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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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Abstract:

This paper investigates the pattern of woody plant association to the two-phase mosaic in semi-arid slopes dominated by the tussock grass *Stipa tenacissima* L. and the woody plant performance after a severe drought event. The establishment and development of the plants of *S. tenacissima* organise a source-sink pattern of water and sediments from bareground areas to tussocks on mountain slopes, forming a tread or small terrace in the upslope of the tussock. We hypothesized that the treads may facilitate woody plants, and so plant association to the treads may be positive and plant performance may be higher in relation to the bareground. We studied these questions in three localities of south-east Spain after a severe drought period that occurred from 1993 to 1995.

The spatial association of plant individuals and the pattern of plant mortality supports the hypothesis that in semi-arid slopes the treads formed by *S. tenacissima* facilitate woody plants. Likewise the prediction that facilitation dominates over interference during a hars period, as a severe drought period, was also supported by the results of plant performance. Despite it, drought effects alone cannot explain the spatial pattern of plant distribution in these slopes and new research is needed to explore other forces causing spatial association.

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Nomenclature: Castroviejo *et al.* (1986-2001) but for the unpublished families we followed Tutin *et al.*, (1964-1980).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 develop 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 start with the colonization of the slopes by pioneer plants, which increase the soil water infiltration capacity in relation to that of the bareground 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 capture sediments and plant debris -including propagules- from the bare areas to the vegetated ones (White, 1971; Whitford *et al.*, 1997; Cerdà, 1997; Agnew, 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 (Gallart *et al.*, 1993; Sánchez & Puigdefábregas, 1994; Wilson & Agnew, 1997). 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; Callaway & Pugnaire, 1999; Aguiar & Sala, 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 and Tielborger & Kadmon, 2000). If so, then we hypothesised 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 analyzed 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 southwestern Europe and north Africa. When the species become dominant, it forms a mosaic of tussocks and bareground zones (Le Houérou, 1969; White, 1983). The establishment and development of the tussocks produces local variations in infiltration (Cerdà, 1997; Cammeraat & Imeson, 1999) and, in consequence, a source-sink pattern of water and sediments is organised from bareground areas to tussocks on mountain slopes (Sánchez & Puigdefábregas, 1994; Puigdefábregas & Sánchez, 1996). Deposition of sediments take place preferably upslope of the *S. tenacissima* tussocks, forming a tread 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 treads 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 treads 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) (38º33'N 0º11'W, 106 m), Minateda (Albacete) (38º28'N 1º30'W 530 m) and Zarzilla de Ramos (Murcia) (37º50'N 1º52'W, 640 m) (Figure 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 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 three 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, being fibre harvest from *S. tenacissima*, grazing by sheep and goats and hunting the main human activities. However, the fibre harvest is from the 60th in full decline due to its replacement by synthetic fibres.

From 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 (Figure 2).

Sampling design and analysis

To know the degree of association of woody plants to the treads originated by *S. tenacissima*, we established one 30 x 30m 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 treads by means of 30 linear transects one metre 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, tread 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 recognised for the old mortality category, but for the recent mortality category we only were able to recognise 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 of 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 treads as a consequence of the period of drought, but the opposite or no pattern during the previous period (old mortality).

Chi-square 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-square 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 x 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 analyzed by Chi-squared tests with the Haber correction (Zar 1996). This analysis was applied to both the recent and the 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 (Figure 2). In Finestrat and Zarzilla de Ramos the precipitation was less than 35% of the average annual precipitation in one of the two 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 the 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 tread sites (Table 1). Also the three plots showed the same pattern of association of woody species to the treads 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 treads, and none of the species showed significant association to the bareground category. This pattern did not varied 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).

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 (Figure 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 analized the percentage of recent mortality of all the woody species pooled they showed higher values in the bareground site category than in the tread one in all the three localities (Figure 3). However, only in two from the seven species in which the recent mortality could be analysed it was significant higher in the bareground site category and no one species showed significant higher mortality in the tread 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 tread 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 (Figure 3).

Discussion

There are a pattern of positive spatial association of the woody species to the treads formed by *S. tenacissima*. The geographic generalization of that pattern in all the three sites supports the hypothesis that in slopes the treads 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 hars 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 treads in all the three study localities and we found the same result in two from five species that we obtain enough data (Figure 3 and Table 3). None species presented the opposite pattern. Again, this mortality seems to be related to the habitat considered (treads 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 treads 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 tread formed by *Stipa tenacissima* because plant mortality was already significatively associated to the bareground site category prior to the drought event in all the three localities (Figure 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 more important component of plant fitness in semi-arid areas (Escós et al. 2000), and then plant performance it 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 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 treads formed by *S. tenacissima* facilitate woody plants. Likewise, our results confirm that an increase of hars conditions, as a severe drought period, also increase the facilitative role of the treads by 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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Table 1. Climatic parameters and plot characteristics of the study localities.

	FINESTRAT	MINATEDA	ZARZILLA
T (ºC)	19.6	14.9	16.8
P average (mm)	293	299	301
Slope angle (degrees)	32	30	40
Stipa tenacissima (% of the plot cover)	22.3	27.4	24.0
Proportion bare/tread 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 treads (ind.m^{-2})	5.9	8.7	8.3

Table 2. Association of the alive individuals of the woody species to the site categories (treads and bareground) before and after the drought event in each of the three localities. The association was analyzed with Chi-squared tests. Bold letters indicate significance level below 0.05.

	FINESTRAT		MINATEDA		ZARZILLA	
	Before	**After**	**Before**	**After**	**Before**	**After**
Anthyllis cytisoides	**TREAD**	**TREAD**	----------	----------	----------	----------
Convolvulus lanuginosus	----------	**TREAD**	----------	----------	----------	----------
Ephedra fragilis	**TREAD**	**TREAD**	----------	----------	----------	----------
Fumana ericoides	----------	**TREAD**	----------	----------	----------	**TREAD**
Fumana laevipes	----------	**TREAD**	----------	**TREAD**	----------	----------
Fumana laevis	----------	----------	----------	----------	----------	**TREAD**
Fumana thymifolia	----------	----------	----------	**TREAD**	----------	**TREAD**
Globularia alypum	**TREAD**	**TREAD**	----------	----------	----------	----------
Helianthemum cinereum	----------	----------	----------	----------	----------	**TREAD**
Helianthemum pilosum	----------	**TREAD**	----------	**TREAD**	----------	**TREAD**
Paronichia argentea	----------	----------	----------	**TREAD**	----------	----------
Phagnalon saxatile	----------	**TREAD**	----------	**TREAD**	----------	BARE
Polygala rupestris	----------	----------	----------	----------	----------	**TREAD**
Rosmarinus officinalis	----------	----------	**TREAD**	**TREAD**	TREAD	TREAD
Satureja montana	----------	----------	----------	TREAD	----------	----------
Sedum sediforme	----------	**TREAD**	----------	**TREAD**	----------	**TREAD**
Teucrium polium	----------	----------	----------	TREAD	----------	**TREAD**
Thymus longiflorus	----------	----------	----------	----------	----------	**TREAD**
Thymus vulgaris	**TREAD**	**TREAD**	**TREAD**	**TREAD**	----------	----------
All the woody species pooled	**TREAD**	**TREAD**	**TREAD**	**TREAD**	**TREAD**	**TREAD**

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

	LOCALITY	TOTAL	BARE	TREADS	X2	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

Figure captions

Figure 1. Localization of the study areas.

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

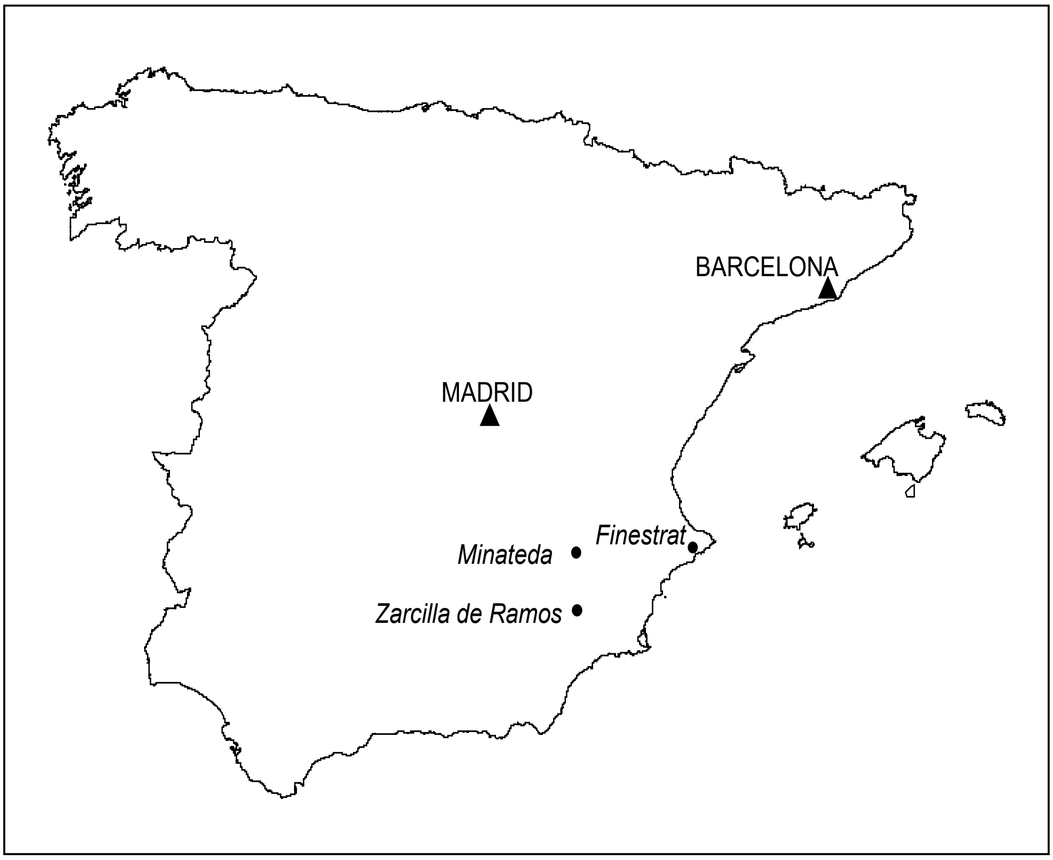

Figure 1.

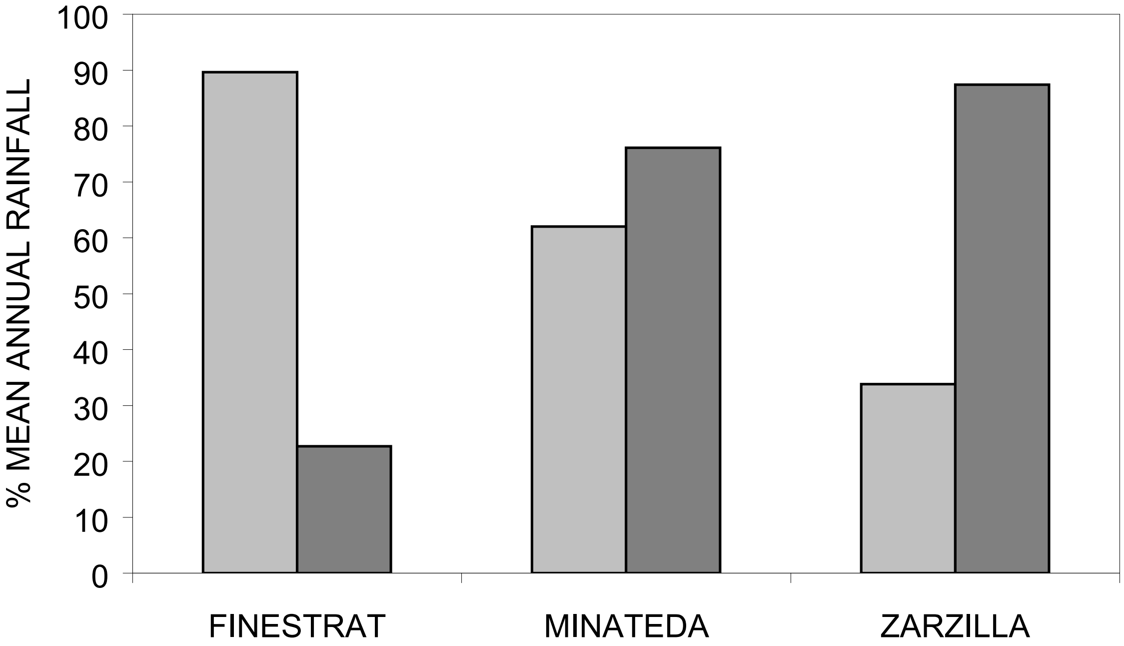
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Figure 2.

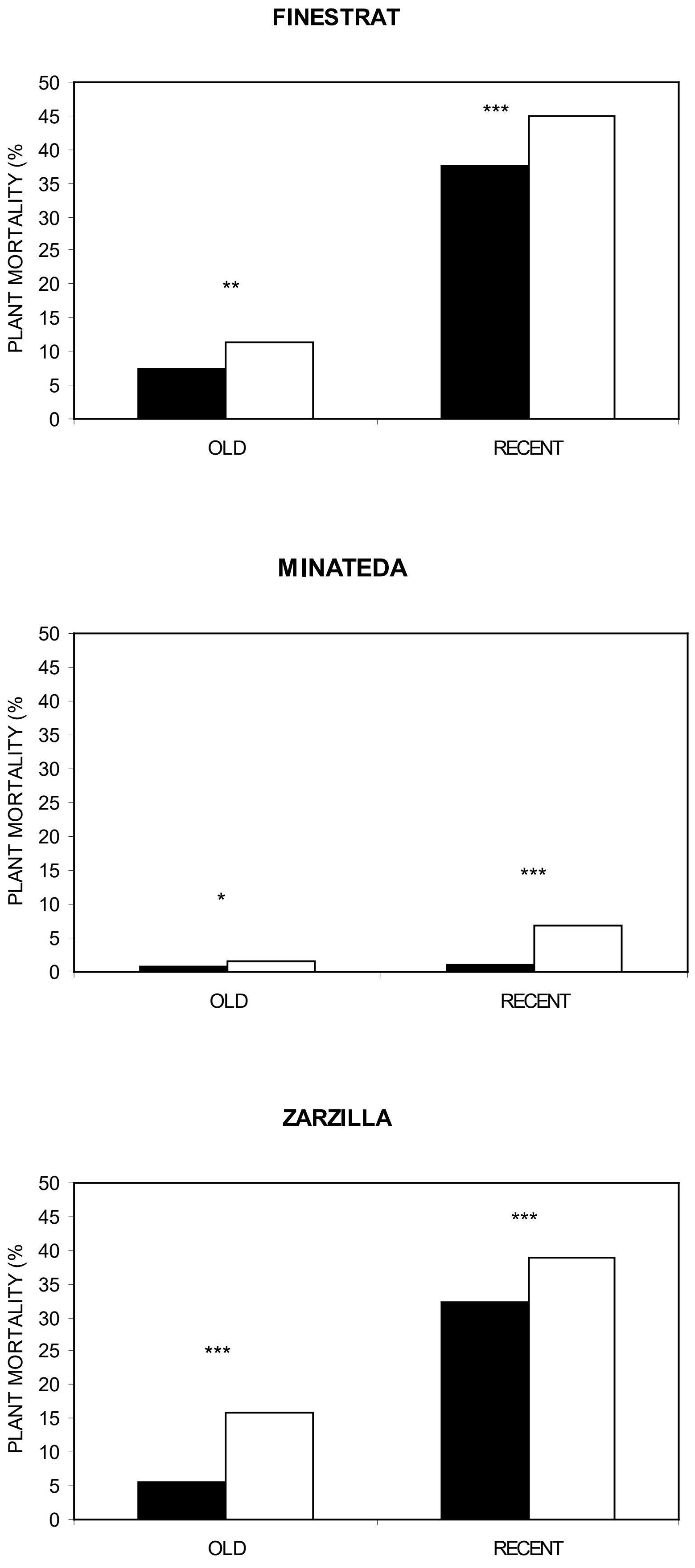
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Figure 3.