

Effects of maternal environmental factors on physical dormancy of *Astragalus nitidiflorus* seeds (Fabaceae), a critically endangered species of SE Spain



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ABSTRACT

The viability and seed dormancy of the critically endangered species *Astragalus nitidiflorus* were tested during eight consecutive years (2006–2013) in order to determine if the high physical seed dormancy described in a previous study is affected by annual or seasonal environmental conditions. Also, the effects of maternal factors – such as fruit position in the inflorescence or seed position in the fruit, the age of the mother plants, and water stress – on seed viability and dormancy were tested. In order to determine the variation in the degree of germinability between years, ripe seeds were harvested each July from 2006 to 2013 and their viability and dormancy were tested. Moreover, in 2013 new seeds were collected to check the effects of the maternal factors mentioned above. A trial with potted plant in greenhouse was performed to corroborate the observed field data about the effect of water stress suffered by the mother plant on seed dormancy. The results show a high variability over the years in the physical dormancy of *A. nitidiflorus* seeds because maternal environmental factors such as drought or mother plant age influence the proportion of seeds that enter dormancy. This in turn determines the proportion of seed that becomes part of the seed bank each year and also the age structure of the natural population. The conservation programs for this critically endangered species should consider these results to implement measures to prevent the extinction of the species.

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1. Introduction

In most plant species, seeds vary in their degree of germination between and within populations and between and within individuals. Some of these variations may be genetic, but many of them are known to be phenotypic (Guterman, 2000). The so-called maternal environmental effects on germination are considered to be the phenotypic effects caused by the environmental conditions that produce seeds that reach different germination percentages and/or have different germination requirements (Shem-Tov and Guterman, 2003; Donohue, 2009). According to Guterman (2000) these conditions consist of a combination of the microenvironment experienced by the seed due to its position on the mother plant and the abiotic environment of the plant (temperature, light, water availability, etc.). As a result, seeds from a single species can vary greatly in dormancy status, depending on when and where they

were collected (Hoyle et al., 2008). The maturation of seeds with different germinability and dormancy on one mother plant has a very important ecological advantage, especially in arid ecosystems (Guterman, 2000). Seed dormancy allows the long-term burial of seeds and consequently the formation of a persistent soil seed bank (Baskin and Baskin, 1998), enhancing seedling survival by delaying germination to avoid competition from established plants or unfavourable weather conditions (Fenner and Thompson, 2005).

Astragalus nitidiflorus Jiménez Mun. et Pau (Leguminosae) is a perennial herb endemic to the province of Murcia (Southern Spain) that was declared extinct in 2003 after nearly 100 years without being observed, but was rediscovered in 2004. Currently it is listed as Critically Endangered, in accordance with IUCN (2001) criteria. After the rediscovery of the species, the first seeds collected (a scarce number in 2005) were analysed and most of them (ca. 90%) showed physical dormancy imposed by a hard coat (Martínez-Sánchez et al., 2011). Hardseededness is a widely occurring feature in Leguminosae (Herranz et al., 1998; Ooi, 2012), that imposes physical seed dormancy by preventing embryo hydration and radicle expansion (Rolston, 1978), and particularly in the genus

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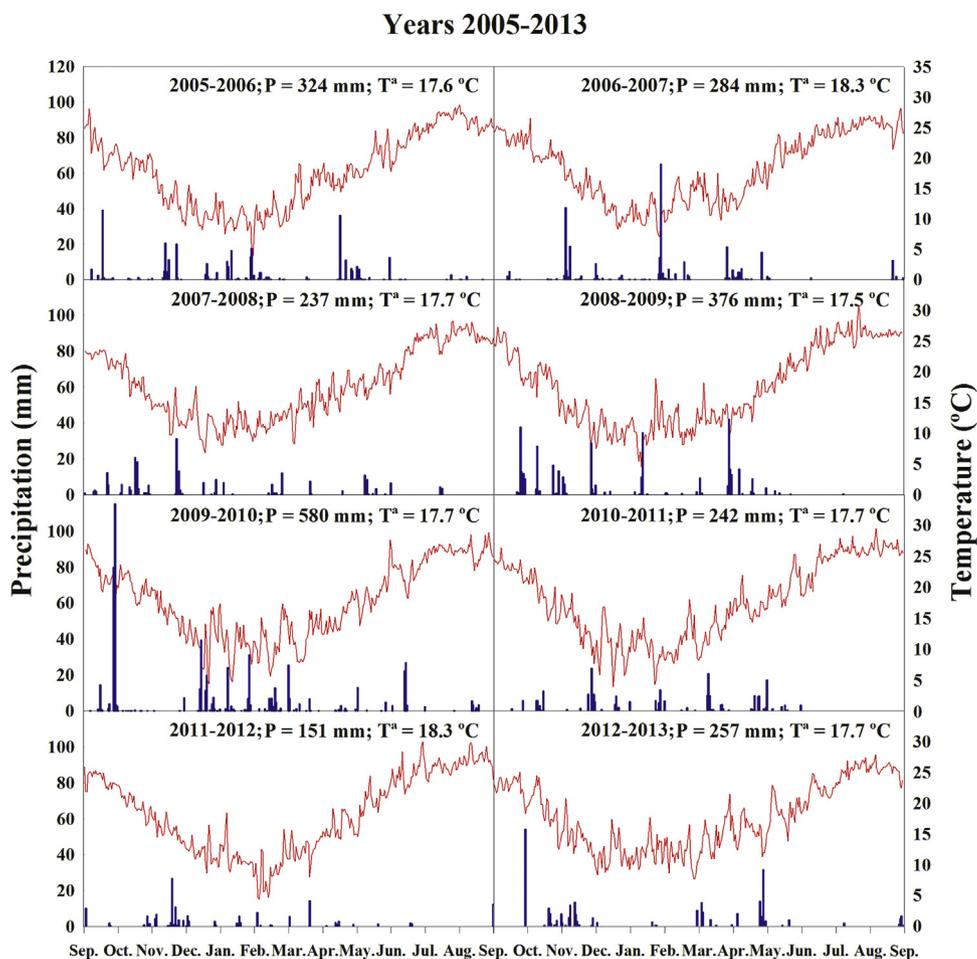


Fig. 1. Daily precipitation (bars) and mean daily temperature (lines) for the periods from September of one year to August of the following year (from September 2005 to August 2013) in the studied area. P = total precipitation; T = mean temperature.

Astragalus (Eisvand et al., 2006; Bacchetta et al., 2011; Martínez-Fernández et al., 2014). In fact, there are evidences in the literature on seed dormancy in 33 *Astragalus* perennial taxa and all of them were reported to have water-impermeable seeds and thus physical dormancy (PY) (Long et al., 2012). Ecologically, physical dormancy has long been proposed to enables plants to survive in unpredictable environments and to prevent seeds from predation, mainly through the formation of persistent seed banks in soil (Baskin and Baskin, 1998). So we considered the physical seed dormancy in *A. nitidiflorus* as a proven fact. However, in 2005 studies on the biology of this species began (Martínez-Sánchez et al., 2011; Vicente et al., 2011; Segura et al., 2014), the latest one showing that the seeds have a hard coat but the species is unable to form a long-term persistent soil seed bank. So, new evidence about the physical dormancy of seeds and the maternal factors that may influence this dormancy is needed to understand the population dynamics, and would contribute to sustainable management and preservation strategies for this species. Also, the seedling stage is the most critical part of the life cycle of *A. nitidiflorus*, since between 70 and 100% of the seedlings which emerge in autumn do not survive the following summer (Martínez-Sánchez et al., 2011). If there were such an effective mechanism, allowing seeds to 'predict' their future success by utilising information about the environment of their mother plant, as proposed by Tielbörger and Petru (2010), it would be very interesting to know whether it exists in this critically endangered species.

The aim of this paper was to analyse the physical dormancy and germination of *A. nitidiflorus* seeds from different harvests

(2006–2013) and to study the effects on seed dormancy of some maternal factors such as (i) fruit position in the inflorescence and seed position in the fruit, (ii) the age of the mother plant and (iii) water stress in the mother plant.

2. Materials and methods

2.1. Plant material and study site

A. nitidiflorus is a perennial herbaceous legume that is short-lived (the plants do not live more than four years) and germinates in autumn. In mature plants (two years old) flowering begins in March and continues until the end of May, being maximal in April. The flowers appear in racemes of up to 30 flowers. The fruits are indehiscent legumes (18 mm × 7 mm) that take about two months to ripen and dispersion take place from early July. The unit of dispersion is the fruit, that may contain up to 19 seeds (Martínez-Sánchez et al., 2011). Currently there is only one metapopulation, composed of four populations very close together (less than 2 km between them). The study area has a Mediterranean type climate with semi-arid conditions. The mean annual rainfall is around 300 mm and the annual potential evapotranspiration 1319 mm. The annual drought period normally lasts five months. The mean annual air temperature is 17.6 °C, the warmest month being August (mean monthly temperature 26.1 °C) and the coldest month January (mean monthly temperature 10.4 °C). The precipitation and temperature data during the study period are shown in Fig. 1.

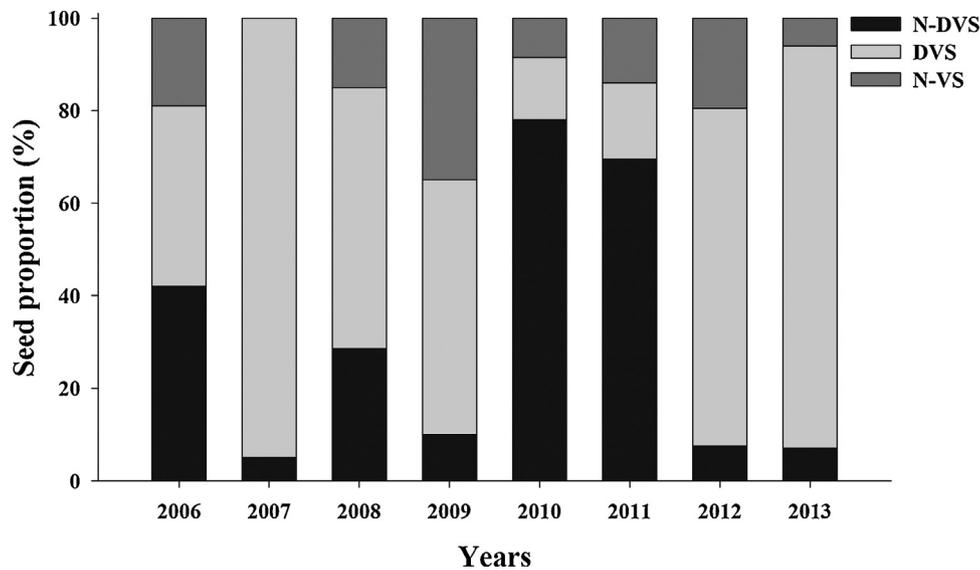


Fig. 2. Proportion of dormant seeds collected in the field population in each year from 2006 to 2013. N-DVS = non-dormant viable seeds; DVS = dormant viable seeds; N-VS = non-viable seeds.

2.2. Germination experiments

To examine the variation in the degree of germinability between years, ripe fruits were harvested each July from 2006 to 2013—from 20 fruiting individuals in the largest known population (37°40'N, 1°08'W). The seeds were removed from the fruits by hand and conserved in the Seed Bank of the Technical University of Cartagena at 4 °C. In July 2013 four replicates (25 seeds each) per year were placed on moistened filter paper in Petri dishes and incubated in a growth chamber with digital temperature and light control system (± 0.1 °C, cool white fluorescent light, 20,000 lx) (Sanyo MLR-351H, Osaka, Japan) at 15 °C and 12-h photoperiod. The number of germinated seeds (2 mm radicle emergence) was registered every two days for one month and recorded as non-dormant viable seeds (N-DVS). From the same test, ungerminated seeds were scarified with sandpaper, to break physical dormancy, and then placed back on moist filter paper for 15 days. Then, the scarified seeds that germinated were recorded as dormant viable seeds (DVS) and those that did not germinate as non-viable seeds (N-VS).

2.3. Maternal environmental effect experiments

To evaluate the effects on germinability of the position of the fruit, positions in the inflorescence and seed positions inside the fruit, 20 two-year-old plants were randomly selected from the field population and their ripened fruits collected in July 2013. From each plant, fruits were collected from five different inflorescences in two morphological positions: the basal and apical positions of the inflorescence. From each fruit, healthy seeds were collected separately from the middle and from the apical end of the fruit (two seeds per fruit and position). At the same time, fruits from 10 two-year-old plants and from the same number of three-year-old plants were collected to test the effect of the age of the mother plant on germinability. The germination response was tested as described above for the seed germination experiments, using four replications of 25 seeds each.

Considering that our study on the germination characteristics was always conducted with seeds collected in the same location and that environmental factors such as temperature, light, altitude and mineral nutrition remained practically constant over the years, we focused on the only environmental factor that varied significantly between years, the rainfall (Fig. 1). So, to check the effect of

rainfall on seed dormancy a correlation was made between seed germination and the annual amount of rainfall, but no correlation was obtained ($F_{1,6} = 1.153$, $P = 0.324$, $R^2 = 0.161$). However, according to Donohue and Schmitt, 1998, germination is highly responsive to environmental stress experienced before dispersal, during seed maturation on the maternal plant, and at least in some species the last 5–15 days of seed maturation is the critical time (Gutterman, 2000). Taking into account that the maximum flowering moment occurs in April and that the fruits take about two months to ripen, the period of maximum influence of the water availability on *A. nitidiflorus* germinability is most likely to occur during May and June. So, another correlation analysis was made between seed germination and the amount of rainfall in May–June.

Also, one experiment was carried out in a greenhouse to test the effect of maternal drought on seed dormancy. For this, *A. nitidiflorus* plants were grown in a greenhouse at the Tomás Ferro Agrifood Experimental Station in Cartagena (37°41'N, 0°57'W). Plants grown from seed collected in July 2011 in the field population were planted in 48 2.5-L PVC pots filled with a mixture of black peat and soil from the habitat (6:1 vol.) and arranged on metal crop tables in six rows of eight pots each. All pots were well irrigated until April 2012, when two irrigation treatments were implemented: “well irrigated plants” (WIP) and “plants stressed by drought” (PSD). For each irrigation treatment, three replicates (eight pots each) were considered. The irrigation was controlled by a system identical to that described by Valdés et al. (2012) at the same experimental station. This system was composed of a CR 1000 data logger, balances (Analytical Sartorius, Model 5201) and an Agrónic 4000 (Sistemas Electrònics PROGRÉS, S.A. Bellpuig, Spain). Each pot had an emitter (2 L h^{-1}). The CR1000 recorded the weight of three pots (one pot per balance) per treatment every 30 min. The substrate water available was estimated at 35% by volume (De Boodt and Verdonck, 1972). So, when the balances detected a loss of weight of 500 mg (a 20% reduction of the water available) in the WIP treatment an irrigation event was triggered while for the PSD treatment this occurred when the pot weight fell by 850 mg (35% of the water available). At the fruiting stage (late July) fruits from both treatments were collected separately (five per pot) and seeds were removed by hand in order to test the germination behaviour. Then, four replicates (of 25 seeds each) per irrigation treatment were plated and their germination responses were tested as in the germination experiments described above.

Table 1
Effect of fruit position in the inflorescence, seed position in the fruit, the age of the mother plant and maternal drought on seed dormancy and viability. *Stat. (M-W)*.

Studied factor	Non-dormant viable seeds (%)	Dormant viable seeds (%)	Non-viable seeds (%)
Fruit position			
Basal	13.1 ± 16.6	51.9 ± 38.3	35.1 ± 41.9
Apical	10.9 ± 26.5	73.2 ± 35.8	15.9 ± 29
	<i>P</i> =0.296	<i>P</i> =0.095	<i>P</i> =0.291
Seed position			
Middle	3 ± 2	62 ± 22.7	35 ± 22.5
Outermost	2 ± 2.3	68 ± 19.9	30 ± 19.2
	<i>P</i> =0.495	<i>P</i> =0.663	<i>P</i> =0.770
Plant age			
Two years	19 ± 6.8B	59 ± 9.4	22 ± 14
Three years	1 ± 2A	74 ± 18	25 ± 18.3
	<i>P</i> =0.018	<i>P</i> =0.180	<i>P</i> =1.000
Maternal drought			
Well-irrigated	87 ± 5B	0A	13 ± 5A
Stressed	19 ± 8.9A	39 ± 2B	42 ± 8.3B
	<i>P</i> =0.020	<i>P</i> =0.011	<i>P</i> =0.020

2.4. Statistical analysis

The germination data did not fit a normal distribution, so comparisons of non-dormant viable seeds (N-DVS), dormant viable seeds (DVS) and non-viable seeds (N-VS) between years were performed using the Kruskal–Wallis non-parametric test at $P < 0.05$. To analyse the effects of fruit and seed position, plant age and water availability on these germination variables a Mann–Whitney U non-parametric test at $P < 0.05$ was performed. A logarithmic transformation was performed with percentages of N-DVS, DVS, N-VS in order to calculate the correlation between the proportion of these type of seeds and rainfall amount. After data transformation regressions were analyzed using the Curve Estimation Method (SPSS, 2011).

All data were analysed using the statistical package SPSS 20.0 (IBM Corp., Armonk, NY) for Windows, and the graph-analysis was performed by the software Sigmaplot Version 10.0 (Systat Software Inc., Point Richmond, CA).

3. Results

The seed germination of *A. nitidiflorus* varied greatly depending on the year in which the seeds were collected ($P < 0.001$). In 2007,

2012 and 2013 the proportions of seeds with physical dormancy (DVS) were 97%, 73% and 87%, respectively, but in 2010 and 2011 only 13% and 16% (Fig. 2).

The results also show that fruit position on the inflorescence had no effect on the proportion of dormant seed ($P = 0.095$) and the same happened regarding the seed position in the fruit ($P = 0.663$) (Table 1). However, the age of the mother plant had a significant effect on the proportion of non-dormant viable seeds ($P = 0.018$) and plants at the first fruiting produced seeds with germination percentages (19 ± 6.8%) higher than those of the oldest plants (1 ± 2%; Table 1). But the most influential effect on seed germination characteristics was the availability of water at the fruiting stage. Seeds from well irrigated plants showed a total absence of dormancy (all viable seeds – 87% – were non-dormant) while those from plants stressed by drought showed lower viability (only 68% were viable) and the proportion of non-dormant seed did not reach 20% (Table 1).

In the natural population, the percentage of germinated seeds was also significantly affected by the amount of rainfall during the May–June period ($P < 0.001$), and proportion of N-DVS increasing with the amount of rainfall according to a power curve ($F_{1,6} = 110.005$, $P \leq 0.001$, $R^2 = 0.948$; Fig. 3A). When the rainfall was less than 10 mm in the period from May to June (“dry springs” in

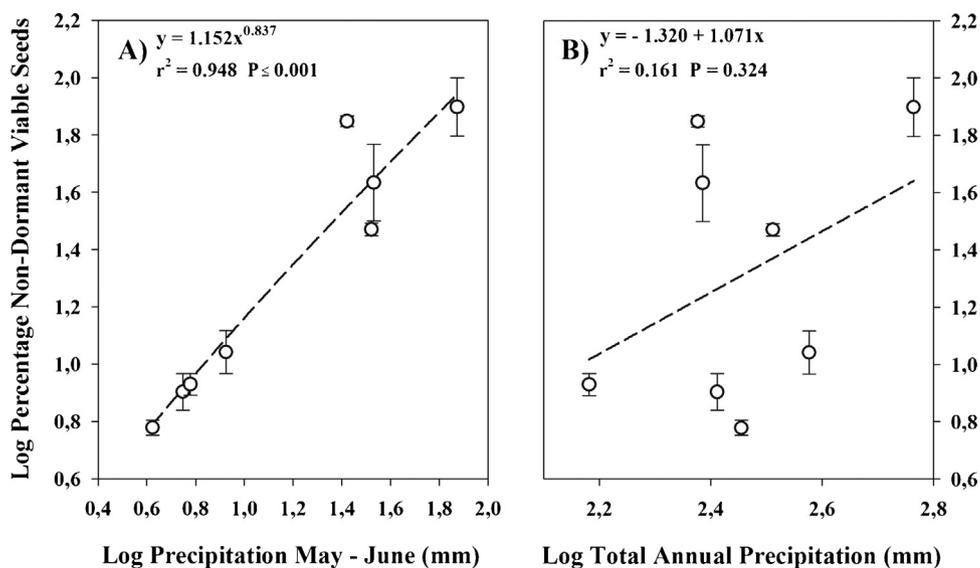


Fig. 3. Relationship between proportion of Non-dormant viable seeds and the precipitation recorded in the May–June (A) or annual (B) period in the eight years sampled.

2007, 2009, 2012 and 2013) the proportion of N-DVS was $7.4 \pm 1\%$; when rainfall exceeded 25 mm (“wet springs” in 2006, 2008, 2010 and 2011) this value increased to $54.5 \pm 11.6\%$. However, the proportion of N-DVS was not affected by the total annual rainfall ($F_{1,6} = 1.153$, $P = 0.324$, $R^2 = 0.161$; Fig. 3B). Proportions of N-VS and DVS were not significantly affected by the May–June rainfall ($P = 0.926$; $R^2 = 0.161$ and $P = 0.409$; $R^2 = 0.479$ respectively).

4. Discussion

Results obtained in this work concerning seed germination are in agreement with results obtained for other species of the genus *Astragalus* in which most of seeds are dormant due to the impermeability of the seed coat to water (Eisvand et al., 2006; Kim et al., 2008; Bacchetta et al., 2011; Long et al., 2012). Also, Martínez-Fernández et al. (2014) showed that seeds from different plants of *Astragalus gines-lopezii* (a species closely related with *A. nitidiflorus*) have not the same germination behaviour even though seeds were collected in the same population and year. But this study has not explained the causes of this intrapopulation variation in seed germination because they did not studied the age effects or water stress effects. However, our results show that the age of the mother plant has an effect on seed germination: older plants produce viable seeds with lower germination percentages than those from younger plants. This is known to occur for a large number of annual species and many examples are cited in Gutterman (2000), supporting the idea that senescence influences seed dormancy. But the senescence effect is not a good explication in the case of *A. nitidiflorus* because it is a perennial herbaceous species and seeds from plants of different ages were collected at the same time. Taking into account that *A. nitidiflorus* plants at the first fruiting stage (two years old) produced an average of 1500–3000 seeds per plant while plants at the second fruiting stage (three years old) produced 8000–10,500 seeds (Martínez-Sánchez et al., 2011), we can explain our result by taking into account the likely negative relationship between maternal fecundity and offspring germination fraction because the risk of sibling competition increases with increasing seed family size (the sibling competition hypothesis in Eberhart and Tielbörger, 2012). But the same authors have shown that in semi-arid land there is no relationship between maternal fecundity and germination. Regardless of the factors that cause the differing germination behaviour of seeds from plants of different age, our results suggest that the age structure of the population should be an important factor to be considered when estimating the annual replenishment of soil seed banks. At the same time, in perennial species, maternal effects have the potential to influence the age structure of populations, which in turn would influence the projected population growth rates, probability of population extinction and genetic variation (Tonsor et al., 1993).

The seed coat is considered one of the main ways in which information is transmitted to the following generation, as it develops entirely from maternal tissues (Luzuriaga et al., 2006). Changes in the structure and thickness of the seed coat have been described by Lacey et al. (1997), among many other authors. But there are discrepancies among the reports on the impact of drought on seed dormancy (Baskin and Baskin, 1998). The type of response to drought conditions during seed development seems dependent on the kind of dormancy involved. Seeds of *A. nitidiflorus* are known to have physical dormancy due to their suberized and water impermeable seed coat; this is commonly known as hardseededness and is typical of many species from families such as the Leguminosae, Malvaceae, Chenopodiaceae and Liliaceae (Copeland and McDonald, 2001). When dormancy is imposed mechanically by a thick seed coat, as in our case, drought usually increases its thickness, thereby contributing to reduced germinability (Fenner, 1991; Baskin and

Baskin, 1998). In fact, our results are supported by some studies in which parental drought increased dormancy in other legumes such as *Glycine max* (Dornbos and Mullen, 1991), *Arachis hypogea* (Pallas et al., 1977) and *Acacia saligna* (Tozer and Ooi, 2014). However, other studies found that parental drought decreased dormancy in *Sorghum halepense* (Arnold et al., 1992), *Raphanus rapahistrum* (Eslami et al., 2010) and *Sinapis arvensis* (Wright et al., 1999; Luzuriaga et al., 2006) among many other species. Tielbörger and Petru (2010) assumed that competition is the ultimate reason for the existence of such maternal environmental effects and hypothesised that there is a negative relationship between favourable seasons and seed germination; then, the offspring may reduce the negative effects of crowding in the following year (Tielbörger and Valleriani, 2005; Valleriani and Tielbörger, 2006). However, this hypothesis is valid in climates with high precipitation but not in semi-arid ecosystems where plant interactions can be neutral or positive (Holzapfel et al., 2006). The total annual rainfall, the amount of rain in each rainfall event and the time between rainfall events are highly variable in semi-arid areas (Shem-Tov and Gutterman, 2003). This is the case for our study, where the annual rainfall from 2005 to 2013 averaged 306 mm (Fig. 1) and massive offspring germination was observed in some autumns. The ecological implication of these differences is that seeds produced in a dry spring are likely to have a slower rate of dormancy release than those produced in a wet spring. Thus, seeds from a dry year may be more likely to become part of the persistent soil seed bank than those produced in a wet year, which are more water permeable and will be able to germinate when the environmental conditions are favourable. This mechanism is responsible for long-term seed dormancy but also provides sufficient germinable seeds for colonisation when conditions become favourable (Eslami et al., 2010). Our findings show that drought from May to June could prevent the emergence of most of the offspring with the first autumn rains. The results shown in this paper are consistent with the population dynamics of *A. nitidiflorus*, characterised by highly variable population censuses between years and specific episodes of massive emergence of seedlings as well as great oscillations of the soil seed bank, depending on the demographic fluctuations in the short-term population shown by Segura et al. (2014). The maximum life span of an *A. nitidiflorus* plant is four years and in that time the plant is fruitful three times, so the probability that different seed yields are affected by plant age or different drought periods is very high. Then, the offspring will have a very high plasticity, to closely match the changing conditions of this unpredictable environment.

In conclusion, the production of dormant seed in *A. nitidiflorus* could be very variable over the years because maternal environmental factors, such as drought or mother plant age, influence the proportion of seeds that enter dormancy and become part of the seed bank. So, the age structure of the population is an important factor to be considered when estimating the annual replenishment of soil seed banks. Besides, the amount of rainfall in late spring needs to be considered in order to plan strategies to manage the endangered populations of *A. nitidiflorus* and of other species with similar characteristics.

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References

- Arnold, R.L.B., Fenner, M., Edwards, P.J., 1992. Changes in dormancy level in *Sorghum halepense* seeds induced by water stress during seed development. *Funct. Ecol.* 6, 596–605.

- Bacchetta, G., Fenu, G., Mattana, E., Pontecorvo, C., 2011. Ecological remarks on *Astragalus maritimus* and *A. verrucosus*, two threatened exclusive endemic species of Sardinia. *Acta Bot. Gallica* 158, 79–91.
- Baskin, C.C., Baskin, J.M., 1998. Seeds. In: *Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.
- Copeland, O.L., McDonald, M.B., 2001. *Principles of Seed Science and Technology*, fourth ed. Kluwer Academic Press, New York.
- De Boodt, M., Verdonck, O., 1972. The physical properties of the substrates in horticulture. *Acta Hort.* 26, 37–44.
- Donohue, K., 2009. Completing the cycle: maternal effects as the missing link in plant life histories. *Phil. Trans. R. Soc. B* 364, 1059–1074.
- Donohue, K., Schmitt, J., 1998. Maternal environmental effects in plants. *Adaptive plasticity?* In: Mousseau, T.A., Fox, C.W. (Eds.), *Maternal Effects as Adaptation*. Oxford University Press, Oxford, UK, pp. 137–158.
- Dornbos, D.L., Mullen, R.E., 1991. Influence of stress during soybean seed fill on seed weight, germination, and seedling growth rate. *Can. J. Sci.* 71, 373–383.
- Eberhart, A., Tielbörger, K., 2012. Maternal fecundity does not affect offspring germination—an empirical test of the sibling competition hypothesis. *J. Arid Environ.* 76, 23–29.
- Eisvand, H.R., Arefi, H.M., Tavakol, R., 2006. Effects of various treatments in breaking seed dormancy of *Astragalus siliquosus*. *Seed Sci. Technol.* 34, 747–752.
- Eslami, S.V., Gill, G.S., McDonald, G., 2010. Effect of water stress during seed development on morphometric characteristics and dormancy of wild radish (*Raphanus raphanistrum* L.) seeds. *Int. J. Plant Prod.* 4, 159–168.
- Fenner, M., 1991. The effects of the parent environment on seed germinability. *Seed Sci. Res.* 1, 75–84.
- Fenner, M., Thompson, K., 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, UK.
- Gutterman, Y., 2000. Maternal effects on seeds during development. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CABI Publishing, Wallingford, UK, pp. 59–84.
- Herranz, J.M., Ferrandis, P., Martínez-Sánchez, J.J., 1998. Influence of heat on seed germination of seven Mediterranean Leguminosae species. *Plant Ecol.* 136, 95–103.
- Hoyle, G.L., Steadman, K.J., Daws, M.I., Adkins, S.W., 2008. Pre- and post-harvest influences of seed dormancy status of an Australian Goodeniaceae species, *Goodenia fascicularis*. *Ann. Bot.* 102, 93–101.
- Holzappel, C., Tielbörger, K., Parag, H.A., Kigel, J., Stenberg, M., 2006. Annual plant–shrub interactions along an aridity gradient. *Basic Appl. Ecol.* 7, 268–279.
- Kim, S.Y., Oh, S.H., Hwang, W.H., Kim, S.M., Choi, K.J., Kang, H.W., 2008. Physical dormancy in seeds of Chinese milk vetch (*Astragalus sinicus* L.) from Korea. *Korean J. Crop Sci.* 53, 421–426.
- Lacey, E.P., Smith, S., Case, A.L., 1997. Parental effects on seed mass: seed coat but not embryo/endosperm effects. *Am. J. Bot.* 84, 1617–1620.
- Long, Y., Tan, D.Y., Baskin, C.C., Baskin, J.M., 2012. Seed dormancy and germination characteristics of *Astragalus arpilobus* (Fabaceae, subfamily Papilionoideae), a central Asian desert annual ephemeral. *S. Afr. J. Bot.* 83, 68–77.
- Luzuriaga, A.L., Escudero, A., Pérez-García, F., 2006. Environmental maternal effects on seed morphology and germination in *Sinapis arvensis* (Cruciferae). *Weed Res.* 46, 163–174.
- Martínez-Fernández, V., Martínez-García, F., Pérez-García, F., 2014. Census, reproductive biology, and germination of *Astragalus gines-lopezii* (Fabaceae), a narrow and endangered endemic species of SW Spain. *Turk. J. Bot.* 38, 686–695.
- Martínez-Sánchez, J.J., Segura, F., Aguado, M., Franco, J.A., Vicente, M.J., 2011. Life history and demographic features of *Astragalus nitidiflorus*, a critically endangered species. *Flora* 206, 423–432.
- Ooi, M.K.J., 2012. Seed bank persistence and climate change. *Seed Sci. Res.* 22, 53–60.
- Pallas, J.E., Stansell, J.R., Bruce, R.R., 1977. Peanut seed germination as related to soil water regime during pot development. *Agron. J.* 69, 381–383.
- Rolston, M.P., 1978. Water impermeable seed dormancy. *Bot. Rev.* 44, 365–396.
- Segura, F., Martínez-Sánchez, J.J., Aguado, M., Franco, J.A., Vicente, M., 2014. Could recently locally extinct population patches of *Astragalus nitidiflorus* regenerate from the soil seed bank? *J. Arid Environ.* 110, 75–78.
- Shem-Tov, S., Gutterman, Y., 2003. Influence of water regime and photoperiod treatments on resource allocation and reproductive successes of two annuals occurring in the Negev Desert of Israel. *J. Arid Environ.* 55, 123–142.
- SPSS, 2011. Statistical package for social sciences. In: 20.0. User Manual. SPSS Inc., Chicago.
- Tielbörger, K., Petru, M., 2010. An experimental test for effects of the maternal environment on delayed germination. *J. Ecol.* 98, 1216–1223.
- Tielbörger, K., Valleriani, A., 2005. Can seeds predict their future? Germination strategies of density-regulated desert annuals. *Oikos* 111, 235–244.
- Tonsor, S.J., Kalisz, S., Fisher, J., Holtsford, T.P., 1993. A life-history based study of population genetic structure: seed bank to adults in *Plantago lanceolata*. *Evolution* 47, 833–843.
- Tozer, M.G., Ooi, M.K.G., 2014. Humidity-regulated dormancy onset in the Fabaceae: a conceptual model and its ecological implications for the Australian wattle *Acacia saligna*. *Ann. Bot.* 114, 579–590.
- IUCN, 2001. IUCN red list categories and criteria. Version 3.1 <http://www.iucn.org/themes/ssc/red-list.htm>.
- Valdés, R., Miralles, J., Ochoa, J., Sánchez-Blanco, M.J., Bañón, B., 2012. Saline reclaimed wastewater can be used to produce potted weeping fig (*Ficus benjamina* L.) with minimal effects on plant quality. *Span. J. Agric. Res.* 10, 1167–1175.
- Valleriani, A., Tielbörger, K., 2006. Effect of age on germination of dormant seeds. *Theor. Popul. Biol.* 70 (1), 1–9.
- Vicente, M.J., Segura, F., Aguado, M., Migliaro, D., Franco, J.A., Martínez-Sánchez, J.J., 2011. Genetic diversity of *Astragalus nitidiflorus*, a critically endangered endemic of SE Spain, and implications for its conservation. *Biochem. Syst. Ecol.* 39, 175–182.
- Wright, K.J., Seavers, G.P., Peters, N.C.B., Marshall, M.A., 1999. Influence of soil moisture on the competitive ability and seed dormancy of *Sinapis arvensis* in spring wheat. *Weed Res.* 39, 309–317.