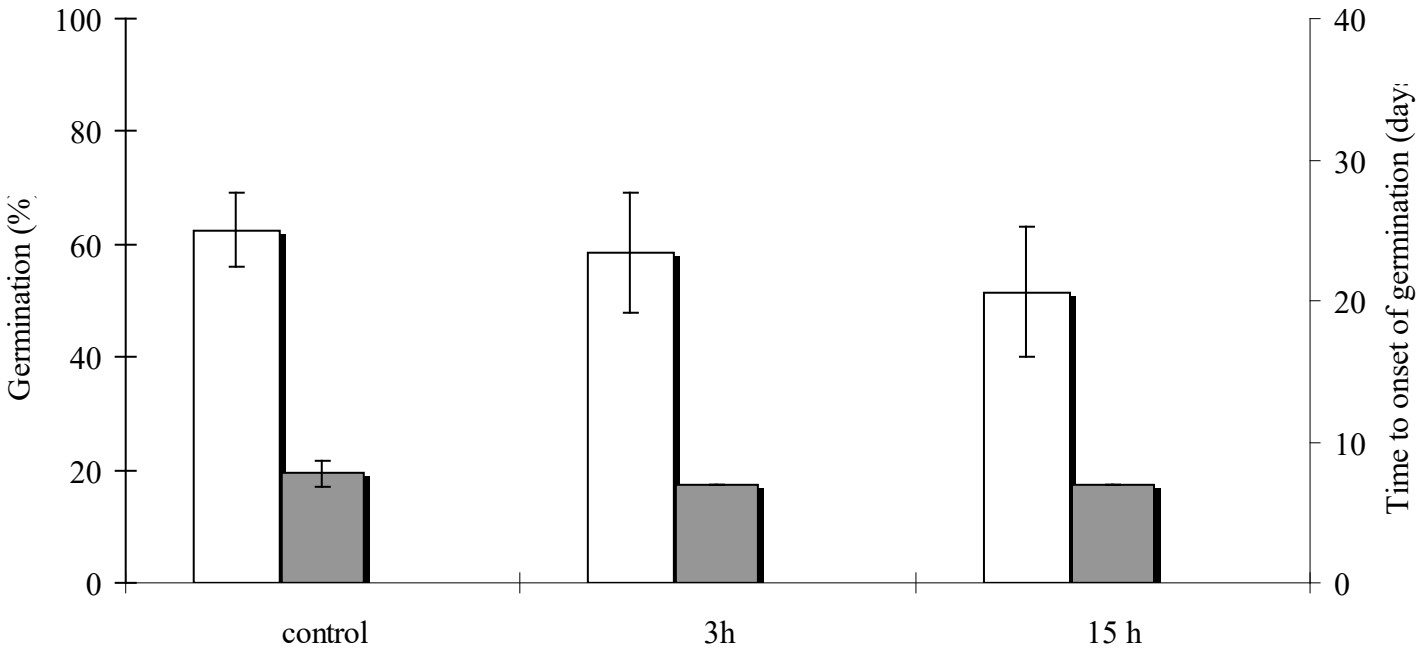
100
80
60
40
20
0
Germination (%
40
30
20
10
0
Time to onset of germination (day
control
3h
15 h

Figure 4

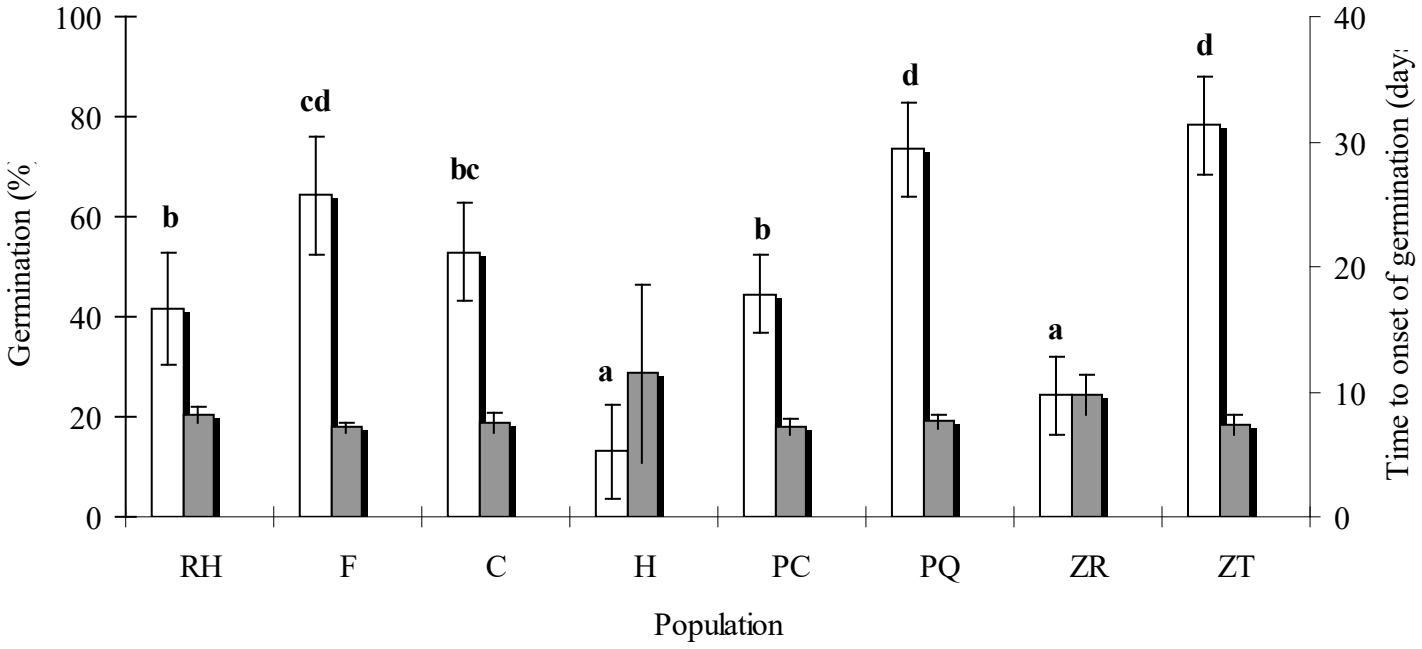
100
80
60
40
20
0
Germination (%
40
30
20
10
0
Time to onset of germination (day
b
cd
bc
a
b
d
a
d
RH
F
C
H
PC
PQ
ZR
ZT
Population

Figure 5

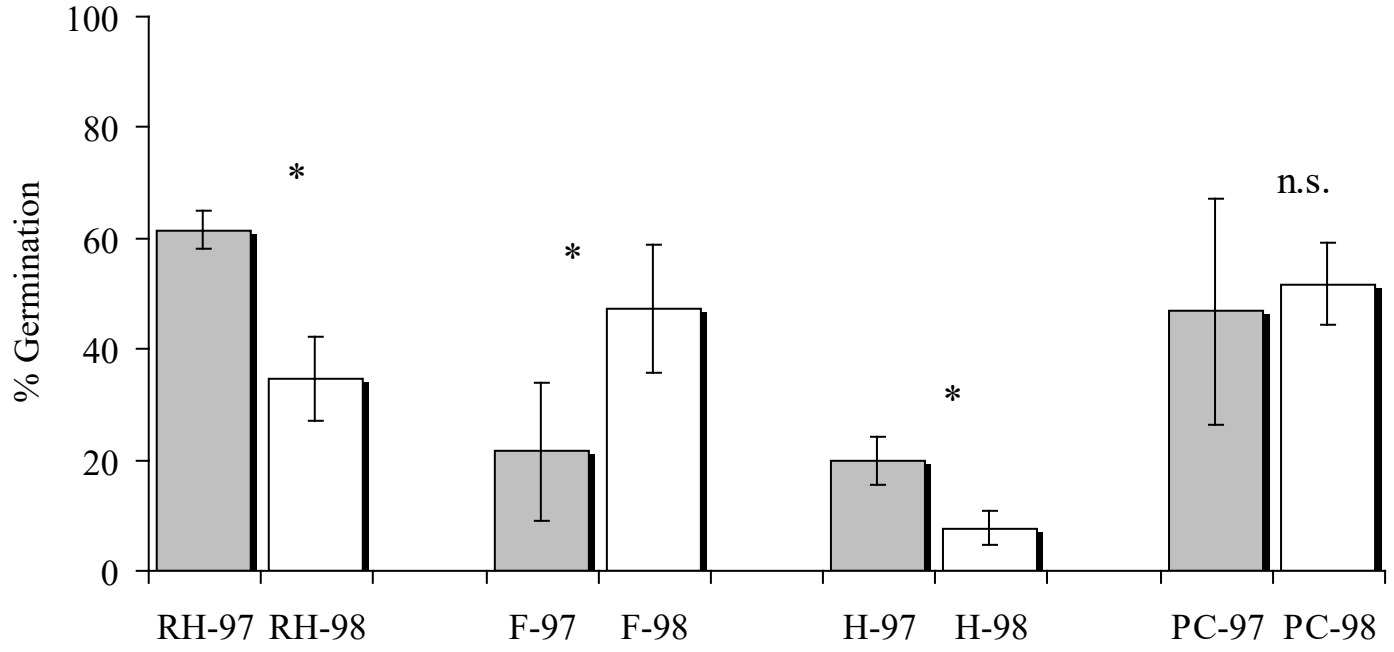

Figure 6a

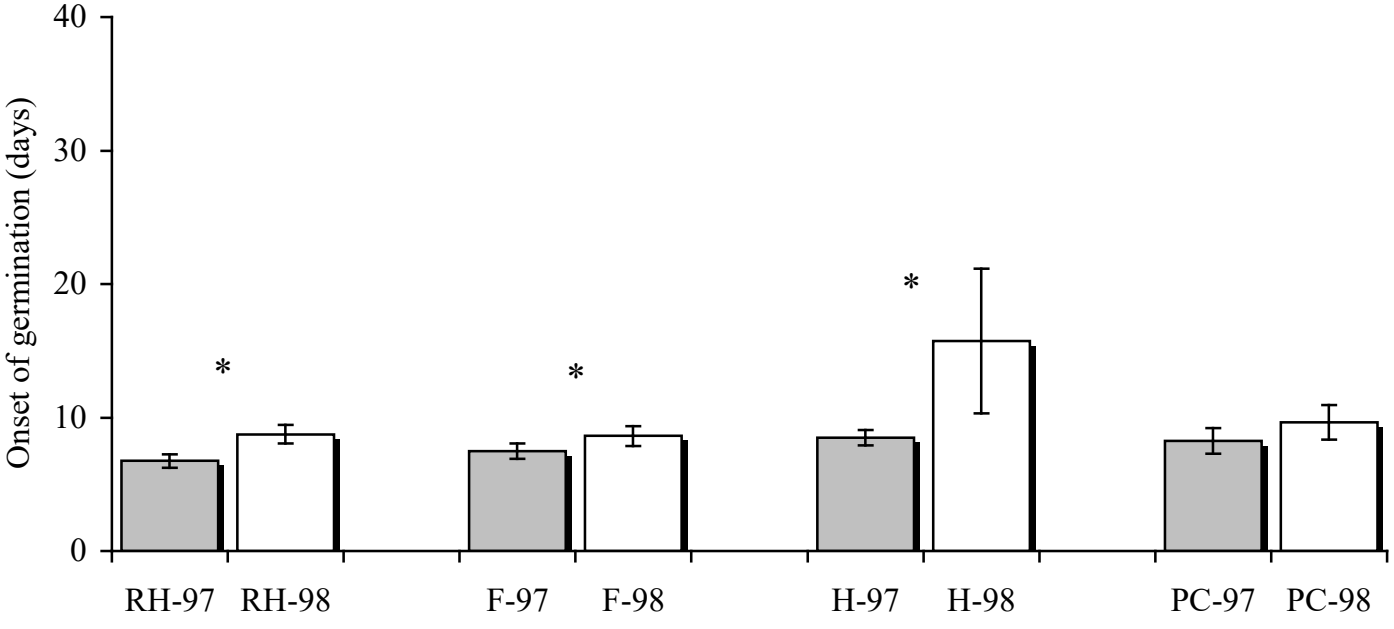

Figure 6b

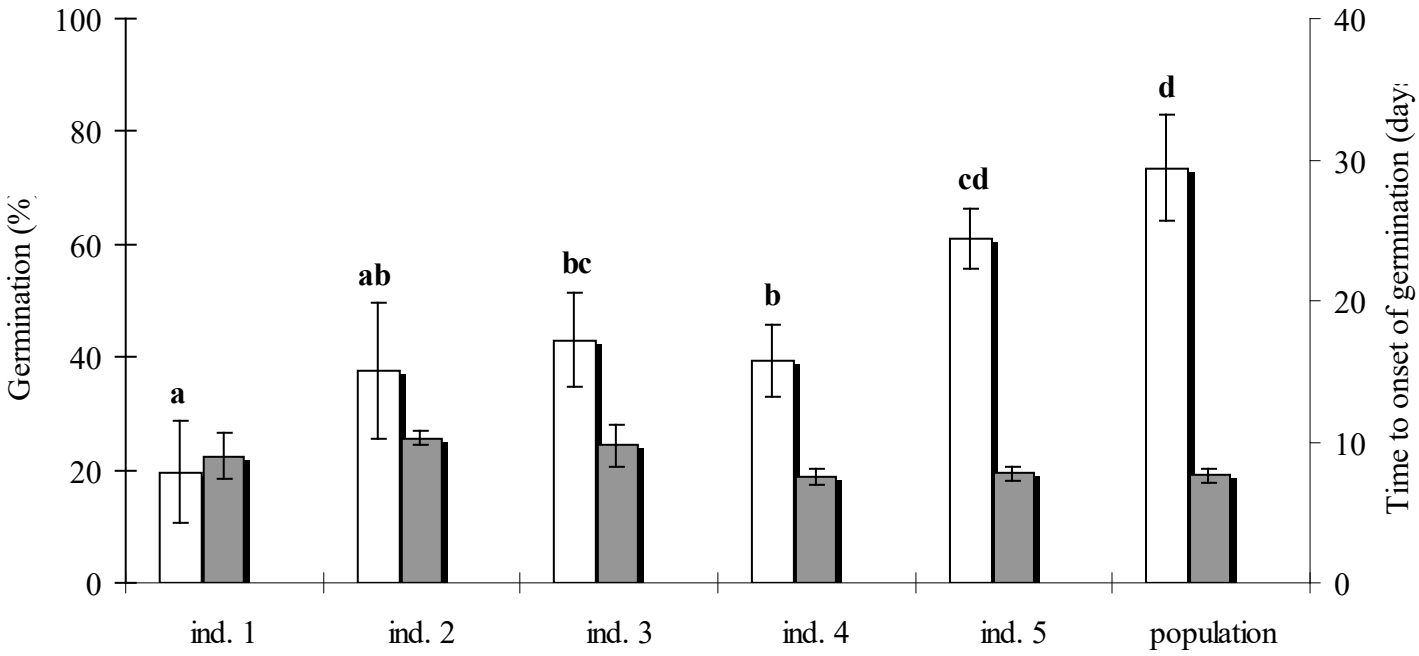
100
80
60
40
20
0
Germination (%
40
30
20
10
0
Time to onset of germination (day
a
ab
bc
b
cd
d
ind. 1
ind. 2
ind. 3
ind. 4
ind. 5
population

Figure 7