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Consequences of a severe drought on spatial patterns of woody plants in a two-phase mosaic steppe of *Stipa tenacissima* L.

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The establishment and development of the plants of *S. tenacissima* L. organize a source–sink pattern of water and sediments from bare soil areas to tussocks on mountain slopes forming small terraces or terracettes upslope of tussocks. We hypothesized that terracettes enhance woody plant survival compared with woody plants on bare soil. We examined this hypothesis at three locations in south-eastern Spain after a severe drought from 1993 to 1995.

The spatial association of individual plants and the pattern of plant mortality support the hypothesis that the terracettes formed by *S. tenacissima* tussocks facilitate woody plants. The prediction that facilitation dominates interference during stress periods such as drought was supported by mortality patterns. Drought effects alone do not explain spatial patterns of woody plants in the two-phase mosaic steppe of *Stipa tenacissima*.

Keywords: spatial association; facilitation; plant mortality; semi-arid; drought; *Stipa tenacissima*; SE Spain

Nomenclature: Castroviejo *et al.* (1986–2001) but for the unpublished families we followed Tutin *et al.* (1964–1980).

Introduction

Two-phase mosaics of densely vegetated areas and bareground or almost bareground areas have been commonly reported from many arid and semi-arid regions of the world (Aguiar & Sala, 1999; Valentin *et al.*, 1999). Two main types of vegetation pattern have been described—banded and spotted vegetation. The first type includes patches such as arcs, bands and stripes, whereas the second type refers to patches that are irregular in shape and distribution.

On the banded pattern, the vegetation develops perpendicular to the angle of the slope, being water, but sometimes wind, the main driving force (Valentin *et al.*, 1999). The formation of the patch starts with the colonization of the slopes by pioneer plants, which increase the soil-water infiltration capacity in relation to that of the bareground

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areas. During long and high-energy rainfall events the water infiltration capacity of the soils of the bareground areas is exceeded, then initiating a runoff flow that captures sediments and plant debris—including propagules—from the bare areas to the vegetated ones (White, 1971; Agnew, 1997; Cerdà, 1997; Whitford *et al.*, 1997).

The increase of resources and propagules in the vegetated patches thickens the differences in soil development in relation to the bareground areas, re-enforces the previously installed species or even facilitates the colonization and development of new species (Mauchamp *et al.*, 1993; Callaway, 1995). The frequency, intensity and amount of the rainfall events and the local topography modulated these processes (Wilson & Agnew, 1992; Gallart *et al.*, 1993; Sánchez & Puigdefábregas, 1994). As sediment and organic matter (litter) deposition increases in the vegetated patches the water storage capacity also increases. After rainy seasons the soil water reserves per surface unit of the vegetated patches can be many times the water reserves of the bare soils and also they are less exposed to the direct soil evaporation (Puigdefábregas & Sánchez, 1996). Despite it, the higher plant transpiration and the higher competition for water in the vegetated patches may reduce these advantages, and the same may occur for nutrients. However, the whole balance may be positive for the vegetated patches, which have a biomass production per unit area many times as higher as that of vegetation types with similar resources and climate but with a homogeneous disposition (Aguiar & Sala, 1999; Valentin & d'Herbès, 1999).

Although a lot of scientific literature have been devoted to report the processes of plant facilitation in these vegetation types (see reviews of Callaway, 1995; Aguiar & Sala, 1999; Callaway & Pugnaire, 1999) most of them refer to the establishment, performance and survival of the seedlings of the facilitated plants and only very few papers focus on performance and survival of adults. According to predictions from theory about plant interactions it is expected that facilitation processes dominate over interference processes under harsh conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997; Holmgren *et al.*, 1997; but see Olofson *et al.*, 1999; Tielborger & Kadmon, 2000). If so, then we hypothesized that during severe drought periods plant survival should be higher in the vegetated patches than on the bareground matrix and then drought may be considered as a mechanism of plant facilitation.

Information about these processes is also pertinent because present data and predictions of climate warming on these regions point to an increase of the recurrence and severity of the drought events (Cubasch *et al.*, 1996; De Luis *et al.* 2001).

In the present paper, we first analysed the spatial association of woody plants to both habitats of a two-phase mosaic of vegetation dominated by a perennial grass under the assumption that facilitation processes dominate in the vegetated phase of the mosaic. Second, we compare the spatial association of woody plants and their percentages of mortality on both habitats after a severe drought event under the assumption that during harsh conditions facilitation processes dominate in the vegetated phase of the mosaic. Although we are aware that census data and pattern analysis do not distinguish mechanisms and thus the proposed factors need to be evaluated by experimentation, pattern analysis under assumed hypothesis about natural phenomena can be also informative on the underlying processes (Silvertown & Wilson, 1994).

Methods

Description of the system

Stipa tenacissima L. (Poaceae) (alfa-grass or esparto) is a perennial tussock grass covering large areas in semi-arid landscapes of south-western Europe and north Africa. When the species becomes dominant, it forms a mosaic of tussocks and bareground zones (Le Houérou, 1969; White, 1983). The establishment and development of the tussocks produce local variations in infiltration (Cerdà, 1997; Cammeraat & Imeson, 1999) and, in consequence, a source–sink pattern of water and sediments is organized from bareground areas to tussocks on mountain slopes (Sánchez & Puigdefábregas, 1994; Puigdefábregas & Sánchez, 1996). Deposition of sediments takes place preferably upslope of the *S. tenacissima* tussocks, forming a terracette or small terrace, which changes the topography and angle of the slope at this point and thus reinforcing the spatial structure (Sánchez & Puigdefábregas, 1994). Soil properties below the tussocks and in the terracettes have been reported to be different to the soils of the bareground, being more rich in fine particles and organic matter and less resistant to penetration (Puigdefábregas & Sánchez, 1996; Bochet *et al.*, 1998). Studies on soil hydraulic properties and moisture dynamics showed that *S. tenacissima* enhances water infiltration and a deeper penetration of wetting front in terracettes than in the bareground resulting in a higher water storage capacity (Puigdefábregas & Sánchez, 1996; Cerdà, 1997; Cammeraat & Imeson, 1999).

Study sites

The study was conduced in three localities on the south-east of Spain, Finestrat (Alicante) (38°33′N; 0°11′W, 106 m), Minateda (Albacete) (38°28′N; 1°30′W, 530 m) and Zarzilla de Ramos (Murcia) (37°50′N; 1°52′W, 640 m) (Fig. 1). These localities have the same vegetation, a steppe dominated by *Stipa tenacissima* with small shrubs and herbs of the plant families Labiatae, Cistaceae, Poaceae, Asteraceae, Caryophyllaceae, Liliaceae, Crassulaceae, etc., and scattered individuals of tall shrubs such as *Juniperus oxycedrus* L., *Salsola genistoides* Juss. ex Poirr., *Rhamnus lycioides* L. and *Pistacia lentiscus* L.

Climate is similar in all the three areas. It is Mediterranean semi-arid, with hot summers, mild winters and a dry season longer than 3 months. Mean annual temperatures and total precipitation are shown in Table 1. Climatological data were supplied by the Instituto Nacional de Meteorología from the nearest meteorological stations of Benidorm (8 years), Jumilla (35 years) and Zarzilla de Ramos (25 years), respectively. Calcareous marls and limestones in all cases constitute the substrate of soils. History of land use has been similar in these areas; fibre harvest from

Figure 1. Localization of the study areas.

Table 1. *Climatic parameters and plot characteristics of the study localities*

	Finestrat	Minateda	Zarzilla
T (°C)	19·6	14·9	16·8
P average (mm)	293	299	301
Slope angle (deg)	32	30	40
Stipa tenacissima (% of the plot cover)	22·3	27·4	24·0
Proportion bare/terracette surface	3	2·3	3
Plant density in the plot (ind m^{-2})	3·8	5·8	6·9
Plant density in bareground (ind m^{-2})	3·1	4·7	6·4
Plant density in terracettes (ind m^{-2})	5·9	8·7	8·3

S. tenacissima, grazing of sheep and goats and hunting are the main human activities. However, the fibre harvest from the 1960s is in full decline due to its replacement by synthetic fibres.

From the summer of 1993 to the end of the summer of 1995 the south and south-east areas of Spain suffered one of the most severe drought period of the last decades (Erena & Rincón, 2000). Nevertheless, the rainfall data of this period showed an important spatio-temporal variation of the severity of the drought event among the studied areas (Fig. 2).

Sampling design and analysis

To know the degree of association of woody plants to the terracettes originated by *S. tenacissima*, we established one 30 × 30 m plot on a representative hill in each of the three localities. All the plots were located in the middle part of south-oriented slopes of similar angle. They were sampled in the spring of 1996 (Finestrat and Zarzilla de Ramos) and in the early spring of 1997 (Minateda). In each plot we determined the relative cover of *S. tenacissima*, bareground and terracettes by means of 30 linear transects 1 m apart each and placed perpendicular to the slope.

All the alive and dead individuals of woody species in the plots were counted and assigned to one-site category, terracette or bareground. As the probability to detect remnants of dead woody plants decreased with the time that death occur we assumed that dead individuals with remnants of bark, leaves or reproductive structures died recently (recent mortality), but those individuals without any remnants were considered that they died before the drought event (old mortality). No species were recognized for the old mortality category, but for the recent mortality category we only were able to recognize remnants belonging to *Anthyllis cytisoides*, *Ephedra fragilis*, *Globularia alypum*, *Rosmarinus officinalis* and *Thymus vulgaris*.

It is true that mortality can have different causes, as disease, senescence, predation or drought, and so whatever combination of all these causes may be responsible for the mortality patterns, but as drought was the most intense factor of stress immediately before the time we did the observations, we assumed it was the main cause of mortality in recently dead plants. Moreover, under the predictions of the hypotheses of facilitation, we expect higher recent mortality percentages on the bare ground than in terracettes as a consequence of the period of drought, but the opposite or no pattern during the previous period (old mortality).

Chi-squared tests with the Yates correction for continuity were carried out to test the null hypothesis that the frequency of the individuals of each species that are present on both site categories are related to the area covered by the sites. Calculations were not applied for individual species that did not fit for the minimum frequency required for the chi-squared analysis. The analysis was performed first with the data of alive and recent dead individuals pooled and then with the alive individuals alone to control if the spatial association of plants to the sites was caused by the drought event. The analysis was applied for the individuals of all the species pooled and also for the species we were able to recognize recent dead individuals.

To analyse the differences in plant mortality between site categories we compared the proportions of dead individuals of all the species pooled by means of 2 × 2 tables of contingency, under the null hypothesis that there were no differences in the proportion of dead individuals in each site category. The contingency tables were analysed by chi-squared tests with the Haber correction (Zar, 1996). This analysis was applied to both the recent and old mortality categories and also individually to the species we were able to recognize recent dead individuals.

Results

Precipitation reduction during the drought period was more pronounced in Finestrat and Zarzilla de Ramos than in the Minateda site and followed a distinct temporal pattern in each of the three localities (Fig. 2). In Finestrat and Zarzilla de Ramos, the precipitation was < 35% of the average annual precipitation in one of the 2 years and about 85% in the other year. In Zarzilla de Ramos, the higher reduction occurred the first year but in Finestrat it did the second year. In the Minateda locality the precipitation was above 60% of the average annual precipitation in both years.

The three plots presented a similar cover of *S. tenacissima*, woody plant density and proportion between the bareground and the terracette sites (Table 1). Also the three plots showed the same pattern of association of woody species to the terracettes formed by the tussocks of *S. tenacissima* (Table 2). All the species in Finestrat, 8 from 10 in Minateda and 9 from 11 species in Zarzilla de Ramos showed positive and significative association to the terracettes, and none of the species showed significant association to the bareground category. This pattern did not vary when we run the analysis with the data of plant distribution before the drought event (alive plus recent dead individuals) and after it (only alive individuals) for the entire community nor for the single species that can be analysed (Table 2).

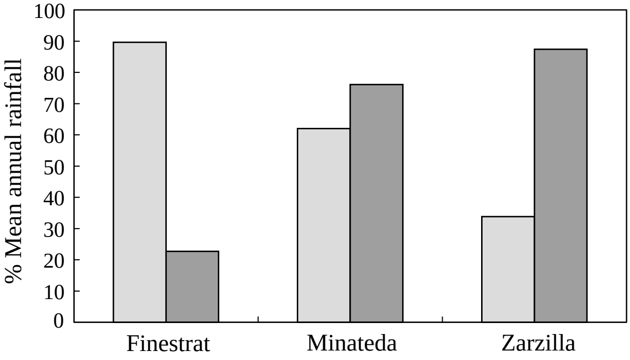


Figure 2. Percentage of precipitation with respect to the average annual precipitation in the three localities from September 1993 to August 1994 (light grey bars) and from September 1994 to August 1995 (dark grey bars).

Table 2. *Association of the alive individuals of the woody species to the site categories (terracettes and bareground) before and after the drought event in each of the three localities*

	Finestrat		Minateda		Zarzilla	
	Before	After	Before	After	Before	After
Anthyllis cytisoides	**Terracette**	**Terracette**	—	—	—	—
Convolvulus lanuginosus	—	**Terracette**	—	—	—	—
Ephedra fragilis	**Terracette**	**Terracette**	—	—	—	—
Fumana ericoides	—	**Terracette**	—	—	—	**Terracette**
Fumana laevipes	—	**Terracette**	—	**Terracette**	—	—
Fumana laevis	—	—	—	—	—	**Terracette**
Fumana thymifolia	—	—	—	**Terracette**	—	**Terracette**
Globularia alypum	**Terracette**	**Terracette**	—	—	—	—
Helianthemum cinereum	—	—	—	—	—	**Terracette**
Helianthemum pilosum	—	**Terracette**	—	**Terracette**	—	**Terracette**
Paronichia argentea	—	—	—	**Terracette**	—	—
Phagnalon saxatile	—	**Terracette**	—	**Terracette**	—	Bare
Polygala rupestris	—	—	—	—	—	**Terracette**
Rosmarinus officinalis	—	—	**Terracette**	**Terracette**	Terracette	Terracette
Satureja montana	—	—	—	Terracette	—	—
Sedum sediforme	—	**Terracette**	—	**Terracette**	—	**Terracette**
Teucrium polium	—	—	—	Terracette	—	**Terracette**
Thymus longiflorus	—	—	—	—	—	**Terracette**
Thymus vulgaris	**Terracette**	**Terracette**	**Terracette**	**Terracette**	—	—
All the woody species pooled	**Terracette**	**Terracette**	**Terracette**	**Terracette**	**Terracette**	**Terracette**

Note: The association was analysed with chi-squared tests. Bold letters indicate significance level below 0·05.

The percentages of recent plant mortality follow the same arrangement among localities than precipitation reduction, but they were one order of magnitude higher in Finestrat and Zarzilla de Ramos than in Minateda (Fig. 3). Likewise, the percentages of recent plant mortality varied highly among species in the same locality and among localities for a given species (Table 3). In Finestrat mortality varied from near 11% for *Ephedra fragilis* to 48% for *Globularia alypum*. On the other hand, *Thymus vulgaris* suffered mortality that varied from 10% in Minateda to 31% in Finestrat.

When we analysed the percentage of recent mortality of all the woody species pooled they showed higher values in the bareground site category than in the terracette one in all the three localities (Fig. 3). However, only in two from the seven species in which the recent mortality could be analysed it was significantly higher in the bareground site category and no one species showed significant higher mortality in the terracette site category (Table 3). *Ephedra fragilis* in Finestrat and *Thymus vulgaris* in Minateda showed 4 and 19 times higher mortality in the bareground than in the terracette site, respectively.

The percentage of old mortality was lower than the percentage of recent mortality in all the three localities but it showed the same significant positive association to the bareground site category (Fig. 3).

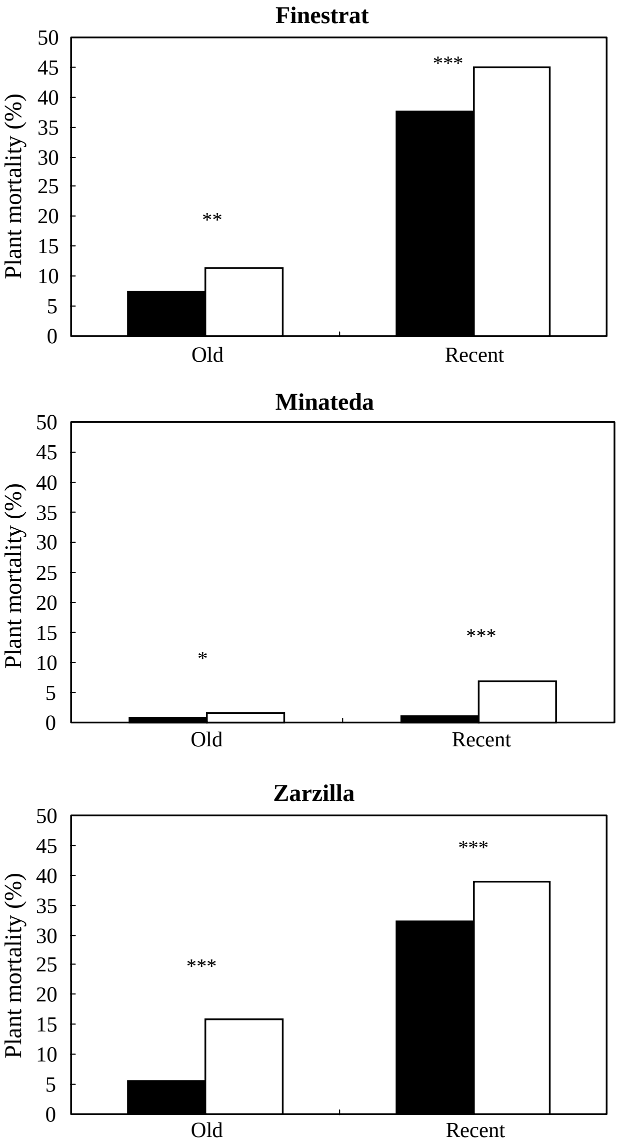
Discussion

There are a pattern of positive spatial association of the woody species to the terracettes formed by *S. tenacissima*. The geographic generalization of that pattern in all the three sites supports the hypothesis that in slopes the terracettes formed by *S. tenacissima* facilitated woody species, as proposed by Sánchez & Puigdefábregas (1994) and Puigdefábregas & Sánchez (1996). However, this pattern was not originated nor modificated by the drought event as the data on spatial pattern previous to the drought event suggest.

The effect of a severe drought event on plant performance was important although it differed among localities and species and it seems to be related to the amount of precipitation reduction in each locality and not to the plant density.

The prediction that facilitation dominates over interference during a harsh period (Bertness & Callaway, 1994; Callaway & Walker, 1997) was supported by the results obtained here on plant performance. The percentage of recent mortality of all the woody species pooled was significantly higher in bareground than in terracettes in all the three study localities and we found the same result for two species from the five species we can obtain enough data (Fig. 3 and Table 3). None of the species presented the opposite pattern. Again, this mortality seems to be related to the habitat considered (terracettes and bareground site categories) and not to the plant density. So, plant mortality in the bareground site was 1·2 times greater than that of the terracettes in Finestrat but plant density was 4·5 times lower.

Differential plant mortality in each site category should not be used to explain the positive association of woody plants to the terracette formed by *Stipa tenacissima* because plant mortality was already significatively associated with the bareground site category prior to the drought event in all the three localities (Fig. 3) and the drought event did not change the associative pattern of any of the species (Table 2). Notwithstanding, plant survival of long-lived plants is considered a very important component of plant fitness in semi-arid areas (Escós *et al.*, 2000), and then plant performance is expected to influence future composition and dynamics of plant communities in these areas. Other components of fitness, as reproduction or germination can also be affected by site categories but they also can vary with year


Finestrat

Minateda

Zarzilla

Figure 3. Differences in the percentage of old and recent plant mortality between terracettes (black bars) and bareground (white bars) of all the woody species pooled in each of the study localities. For differences between site categories (chi-squared test with the Haber correction for contingency tables), n.s. = not significant; * = $p < 0{\cdot}05$; ** = $p < 0{\cdot}01$ and *** = $p < 0{\cdot}001$.

conditions and species (Holmegren *et al.*, 1997; Tielborger & Kadmon, 2000). In this sense, we failed to find differences in the patterns of seed dispersal, germination emergence, and seedling survival between site categories during a more mesic period in Finestrat (1996/1997).

The spatial association of plant individuals and the pattern of plant mortality confirm that in semi-arid slopes the terracettes formed by *S. tenacissima* facilitate woody plants. Likewise, our results confirm that an increase of harsh conditions, such as a severe drought period, also increases the facilitative role of the terracettes by

Table 3. *Recent plant mortality (%) of woody species in the three localities and in both site categories after severe drought*

	Locality	Total	Bare	Terracettes	χ^2	p
Anthyllis cytisoides	Finestrat	19·4	13·1	25·6	3·76	0·0525
Ephedra fragilis	Finestrat	10·8	22·2	5·4	6·67	0·0098
Globularia alypum	Finestrat	48·2	52·1	43·9	0·72	0·3954
Rosmarinus officinalis	Minateda	4·4	6·5	1·5	3·76	0·0524
Rosmarinus officinalis	Zarzilla	1·9	1·3	3·6	0·61	0·4357
Thymus vulgaris	Finestrat	31·3	29·4	34·5	1·55	0·2135
Thymus vulgaris	Minateda	9·9	15·5	0·8	17·34	<0·0001

sharpening the differences in plant mortality. Notwithstanding, drought effects per se cannot explain the spatial pattern of plant distribution in these slopes and new research is needed to explore and test other forces causing this spatial association.

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