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Evidence for species specific impacts of resprouters on herbal vegetation patterns during post-fire succession in south-eastern Spain

Constanze Buhk[1] & Isabell Hensen[2]

[1] University of Trier, Department of Geobotany, Behringstr. 21, 54296 Trier, Germany

[2] University of Halle, Department of Geobotany, Am Kirchtor 1, 06108 Halle, Germany

Email: buhk@uni-trier.de

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Abstract

Plant interactions - be they positive or negative - are known to strongly influence successional pathways. On early post-fire sites in south-eastern Spain, resprouting shrubs and perennial grasses regenerate rapidly and may reach their original size after only the second year of succession. The present study aims to analyze if an influence of dominant resprouting species on herbal regeneration patterns exists. Therefore, we used a grid design of several subplots of a 4 m² plot with one of the following species located in the centre: *Calicotome intermedia* C. Presl., *Periploca angustifolia* Labill. or *Stipa tenacissima* L. Our results show that the effect of the canopy on the number of herbal plants is different between the species studied: *Calicotome intermedia* serves as a nurse plant, whereas *Periploca angustifolia* has a significantly negative impact on the establishment of non-woody plants, possibly due to allelopathic effects. The influence of *Stipa tenacissima* is dependent on the location and varies between a slightly negative influence and a significant facilitation effect; the influence was found to be positive at sites with enhanced soil nutrient levels under the *Stipa* canopies as compared to the surrounding area. We conclude that plant interactions are of great importance to the vegetation development of post-fire ecosystems under semi-arid conditions.

Keywords: facilitation, allelopathy, plant-plant interaction, safe sites

Zusammenfassung

Pflanzen-Interaktionen, ob positive oder negative, spielen bei Sukzessionsprozessen eine große Rolle. Auf Feuerflächen in Südostspanien regenerieren Büsche und Horstgräser ausgesprochen erfolgreich bereits kurz nach Brandereignissen durch vegetativen Wiederaustrieb und erreichen so bereits im zweiten Jahr annähernd ihre ursprüngliche Größe. Die vorliegende Untersuchung hat zum Ziel den Einfluss dieser dominanten, austreibenden Pflanzen auf die Regenerationsmuster der übrigen krautigen

Vegetation zu analysieren. Wir nutzen ein Rasterdesign von mehreren Teilflächen innerhalb größerer 4 m² Flächen in deren Mitte jeweils eine der folgenden Arten wächst: *Calicotome intermedia* C. Presl., *Periploca angustifolia* Labill. oder *Stipa tenacissima* L. Unsere Ergebnisse zeigen unter der Beschirmung durch die getesteten austreibenden Arten unterschiedliche Beeinflussung der krautigen Vegetation: *Calicotome intermedia* wirkt fördernd auf die Besiedlung, *Periploca angustifolia* hat einen negativen Einfluss auf krautige Pflanzen, möglicherweise durch allelopathische Effekte. *Stipa tenacissima* wirkt unterschiedlich je nach Standort und variiert zwischen einem leicht negativen Effekt und einem signifikant positiven Effekt. Dieser wurde besonders an Stellen festgestellt, an denen im Vergleich zur Umgebung erhöhte Nährstoffkonzentrationen im Boden unter der Pflanze gemessen wurden. Wir schließen aus der Studie, dass Pflanzen-Interaktionen artspezifisch sind und auf Feuerflächen semiarider Landschaften für die Vegetationsentwicklung von großer Bedeutung sind und bei Analysen der Regeneration dringend beachtet werden müssen.

Schlüsselbegriffe: Positive Interaktionen, Allelopathie, Pflanze-Pflanze Interaktion, geschützte Bereiche zur Etablierung

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Introduction

Initial plant-plant interactions are known to strongly influence successional development (Sans et al. 2002, Bruno et al. 2003). Potential positive interactions include facilitation due to nutrient enrichment (Haase et al. 1997) or water retention under shrubs (Verdú et al. 2004), differential seed accumulation (Bullock & Moy 2004), stress reduction by the canopy like shading, the promotion of a favourable microflora (Maestre et al. 2002) or pollinator visits (Ryser 1993), transfer of resources (Pugnaire & Haase 1996), fixation of carbon via mycorrhizae and the protection against grazing (Callaway 1995, Facelli & Temby 2002, Tirado & Pugnaire 2003). Negative impacts comprise allelopathic effects and competition for water, nutrients or light (Flores & Jurado 2003). Especially in highly disturbed communities, facilitation has been found to be more abundant than competition (Bertness & Leonard 1997, Brooker & Callaghan 1998).

On post-fire sites, some important factors influencing plant interactions are altered. In particular, the distribution of nutrients is different in comparison to undisturbed stands where organic debris accumulates over years below long-lived plant species (Pugnaire & Haase 1996). After fire, the former plant coverage, including the organic layer, is mineralized, and charred material and ash are easily washed out and transported. In south-eastern Spain, lowest soil nutrient levels were found about 3 years after a fire, especially on south-facing slopes, due to water runoff and leaching (Herranz et al. 1991, de las Heras et al. 1993). These findings indicate a specific situation which influences plant interactions during regeneration in post-fire areas.

In the coastal area of the province of Murcia, the tussock grass *Stipa tenacissima* L., the thorny Fabaceae *Calicotome intermedia* C. Presl. and the Asclepiadaceae *Periploca angustifolia*

Labill. are among the most successful resprouters (Götzenberger et al. 2003). Our study aims to analyze the impact of these species on the regeneration success of non-woody vegetation regenerating mainly from seed after fire. We assessed the following questions:

Does the growth pattern of mainly seed-dependent herbs during early post-fire succession in south-eastern Spain give evidence for positive or negative impacts of resprouters? Do abundant resprouting shrubs or tussock grasses serve as safe sites for the herbal vegetation? Is the impact species specific?

Finally, the factors slope inclination, aspect, location and trends of the distribution of nutrients are compared to the patterns of herbal plants found under *Stipa tenacissima*.

Methods

The study sites are situated in south-eastern Spain in the province of Murcia (Fig. 1).

Three plant species that were dominant during early post-fire regeneration were selected to document their impact on the abundance of herbal vegetation: the tussock grass *Stipa tenacissima* (Poaceae) and the shrubs *Calicotome intermedia* (Fabaceae) and *Periploca angustifolia* (Asclepiadaceae). These species resprout effectively after fire and plants regenerate almost to pre-fire size after the second year (Buhk et al. 2005). *Calicotome intermedia* and *Periploca angustifolia* were studied in two burnt areas located close to the coast (Alumbres: 2 years post-fire, Portman: 5 years post-fire). The climate in this region is thermo-Mediterranean with 200-300 mm of annual precipitation and a dry period

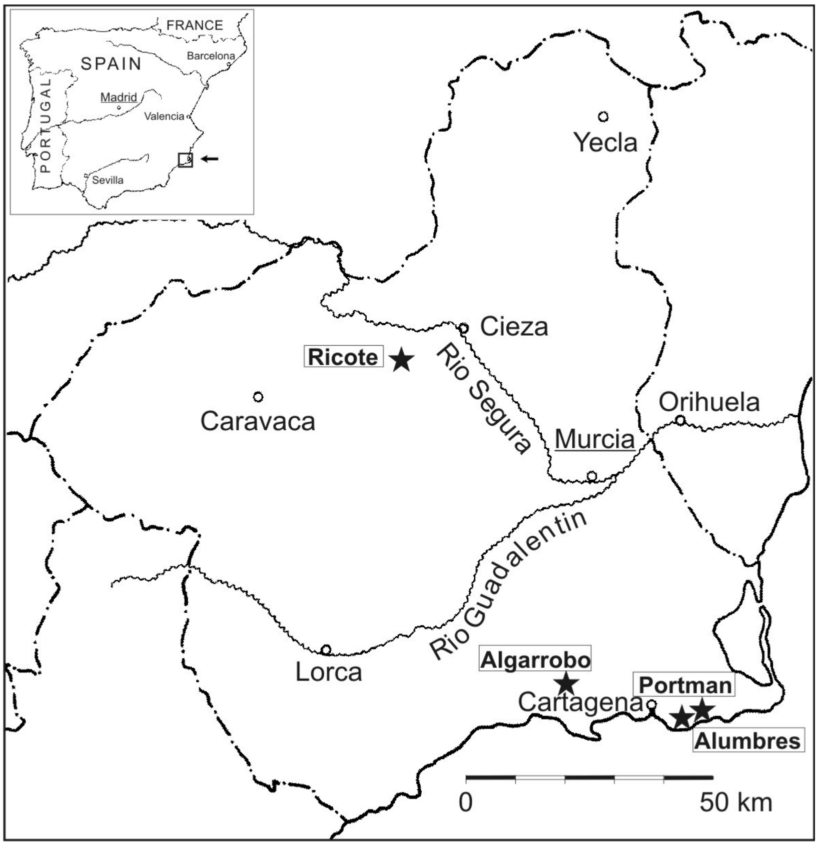

Fig. 1: *Location of the four research areas in south-eastern Spain (Province of Murcia)*

of 7-11 months. The vegetation is dominated by shrubs of the Periplocion angustifoliae Rivas Martínez 1975. As *Stipa tenacissima* is more widespread in the area than the other two species, two supplementary fire sites were included in the analysis: Algarrobo (2 years post-fire), another thermo-Mediterranean location, and Ricote (3 years post-fire) which is located in the meso-Mediterranean mountainous region (700m a.s.l., 400 mm annual precipitation, dry period 6-8 months), where open *Pinus halepensis* woodland with *Quercus coccifera* and *Stipa tenacissima* prevail (Carrión Vilches et al. 2003).

The bedrock of the research areas consists primarily of limestone and dolomite of Triassic origin at the coast and Jurassic origin in the Ricote Mountains (Fontbote 1983, 1983).
Sample plants were selected randomly, excluding individuals < 50 cm in diameter or sites with a rock coverage > 50% below the target species. The sample design is illustrated in Fig. 2.

The number of all individual herbal plants (therophytes, hemicryptophytes and geophytes) was recorded in 36-64 subplots (25cm x 25cm; number depending on plant size and rock cover) in the space around and under the selected individuals (*Stipa tenacissima*, N=19; *Calicotome intermedia*, N=6; *Periploca angustifolia*, N=5; hereafter referred to as "under the canopy" and "outside the canopy"). The percentage cover of the sample shrub or grass and the percentage of rocks in each subplot were recorded. The influence of the surrounding vegetation and the presence of rocks was minimized by excluding from the analysis: a) subplots with a rock coverage > 50%; b) subplots influenced by other woody plants or non-target *Stipa tenacissima* tussocks; and c) subplots with shrubs or *Stipa* coverage > 80%.

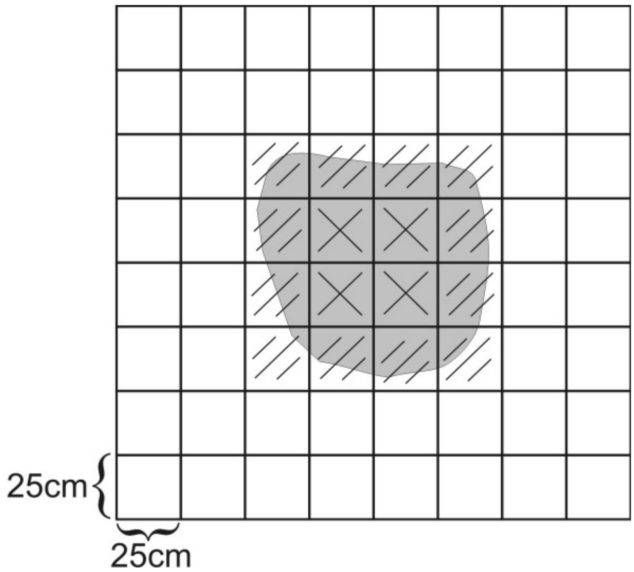

Fig. 2: *Sample design*

(Subplots of 25x25cm were set up around the randomly selected sample plants [shaded area]. White areas: subplots outside the canopy of the target plant; ///: subplots below 10-80% canopy of the target plant; X: subplots excluded from the analyses)

For all sites of *Stipa tenacissima*, slope inclination and aspect were noted and soil analyses were carried out. Mixed soil samples at the site scale of 10 sub-samples each were taken upslope and downslope the centre of the *Stipa* individuals as well as in gaps between the plants. The following nutrients were analyzed: Total C and N (Dumas method; CN Analyser Vario EL, ELEMENTAR, Germany); Ca^{2+} and Mg^{2+} (atomic absorption spectrometry, Flame-AAS Vario 6, Analytik Jena, Germany); K^+ and Na^+ (flame spectrometry; Flame-AAS Vario 6); pH value (20g soil in 50ml H_2O; SenTix 21, WTW, Germany); and conductivity (Cond 315 i, WTW, Germany). All data refer to dry (105°C) fine soil (particle size < 2mm).

Statistical analysis

Numbers of non-woody plants were pooled (average of the subplots) for each replicate. Two groups (a and b) were distinguished and analyzed as paired samples (paired t-test; $p<0.05$): a) subplots located in gaps without the influence of a shrub or tussock; b) subplots located under 10-80% canopy cover of a shrub or tussock.

The data was log-transformed to assure normality. General linear models were analyzed at a site scale including location (the 4 study sites); and at a plant scale including slope inclination (3 classes: 0-10°, 15-20°, 25-30°) and aspect (N/S). For multivariate models at the within-plant scale the response variables "number of non-woody plants" a) below *Stipa* and b) in between *Stipa*-plants were included; for univariate analysis the response variable "diff" was used: number of herbal plants below *Stipa* minus the number of herbal plants in gaps quantifying the strength of facilitation (positive values) or competition (negative values). Statistical analyses were carried out using SPSS 12 (SPSS inc. 1998-2003).

Results

The effects of the species studied on herbal plant growth are different: *Calicotome intermedia* seems to facilitate non-woody plants whereas significant lower numbers of herbs were found under rather than outside the canopy of *Periploca angustifolia* (Fig. 3). We did not confirm any significant effect of *Stipa tenacissima* on herbal plant numbers if all sites and aspects are included in the analysis. However, patterns were different in different locations (Fig. 4), varying from a slightly negative impact on other herbal

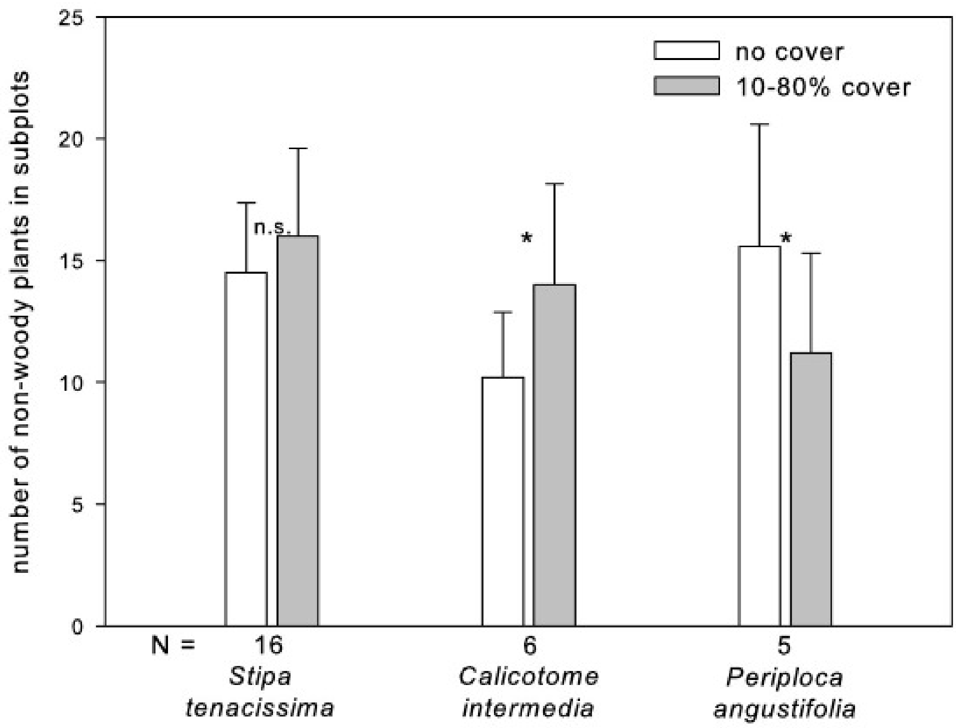

Fig. 3: *Comparison of the mean number of non-woody plants in the subplots outside the canopy and below 10-80% coverage of the sample plants (paired t-Test, p< 0.05)*

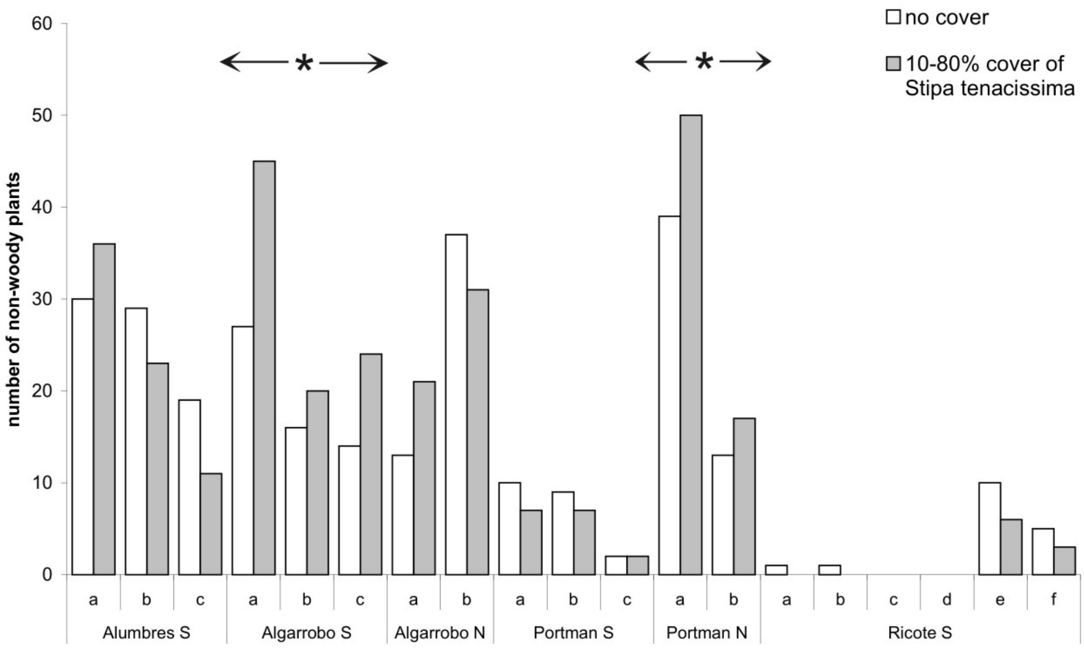

Fig. 4: *Detailed comparison of the number of non-woody plants in the subplots outside the canopy and below 10-80% canopy coverage of Stipa tenacissima.*

(Plots = plants are sorted according to the different locations and aspects. The two sites with significant higher abundance of herbs below *Stipa* than in gaps are marked [paired t-test on the log-transformed data, p<0.01]).

plants to a possible facilitation effect on the sites of Algarrobo (south-exposed) and Portman (north-exposed). The mountainous site of Ricote is characterized by very low numbers of non-woody plants, even three years after fire.

As regards *Stipa tenacissima*, none of the general linear models brought significant results, which shows that neither slope inclination, aspect, location nor combinations of the factors contribute in a linear way to the explanation of the facilitation pattern observed (best fitted model, F 2.15; p=0.16). Nutrient levels upslope and downslope of the tussock did not follow regular trends (Tab. 1).

However, a trend towards higher nutrient levels below compared to the area outside the tussock canopy was found for three of the sites studied (shaded values in Tab. 1). Two of these locations are identical with those where a facilitation effect of *Stipa* was observed (south-facing Algarrobo and north-facing Portman; Fig. 4).

Discussion

Plant interactions are of great importance to post-fire regeneration, as shown exemplarily for *Calicotome intermedia*, *Periploca angustifolia* and *Stipa tenacissima*, which are dominant resprouting species after fire in south-eastern Spain. The impact of the target species on the herbal layer ranges from negative effects (*Periploca angustifolia*) to facilitation (*Calicotome intermedia*). However, it is difficult to distinguish the various factors that contribute to the overall pattern of plant interaction without employing more detailed analyses e.g. on the herbal

***Tab. 1:** Summary of the nutrient analysis*
(Ca^{2+}[mg/kg], Mg^{2+}[mg/kg], K^{+}[mg/kg], Na^{+}[mg/kg], conductivity [µs/cm], total N[%] and C[%]) at the different locations and aspects at three sample positions: mixed samples were taken from a) upslope and b) downslope the centre of the *Stipa* tussock, but still within the influence sphere of the canopy, as well as c) outside the influence sphere of the *Stipa tenacissima* canopy. Results indicating a trend towards increased nutrient contents below *Stipa* in comparison to the conditions in gaps are shaded in grey.

location and aspect	sample position	Ca mg/kg	Mg mg/kg	Na mg/kg	K mg/kg	LF [µs/cm]	N%	C%	C/N	pH (H²O)
Alumbres S	upslope	1638	236	80.7	216	488	0.59	8.15	13.8	7.43
	downslope	1690	392	15.6	310	223	0.56	7.62	13.6	7.15
	outside the canopy	1706	273	120	212	813	0.61	8.02	13.1	7.67
Algarrobo S	upslope	1962	298	38.2	320	301	0.47	7.33	15.6	7.87
	downslope	1800	285	40.6	261	284	0.47	6.93	14.7	7.91
	outside the canopy	1928	153	42.5	177	159	0.36	4.17	11.6	7.89
Algarrobo N	upslope	2040	282	69.5	319	309	0.46	8.12	17.7	7.91
	downslope	1838	264	37	378	284	0.54	7.28	13.5	7.83
	outside the canopy	1990	4364	72.1	292	368	0.62	8.98	14.5	7.94
Portman S	upslope	2120	4948	72.2	414	205	0.56	5.77	10.3	7.71
	downslope	2060	5216	109	462	287	0.59	5.8	9.83	7.72
	outside the canopy	1368	411	121	468	314	0.42	6.6	15.7	7.4
Portman N	upslope	2160	4352	104	489	591	0.68	6.76	9.94	7.56
	downslope	2160	4552	150	456	477	0.52	5.35	10.3	7.64
	outside the canopy	1772	419	73	414	405	0.41	5.3	12.9	7.2
Ricote S	upslope	2320	156	43.4	262	231	0.62	10.6	17.1	7.77
	downslope	2480	166	75.4	372	404	0.62	10.2	16.4	7.74
	outside the canopy	2240	131	33.6	378	209	0.52	8.84	17	7.82

species level (Goldberg et al. 2001).

The variable response of herbs to the coverage of the different resprouting species might be explained by species-specific characteristics promoting or hampering regeneration (Callaway 1995, Callaway 1998). As grazing pressure by sheep or goats is not important in the whole study area, we rule out a possible protection by the thorny shrub *Calicotome intermedia* in contrast to the unarmed *Periploca angustifolia* or *Stipa tenacissima* (Rebollo et al. 2002). The nurse plant syndrome (Callaway 1995) of the Fabaceae *Calicotome intermedia* is supposed to be an effect of nitrogen fixation by microorganisms (Rodríges Echeverría & Pérez Fernández 2003). Asclepiadaceae like *Periploca angustifolia* have been described previously to exert an allelopathic effect (sensu Inderjit & Duke 2003) on surrounding plants (Hegazi & Alsubaey 1994). However, such differences in plant-plant interactions at a species level are not self-evident, as Turner et al. (1966) found equal proportions of seedlings under 15 potential nurse species, which indicates that no species-specific biotic factor is involved. He concluded that nurse plant associations might be only a by-product of microclimatic changes under canopies.

The impact of *Stipa tenacissima* on herbal regeneration was highly variable probably due to a complex co-occurrence of competition and facilitation (Callaway & Walker 1997, Wilson & Nisbet 1997). Poaceae in arid to semi-arid environments have hardly ever been described to be safe-site builders (Flores & Jurado 2003). However, in two of the selected sample areas, a significantly higher number of herbal plants was found below rather than outside the canopy influence sphere. The soil analysis indicates a possible relationship between nutrient enrichment below *Stipa* and the abundance of herbal plants. This is noteworthy, as on a larger scale differences in soil characteristics between slopes in the area were found to be of little importance in explanation of the vegetation patterns (Buhk et al. 2006, Götzenberger et al. 2003). Instead, much of the variability in post-fire species composition and regeneration speed was explained by climatic differences between the coastal and mountainous areas, and by microclimatic variation of southern and northern exposures (Buhk et al. 2006). Virtually all types of ecological interactions have been shown to vary with changes in the abiotic environment (Schenk et al. 2003, Maestre & Cortina 2004), and facilitative effects are supposed to become stronger as abiotic stress increases (Bertness & Callaway 1994, Callaway 1997, Pugnaire & Luque 2001) though this issue is discussed controversially (Goldberg et al. 1999). Although an accumulation of nutrients and seeds underneath the plants by wind and erosion is likely to occur in semi-arid environments (Garner & Steinberger 1989, Pugnaire & Haase 1996, Jones et al. 1997), the period of time since the fire has possibly not been long enough to create such patterns: It is remarkable that patterns of nutrient accumulation under the canopy of *Stipa tenacissima* are highly variable in the study area, regardless of the similar overall nutrient availability on the different sites and aspects. Regeneration age, possibly combined with slope inclination and prevailing wind direction, might therefore be an important factor. In addition, as nutrient enrichment under the canopy of *Stipa* tussocks does not necessarily relate to facilitation, we assume that other factors might be more important to the pattern observed. The most probable one is limitation of water, as water is the prominent limiting factor in semi-arid environments (Pugnaire & Luque 2001). Effects of soil water and fertility probably contribute to facilitation simultaneously as the build-up of organic matter changes physical soil properties and improves soil water retention (Pugnaire et al. 2004). Holmgren et al. (1997) presented a light-water model showing that facilitation only occurs when the improvements of plant water relations under the canopy exceeds the costs caused by lower light levels. Further analyses of soil organic matter, nutrient distribution and water availability as well as manipulating experiments across gradients of physical stress and disturbance (Bertness 1998) have to be carried out to understand the function of facilitation between resprouters and herbal plants at early post-fire sites in south-eastern Spain in more detail (compare to Brooker et al. 2008).

References

Bertness, M.D., 1998: Searching for the role of positive interactions in plant communities. Trends in Ecology and Evolution 13, 133-134.

Bertness, M.D., Callaway, R., 1994: Positive interactions in communities. Trends in Ecology and Evolution 9, 187-191.

Bertness, M.D., Leonard, G.H., 1997: The role of positive interactions in communities: Lessons from intertidal habitats. Ecology 78, 1976-1989.

Brooker, R.W., Callaghan, F.V., 1998: The balance between positive and negative interaction and its relationship to environmental gradients: a model. Oikos 81, 196-207.

Brooker, R.W., Maestre, F.T., Callaway, R.M., et al., 2008: Facilitation in plant communities: the past, the present and the future. Journal of Ecology 96, 18-34.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003: Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18, 119-125.

Buhk, C., Sánchez Gómez, P., Hensen, I., 2005: Plant regeneration mechanisms during early post-fire succession in south-eastern Spain. Feddes Repertorium 116, 392-404.

Buhk, C., Götzenberger, L., Wesche, K., Sánchez Gómez, P., Hensen, I., 2006: Post-fire regeneration in a Mediterranean pine forest with historically low fire frequency. Acta Oecologica 30, 288-298.

Bullock, J.M., Moy, I.L., 2004: Plants as seed traps: inter-specific interference with dispersal. Acta Oecologica 25, 35-41.

Callaway, R.M., 1995: Positive interactions among plants. Botanical Review 61, 306-349.

Callaway, R.M., 1997: Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112, 143-149.

Callaway, R.M., 1998: Are positive interactions species-specific? Oikos 82, 202-207.

Callaway, R.M. & Walker, L.R., 1997: Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78 (7): 1958-1965.

Carrión Vilches, M.A., Coy Cómez, E., S., F.J., Guerra Montes, J., Hernández Gonzáles, A., Jiménez Martínez, J.F., López Espinosa, J.A., Sánchez Gómez, P., Vera Pérez, J.B., 2003: Nueva Flora de Murcia. Diego Marin, Murcia.

de las Heras, J., Martínez Sanchez, J.J., Herranz, J.M., del Pozo, E., 1993: Erosion tras incendio en el SE de España: Proteccion de los suelos por la cubierta vegetal colonizadora durante las primeras etapas de la sucesion. Ecología 7, 3-10.

Facelli, J.M., Temby, A.M., 2002: Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral Ecology 27, 422-432.

Flores, J. & Jurado, E., 2003: Are nurse-protege interactions more common among plants from arid environments? Journal of Vegetation Science 14, 911-916.

Fontbote, J.M., 1983[a]: Mapa Geologico E. 1:200000. Elche. 72. Instituto Geologico y Minero de España, Madrid.

Fontbote, J.M., 1983[b]: Mapa Geologico E. 1:200000. Murcia. 79. Instituto Geologico y Minero de España, Madrid.

Garner, W., Steinberger, Y., 1989: A proposed mechanism for the formation of "fertile islands" in the desert ecosystem. Journal of Arid Environments 16, 257-262.

Goldberg, D.E., Rajaniemi, T.D., Gurevich, J., Stewart-Oaten, A., 1999: Empirical approaches to quantifying interaction intensity: Competition and facilitation along productivity gradients. Ecology 80, 1118-1131.

Goldberg, D.E., Turkington, R., Olsvig-Whittaker, Dyer, A.R., 2001: Density dependency in an annual plant community: variations among life history stages. Ecological Monographs 71, 423-446.

Götzenberger, L., Ohl, C., Hensen, I., Sánchez Gómez, P., Wesche, K., 2003: Postfire regeneration of a thermomediterranean shrubland area in south-eastern Spain. Anales de Biología 25, 21-28.

Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1997: Spatial pattern in *Anthyllis cytisoides* shrubland on abandoned land in southeastern Spain. Journal of Vegetation Science 8, 627-634.

Hegazi, A.K., Alsubaey, A.A.A., 1994: Allelopathic effect of *Glossonema edule* (Asclepiadaceae) on associated flowering plants and rhizospere fungi in Qatar. Qatar University Science Journal 14, 165-168.

Herranz, J.M., de las Heras Ibáñez, J., Martínez Sánchez, J.J., 1991: Efecto de la orientation sobre la recuperacion de la vegetacion natural tras el fuego en el valle del rio Tus (Yeste, Albacete). Ecología 5, 111-123.

Holmgren, M., Scheffer, M., Huston, M.A., 1997: The interplay of facilitation and competition in plant communities. Ecology 78, 1966-1975.

Inderjit, Duke, S.O., 2003: Ecophysiological aspects of allelopathy. Planta 217, 529-539.

Jones, C.G., Lawton, J.H., Shachak, M., 1997: Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946-1957.

Maestre, F.T., Cortina, J., 2004: Do positive interactions increase with abiotic stres? A test from a semi-arid steppe. Proceedings of the Royal Society 271, 331-333.

Maestre, F.T., Huesca, M., Zaady, E., Bautista, S., Cortina, J., 2002: Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. Soil Biology and Biochemistry 34, 895-898.

Pugnaire, F.I., Armas, C., Valladares, F., 2004: Soil as a mediator in plant-plant interactions in a semi-arid community. Journal of Vegetation Science 15, 85-92.

Pugnaire, F.I., Haase, P., 1996: Facilitation between higher plant species in a semiarid environment. Ecology 77, 1420-1426.

Pugnaire, F.I., Luque, M.T., 2001: Changes in plant interactions along a gradient of environmental stress. Oikos 93, 42-49.

Rebollo, S., Milchunas, D.G., Noy-Meir, I., Chapman, P.L., 2002: The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos 98, 53-64.

Rodríges Echeverría, S., Pérez Fernández, M.A., 2003: Soil fertility and herb facilitation mediated by *Retama sphaerocarpa*. Journal of Vegetation Science 14, 807-814.

Ryser, P., 1993: Influences of neighbouring plants on seedling establishment in limestone grassland. Journal of Vegetation Science 4, 195-202.

Sans, F.X., Escarre, J., Lepart, J., Hopkins, F., 2002: Positive vs. negative interactions in Picris hieracioides L., a mid-successional species of Mediterranean secondary succession. Plant Ecology 162, 109-122.

Schenk, H.J., Holzapfel, C., Hamilton, J.G., Mahall, B.E., 2003: Spatial ecology of a small desert shrub on adjacent geological substrates. Journal of Ecology 91, 383-395.

Tirado, R., Pugnaire, F.I., 2003: Shrub spatial aggregation and consequences for reproductive success. Oecologia 136, 296-301.

Turner, R.M., Alcorn, S.M., Olin, G., Booth, J.A., 1966: The influence of shade, soil, and water on saguaro seedling establishment. Botanical Gazette 127, 95-102.

Verdu, M., Villar, S.P., Garcia, F.P., 2004: Gender effects on the post-facilitation performance of two dioecious *Juniperus* species. Functional Ecology 18, 87-93.

Wilson, W.G., Nisbet, R.M., 1997: Cooperation and competition along smooth environmental gradients. Ecology 78, 2004-2017.