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Original article

Seed vs. microsite limitation for seedling emergence in the perennial grass *Stipa tenacissima* L. (Poaceae)

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ABSTRACT

This paper examines the relative influence of seed and microsite availability in the seedling emergence of *Stipa tenacissima*, a perennial grass inhabiting semi-arid Mediterranean steppes. A correlative approximation was used to establish 21 (10 × 10 m) plots along a climatic gradient in the Northern limit of the geographic distribution in East Spain. Seed production, seed removal by ants, ant nest density, and the relative cover of *S. tenacissima*, other perennial plants and bare ground, as explanatory variables, were measured in each plot. Multiple linear regression with forward stepwise selection procedure was used to analyze the relationships between seedling emergence and the explanatory variables. There was large variation between and within plots of all the studied variables, but cover of perennial plants was the only explanatory variable included in the regression model when all the plots were used for the analysis. We suggest that this result was the consequence that high annual precipitation on the Northernmost plots had on the cover of perennial plants and it is consistent with the experimental evidence that shadowing by perennial plants negatively affects germination and performance of the *S. tenacissima* seedlings. Once the Northernmost plots were removed from the model of regression then seed production, seed removal by ants and ant nest density significantly affected seedling emergence. We concluded that microsite quality, defined in relation to the shadowing capacity of perennial species, was more influential than seed and microsite availability at the Northern limit of the geographic distribution of *S. tenacissima*.

1. Introduction

Seed and microsite availability are the main factors controlling seedling establishment in plants (Eriksson and Ehrlén, 1992; Turnbull et al., 2000). Seed availability depends on seed production and on pre- and post-dispersal seed predation, whereas microsite availability depends on the quantity and quality of microsites available for a seed to germinate in and a seedling to survive and develop (Andersen, 1989; Eriksson and Ehrlén, 1992). Microsite requirements can differ throughout the life of long-lived species (Schupp, 1995) and across the distribution range (Austin and Smith, 1989; Barton, 1993).

Iteroparous plants in arid and semi-arid ecosystems must take advantage of the scarce spatial and periodical recruitment opportunities open to them to colonize with sufficient frequency to allow population persistence. Alternatively, seed longevity, i.e. the ability to produce permanent soil seed banks, can contribute to population persistence (Venable, 1989) but persistent seed banks are rare in perennial plants in hot arid and semi-arid environments (Kemp, 1989; Pugnaire and Lázaro, 2000).

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Granivory is another important element of the dynamics of arid and semi-arid ecosystems (Davidson, 1993). In the semi-arid areas of the Mediterranean basin, ants are the most important group of seed consumers during the late spring and summer (Diaz, 1992, 1994), when grass species disperse their seeds. The seasonal and spatial patterns of ant collection are positive correlated with seed size and availability (Crist and MacMahon, 1992; Wilby and Shachak, 2000). Granivory by ants influences the abundance and local distributions of plants by selectively harvesting the seeds of particular species (Mull and MacMahon, 1996; MacMahon et al., 2000, but see Acosta et al., 1992; Brown and Human, 1997).

Requirements for germination and establishment in arid and semi-arid habitats are dependent on environmental and biotic factors that are spatially and temporally variable, such as soil moisture, light, nutrient availability and competition (Lauenroth et al., 1994; Bowers et al., 1995). However, even if the environmental conditions are suitable for germination, seedling emergence will be limited by the production and survival of seeds and the amount and quality of available soil space. In most species, recruitment is concentrated during periods of favorable weather conditions and resource availability (Lauenroth et al., 1994; Watson et al., 1997), and it also concentrates spatially in some favorable microsites (Montaña, 1992; Aguiar and Sala, 1999; Maestre et al., 2003). In the transition from semi-arid to temperate climates there is an increase in soil moisture content that is correlated to an increase in plant cover and biomass (Kerkhoff et al., 2004 and references herein). As plant cover increases, light available to juvenile plants decreases and may become a limiting factor (Tilman, 1988).

This paper presents an analysis of the relative role of microsite availability, microsite quality, seed production and seed removal by ants on the seedling recruitment of *Stipa tenacissima*, a reputed long-lived grass species inhabiting Mediterranean semi-arid environments, along its Northern range of distribution.

2. Material and methods

2.1. Study species

S. tenacissima L. (Poaceae) ("esparto grass" or "alfa grass") is a perennial tussock grass widely distributed in semi-arid ecosystems of the southern and western Mediterranean basin, mainly in the Maghreb, establishing virtually monospecific steppes or co-occurring with shrubs and low trees (Le Houérou, 1986). It grows where annual rainfall is between the 100 and 500 mm isohyets (White, 1983).

S. tenacissima tussocks spread laterally by means of stolons while the older parts senesce as they age (Sánchez and Puigdefábregas, 1994). Plants sprouts after disturbance by fire, drought or grazing. In SE Spain flowering is in early spring and the seeds disperse in before the summer starts. The weight of the dispersal unit (caryopsis) is about 10 mg and has a long awn that aids seed buried into the soil (Hensen, 1999). Not all the caryopses contain a viable seed (Gasque and García-Fayos, 2003) as some flowers may remain unpollinated or seeds may abort before filling (pers. obs.). In this paper the term "seed" will be used when referring to the dispersal unit.

Granivorous ants are the main intensive harvester of the seeds of *S. tenacissima* (Haase et al., 1995; Schöning et al., 2004). The ants are predominantly of the genus *Messor*, and include the species *Messor barbarus* L., *Messor capitatus* Latreille, *Messor bouvieri* Bondroit and *Messor timidus* Espadaler (Willot et al., 2000; Hensen 2002; Schöning et al., 2004). These species mostly search for seeds on the soil surface, but may collect seeds on the plant (pers. obs., Hensen, 2002).

S. tenacissima forms transient soil seed banks with germination taking place from autumn to early spring following a 4-month period of after-ripening (Gasque and García-Fayos, 2003). Germination of seeds and seedlings establishment is less than 30% after 3 years; however those in unshaded conditions were more successful than those under the canopy of perennial plants (Gasque and García-Fayos, 2004).

2.2. Study area

The study was located in six places of E and SE Spain (Fig. 1), from the Northern limit of the distribution of *S. tenacissima* to 300 km south (see Vázquez and Devesa, 1996, for the distribution of the species in the Iberian Peninsula). All of the study sites had slopes less than 15%, with soils derived from calcareous marls. The sites were covered by tussocks of *S. tenacissima* with small woody shrubs of the genus *Fumana* and *Helianthemum* (Cistaceae), *Teucrium*, *Thymus* and *Rosmarinus* (Lammiaceae), and some forbs and grasses. The Porta-Coeli site, the Northernmost one, had also individuals of large shrubs such as *Pistacia lentiscus* L. (Anacardiaceae), *Juniperus oxycedrus* L. (Cupressaceae), *Quercus coccifera* L. (Fagaceae) and *Chamaerops humilis* L. (Palmae).

The climate is typical Mediterranean semi-arid, with hot summers, mild winters and a dry season that lasts for more than 3 months (Table 1). The historical use across the region has been fiber harvesting and grazing, although both activities are presently in decline.

2.3. Methods

Seed and microsite availability and seedling emergence were determined through the establishment of 21 (10 × 10 m) permanent plots across the six sites at the start of the spring in 1997. Plots were established before the anthesis of *S. tenacissima* flowers took place and were located at least 30 m apart from each other.

Seed availability was determined by estimating seed production and seed removal by ants in each plot. Gasque (1999) found that the proportion of filled seeds in *S. tenacissima* spikes is related to spike density in the 10 × 10 m surrounding area ($R^2 = 0.974$; $P < 0.05$; $N = 16$). As it was not possible to determine the number of flowers per spike without altering them and, since in the study area this value varies more within populations than between populations and years, we used the average number of flowers per spike obtained from a previous study (1996) of six Spanish populations of *S. tenacissima* in the same area (Gasque, 1999). Therefore, we counted the number of spikes in each plot during the flower-

Fig. 1 – Distribution of the study sites in SE Spain.

Table 1 – Location and environmental characteristics of the study sites

Site (administrative province)	Geographic coordinates	Altitude (m)	Mean annual temperature (°C)	Annual precipitation (mm)	Rainfall during emergence (mm)
Porta-Coeli (Valencia)	39°40′N 0°29′W	200	17.4	467	106.5
Hellín (Albacete)	38°21′N 1°46′W	360	16.0	379	100.7
Zarcilla de Ramos (Murcia)	38°21′N 1°30′W	640	15.5	350	141.2
Zarzadilla de Totana (Murcia)	37°50′N 1°40′W	850	12.5	354	134.5
La Parroquia (Murcia)	37°44′N 1°52′W	500	16.8	276	141.2
Carboneras (Almería)	36°58′N 2°12′W	235	17.7	268	183.5

ing period of 1997 and assigned a constant value of 148.9 flowers per spike to estimate the number of filled seeds produced per plot. Although more than 75% of the seeds of S. *tenacissima* are dispersed up to 4 m from the parent plant (Gasque, 1999), we assumed that these dispersal losses were balanced by the seed input from the plants located outside the plots.

Seed removal by ants was measured for 4 weeks in June 1997 following cessation of seed dispersal. Experiments consisted of five 9 cm diameter plastic Petri dishes per plot, each dish containing six caryopses with their awns glued to the center of the dish to avoid removal by wind. Only filled caryopses were used in this experiment. One week after placement in the field the Petri dishes were inspected, the remaining caryopses were counted and then replaced with another set of five dishes with intact caryopse. Newly placed dishes were arranged in different positions to avoid ants becoming accustomed to their location. Ants that were found feeding on the seeds of S. *tenacissima* were collected for identification. Additionally, nest density of granivorous ants was estimated by counting the number of ant nests within 30 m of each plot.

Microsite availability was defined as the area occupied by bare ground in each plot. Bare ground was taken to be the proportion of soil surface free from S. *tenacissima* tussocks, other perennial plant species and rock outcrops. Microsite quality was defined as the proportion of soil surface covered by perennial plants other than S. *tenacissima*. The relative cover of the different surfaces was measured by the intercept method with 10 transects 1 m apart along each plot.

Seedling emergence of S. *tenacissima* was determined twice by direct censuses 10 days after rainfall events that occurred in November 1997 and March 1998. At each census, all seedlings we removed after counting. The five Hellín site plots and two of the four Porta-Coeli site plots were disturbed for *Pinus halepensis* afforestation, therefore seedling emergence counts could not be obtained in March 1998. Although seedling numbers in the November 1997 and March 1998 cohorts were highly correlated ($r = 0.895$; $P < 0.0001$; $N = 14$), the data of the former cohort was used because it was the most complete data set.

After the March 1998 emergence period, three randomly located soil samples (50 × 50 × 2 cm) were collected from each plot and inspected in the laboratory to determine the size of the soil seed bank. Only filled seeds were considered for determining soil seed bank estimates. As in the case of the seedling cohort of March 1998, the seed bank of the five Hellín site plots and two of the four Porta-Coeli site plots could not be quantified.

General climatic information for each site was obtained from the nearest meteorological station in the *Worldwide Bioclimatic Classification System* database (http://www.globalbioclimatics.org/) (Table 1). The data set was homogenized by using only the nearest meteorological stations with measurement records spanning the period 1950–1989. Rainfall data for the seedling emergence observation period (01/10/

1997 to 28/03/1998) were obtained from automatic weather stations within 20 km of the study sites.

2.4. *Data analysis*

Prior to multiple regression analysis, we inspected the relationships between all the explanatory variables by means of correlation analysis. We used Spearman's Rho correlation index, as some data were semi-quantitative and others did not fit the normal distribution.

Multiple linear regression analysis with normal distribution of errors was used to analyze the relationships between seedling emergence and seed and microsite related variables. The forward stepwise selection procedure was used to build the regression model with an inclusion criterion of 0.05 and an exclusion criterion of 0.10 in the probability of the F value. The number of seedlings emerging in each plot in November 1997 was selected as the response variable and the measures of seed and microsite availability and microsite quality were used as explanatory variables. Explanatory variables included number of seeds produced, percentage of seeds removed by ants, ant nest density, percentage of bare ground and percentage of soil surface occupied by perennial plants in each plot. Precipitation-related variables were not used because all the plots at the same site had the same values. Data were transformed where necessary to make the relationships between the response and the explanatory variables linear and to fulfill the assumption of homoscedasticity of the variances and normality of the residuals. Decimal logarithms were used to transform both the number of seeds and seedlings and the inverse relation was used to transform the percentage of seeds removed by ants. Data were also checked for outliers and for collinearity of the explanatory variables. As there were several plots in each site, and since some factors such as those related with precipitation can produce similar responses in seedling emergence in all the plots of a site, we also analyzed residuals with one-way ANOVA to check for site effects.

The analyses were performed with the 11.0.1 version of the SPSS package, SPSS Inc. Chicago.

3. Results

Production of seeds varied greatly between plots, ranging across three orders of magnitude (Table 2). The proportion of seeds removed by ants in the experiments was moderate and available soil was high, however only a very small proportion of the seeds produced seedlings. All the ants we found collecting seeds of *S. tenacissima* belonged to the species *M. barbarus*, *M. capitatus* and *M. bouvieri*. Seed removal by ants in traps was constant during the 4 weeks the experiment was running. Seedling emergence took place in November 1997 and March 1998 after two periods of rainfall, each exceeding 25 mm. Precipitation amounts varied substantially between sites (Table 1) although there was no difference between sites in the temporal pattern of precipitation. Seedling density of the November cohort differed highly between plots ranging from 0.03 to 6.86 seedling m^{-2} (Table 2). Post-emergence seed banks were small in all the plots, ranging from < 1% to < 7% of the total seed production.

The correlation matrix showed no relationship between microsite availability and quality (Table 3). Seedling emergence was positively correlated with seed production and

Table 2 – Values of the relative cover of *S. tenacissima*, perennial plants (other than *S. tenacissima*) and bare ground, seed production (expressed as seed density), percentage of seed removal by ants, *Messor* sp. nest density, seedling emergence of *S. tenacissima* (for the November 1997 and March 1998 cohorts) and seeds in the soil bank after the emergence period for each plot (PC: Porta-Coeli, H: Hellín, ZR: Zarzilla de Ramos, ZT: Zarzadilla de Totana, PQ: La Parroquia, C: Carboneras. # indicates absence of data)

Plot	*S. tenacissima* (%)	Perennial plants (%)	Bare ground (%)	Seeds m^{-2}	Seed removal by ants (%)	Nests 100 m^{-2}	Seedlings m^{-2} (November 1997)	Seedlings m^{-2} (March 1998)	Soil bank (seeds m^{-2}) (March 1998)
PC1	31.75	11.75	56.20	846.47	48.33	4	0.04	#	#
PC2	53.90	6.50	39.20	982.07	59.17	1	0.79	#	#
PC3	17.20	22.15	43.40	222.89	34.17	1	0.05	0.01	8.00
PC4	19.20	12.90	48.00	92.99	28.33	1	0.03	0.01	1.33
H1	47.55	4.25	48.05	536.69	35.00	1	2.18	#	#
H2	48.15	5.35	43.60	470.77	47.50	1	0.81	#	#
H3	44.75	2.65	50.80	240.57	50.00	1	1.28	#	#
H4	34.90	8.50	56.40	103.55	69.17	1	0.79	#	#
H5	22.95	3.45	73.40	1329.31	68.33	7	0.81	#	#
ZR1	27.60	2.20	70.20	290.35	38.33	5	0.68	0.00	8.00
ZR2	36.65	3.10	60.25	637.20	40.83	5	1.88	0.38	14.67
ZR3	21.45	2.80	75.75	209.42	40.83	1	4.03	0.79	4.00
ZR4	45.95	5.80	47.40	208.08	65.83	5	0.64	0.08	12.00
ZR5	25.60	5.45	68.95	1101.57	14.17	7	6.86	1.40	17.33
ZT1	31.25	10.20	58.05	4.45	22.50	3	0.35	0.06	#
ZT2	19.10	3.85	76.85	22.08	47.50	6	0.21	0.02	#
ZT3	27.45	6.65	65.05	4.87	33.33	4	0.18	0.02	#
PQ1	66.70	0.70	32.60	1542.57	65.83	1	1.63	0.21	10.67
PQ2	58.00	5.60	36.20	1566.98	74.17	2	4.16	0.71	1.33
C1	60.15	0.20	26.95	3415.01	41.67	9	1.54	0.08	8.00
C2	58.85	0.20	39.05	3204.63	65.83	1	1.54	0.19	4.00

Table 3 – Coefficients of correlation between the studied variables in the plots

	Precipitation during the emergence period (mm)	Cover of *S. tenacissima* (%)	Cover of perennial plants (%)	Cover of bare ground (%)	Seed production (seeds m^{-2})	Seed removal by ants (%)	Ant nest density (nest 100 m^{-2})	Seedlings November 1997 (seedling m^{-2})
Mean annual precipitation (mm)	-0.865^{***}	-0.444^{*}	0.689^{**}	0.152 ns	–0.411 ns	–0.161 ns	–0.346 ns	-0.593^{**}
Precipitation emergence period (mm)		0.264 ns	-0.465^{*}	–0.173 ns	0.347 ns	–0.045 ns	0.372 ns	0.339 ns
Cover of *S. tenacissima* (%)			-0.444^{*}	-0.740^{***}	0.622^{**}	0.510^{*}	–0.180 ns	0.459^{*}
Cover of perennial plants (%)				0.073 ns	-0528^{*}	–0.259 ns	–0.171 ns	-0.610^{**}
Cover of bare ground (%)					-0.505^{*}	–0.329 ns	0.377 ns	–0.144 ns
Seed production (seeds m^{-2})						0.429^{*}	0.114 ns	0.603^{**}
Seed removal by ants (%)							–0.119 ns	0.192 ns
Ant nest density (nests 100 m^{-2})								0.007 ns

ns = not significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

cover of *S. tenacissima* and negatively correlated with the cover of perennial plants and annual precipitation. Variables, including the percentage of bare ground, percentage of seed removal by ants and ant nest density, were not correlated with seedling emergence. *S. tenacissima* cover was negatively correlated with amount of precipitation while the cover of perennial plants was strongly correlated with annual precipitation at the sites.

Thus, the higher the annual precipitation, the higher was the cover of other perennial plants and the lower the cover of *S. tenacissima*. There was no relation between seed removal by ants and ant nest density ($r_s = -0.119$; $P = 0.608$).

The regression model with all the plots included only the cover of perennial plants as an explanatory variable (corrected $R^2 = 0.493$; $N = 21$; $P < 0.001$) with a high partial correlation coefficient ($r_{\text{cover-perennial}} = -0.720$; $t = -4.518$; $P < 0.001$). The residuals were distributed normally and they were not significantly affected by site ($F_{5,20} = 1.341$; $P = 0.300$). However, when the residuals of the regression analysis were graphed, the Porta-Coeli plots appeared to be strongly influencing the results of the analysis, and this was confirmed when they were analyzed by Cook's distances (Ramsey and Schafer, 2002). Therefore, the inclusion of microsite quality in the regression model may be caused by the outlier nature of the plots of the Porta-Coeli site. The data were analyzed again but without these plots.

Regression analysis, without the Porta-Coeli plots, showed a strong positive influence of seed production in seedling emergence and a negative influence of the variables related to seed removal (corrected $R^2 = 0.739$; $N = 17$; $P < 0.001$). The partial correlation coefficients were also high, $r_{\text{log(seed-production)}} = 0.875$ ($t = 6.530$; $P < 0.001$) $r_{\text{1/seed removal-by ants}} = 0.711$ ($t = 3.651$; $P = 0.003$) and $r_{\text{ant-nest-density}} = -0.581$ ($t = -2.573$; $P = 0.023$). The residuals were distributed normally, and were not significantly affected by site ($F_{4,16} = 1.024$; $P = 0.434$).

4. Discussion

Seedling emergence was very low, with only 1% of the seeds becoming seedlings. There was a difference of two orders of magnitude in the numbers of seedlings between plots which was related to variables reflecting seed availability and microsite availability and quality. However, only seed availability (i.e. seed production) and microsite quality (i.e. cover of perennial plants other than *S. tenacissima* and the annual average precipitation) were correlated with seedling emergence.

The forward stepwise selection procedure applied to the multiple regression between seedling density and seed and microsite variables produced a model explaining nearly 50% of the variance and identifying the cover of perennial plants as the only explanatory variable included in the model with a negative partial correlation coefficient.

Theoretical models suggest that a trade-off in plants between tolerance of water limitation vs. tolerance of light limitation results in changes in dominant species over gradients of increasing soil moisture and decreasing light at ground level (Tilman, 1988). As with these models, current research suggests that water stress controls lower limits of species along moisture gradients and light the higher limits, although other factors can mask this relationship (Barton, 1993). In the Mediterranean region soil moisture increases from lower to high latitudes (Quézel, 1981), and therefore vegetal cover and development also increases making light a more limiting factor for seedling emergence. The result of the regression analysis presented here, and the negative effect that experimental shadow had on the emergence and performance of *S. tenacissima* seedlings (Gasque and García-Fayos, 2004), is consistent with the importance of cover of perennial plants controlling seedling emergence of *S. tenacissima* at the Northernmost extreme of its geographical distribution.

Analysis of the data without the plots of the most Northerly study site (Porta-Coeli) produced a regression model with higher explanatory power (more than 70%) that included those variables related to seed availability as explanatory variables but none of the variables related to either microsite availability or quality. Seed production had the highest partial correlation, indicating its greater influence in seedling emergence of *S. tenacissima*. Even though seed removal of *S. tenacissima* by *Messor* spp. ants was high (about 50% of the exposed seeds) their influence in determining seedling emergence was minor given the level of seed production. Seeds of *S. tenacissima* are not the main food resource for *Messor* spp. ants, comprising less than 5% of the seed weight in the waste piles in five ant nests studied at the end of the seed dispersal season of *S. tenacissima* in 1997 at the Porta-Coeli site (Gasque, 1999). Furthermore, a small percentage of *S. tenacissima* seeds remained ungerminated in the soil after the germination period, supporting the theory that seed burial of *S. tenacissima* by the hygroscopic movements of the awn may be an adaptative mechanism against seed predation, as proposed by Schöning et al. (2004). These results illustrate that the interpretation of ant removal experiments and other time limited experiments, such as the counts in returning foraging trails, may not accurately reflect the exact impact of seed removal by ants in plant populations. Furthermore, the density of *Messor* spp. nests adjacent to the plots has only a minor influence on seedling emergence. Despite the effect that both ant-related variables had on seedling emergence, they were not correlated to each other.

Microsite availability in this study did not affect seedling establishment of *S. tenacissima*, in contrast to a study by Schöning et al. (2004) which suggested that the establishment of *S. tenacissima* was limited by the number of safe sites and the number of seeds remaining after ant predation. Results of the current study indicate that when climatic conditions are suitable for germination, seedling establishment is primarily limited by seed production and removal by ants.

Seed production is a common determinant of seedling emergence in other species with short-distance dispersal that inhabit water and soil limited environments (Escudero et al., 1999, 2000). Turnbull et al. (2000) also state that seed-limited recruitment is more likely in plant communities that have competition-free microsites, and microsite-limited recruitment is more likely in forest than in ungrazed grassland communities (Oesterheld and Sala, 1990).

As the factors that influence seed germination may differ from those affecting seedling growth and survival, the initial differences between seedling emergence microsites frequently disappear as a consequence of differential seedling mortality or development (Lamont et al., 1993; Bisigato and Bertiller, 2004). Survival and vegetative growth of seedlings and adult reproduction in *S. tenacissima*, however, were both negatively affected by the canopy of other plants (Gasque and García-Fayos, 2004). Therefore, differential *S. tenacissima* seedling emergence between microsites may continue to be expressed in older life-stages of these communities.

Microsite quality, as defined in relation to the shadowing capacity of perennial plants, may be more influential for seedling emergence than seed and microsite availability at the Northernmost extreme of the geographic distribution of *S. tenacissima*, but towards the core of the distribution of the species, seed availability has a stronger influence than microsite quality and availability in the emergence of seedlings. As the cover of perennial plants in the steppes of *S. tenacissima* is positively related to latitude in southeastern Spain (this study; Maestre, 2004) it is proposed that expansion of the *S. tenacissima* steppes to the North is actually limited by the development of shrublands and woodlands.

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