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Stipa tenacissima as a nurse plant of the endemic species *Haplophyllum bastetanum* near Granada, SE Spain

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Question: What is the role of *Stipa tenacissima* as a nurse plant of the rare and threatened endemic species *Haplophyllum bastetanum*?
Location: Semi-arid steppe of the Guadix-Baza basin (SE Spain).
Methods: In the two *H. bastetanum* populations known, we (1) estimated the number of individuals and (2) analysed the influence of the factors 'site' (S1 = Hernán Valle, S2 = Alicún), 'microhabitat' (inside and below the canopy of the *S. tenacissima* tussocks vs. open areas), 'life stage' (vegetative, reproductive), 'aspect' (N, S, E, W, flat) and 'damage' (yes or no), in relation to the distribution of individuals and to the height, number of flowers, number of capsules, and edaphic variables.
Results: The total number of individuals was estimated at 3135. *S. tenacissima* was found to have a positive and significant effect on the distribution of *H. bastetanum*, more pronounced in the sample taken at S2 than S1, where 83.8% of the plants were growing in association with *S. tenacissima*. Similarly, there were more *H. bastetanum* individuals that became reproductive inside *S. tenacissima* tussocks than in the open areas, and *H. bastetanum* individuals had a greater production of flowers and fruits, especially in the sample taken at S1. Organic carbon, nitrogen, and carbon:nitrogen ratio were related to the height and number of flowers and capsules of the plants.
Conclusion: Although new patches were established, with a larger number of individuals, *H. bastetanum* continues to be Critically Endangered (CR). The results support the hypothesis of the facilitation effect of *S. tenacissima* on this rare, endemic species. Facilitation of species of interest in conservation is an aspect that has not previously been clearly reported. We propound this important process as a valuable tool for rehabilitation of populations of threatened plant species in conservation biology projects.

Keywords: Critically endangered species; Facilitation; Plant-soil relationship; Red List; *Rutaceae*; Semi-arid steppe.

Nomenclature: Castroviejo (1986-2003); Valdés et al. (1987).

Introduction

Plant interactions are key processes that strongly influence the composition and structure of plant communities (Callaway 1995; Armas & Pugnaire 2005). In arid and semi-arid environments, positive interactions or facilitation between plants are widespread (Franco-Piñaza et al. 1996; Pugnaire et al. 1996a; Moro et al. 1997a; Flores & Jurado 2003). Nurse plants may improve the microclimate beneath their canopies and protect other plants/seedlings against direct irradiance and overheating (Franco-Piñaza et al. 1996; López-Pintor et al. 2000). The canopy can also enhance water availability and accumulate plant nutrients in the understorey (Vetaas 1992; Chambers 2001) and may also protect against herbivores (grazing and trampling) (Rebollo et al. 2002; Flores & Jurado 2003). Differences in floristic composition between microhabitats under shrubs and trees vs. intercanopy areas have been reported by Pugnaire et al. (1996 b), Moro et al. (1997 a), and Rossi & Villagra (2003).

The relationship between stress and plant interactions has been conceptually formalized in the 'stress-gradient hypothesis', which states that net competitive effects are more important, or at least more intense (Brooker et al. 2005), in relatively benign, low-stress environments, whereas facilitative effects are more important in relatively harsh, high-stress environments (Bertness & Callaway 1994). However, according to Maestre et al. (2005, 2006), despite an enormous body of empirical evidence, spatial and temporal variation of facilitative and competitive interactions in the field, and the way the balance between them is related to species traits and environmental conditions remains unclear.

The role of S. tenacissima tussocks

In the Mediterranean Basin, steppes cover > 400 000 km^2 (Le Houérou 1986), dominated mostly by *Stipa tenacissima* L. (*Poaceae*) (Puigdefábregas & Mendizábal 1998), a long-lived perennial grass (ca. 40-70 cm height). *S. tenacissima* forms large tussocks (ca. 0.5 m^2), has a dense matrix of thin roots concentrated in the first 20 cm of the soil, and has long, narrow leaves (up to 100 cm long and 2-3 mm wide) which can fold along their long axes and curl up during periods of water deficit to avoid evapotranspiration (Armas & Pugnaire 2005). Estimates in the steppes of SE Spain have revealed that the average cover of *S. tenacissima* ranges between 10 and 40 % and the average aboveground phytomass reaches 7 t.ha^{-1} of dry matter (see Gauquelin et al. 1996, 1998), partly by dead leaves remaining in the central or internal part of the tussocks.

Prior studies on *S. tenacissima* communities confirm that *S. tenacissima* tussocks constitute 'islands', where soil fertility and soil water can be sources of facilitation (e.g. Martínez-Sánchez et al. 1994; Sánchez 1995; Cerdà 1997; Bochet et al. 1999; Maestre et al. 2002 a; Maestre & Cortina 2002; García-Fayos & Gasque 2002; Gasque & García-Fayos 2004; Armas & Pugnaire 2005). In addition, amelioration of microclimatic conditions under *S. tenacissima* plants compared with open spaces can lead to facilitative effects on other plants (Maestre et al. 2001, 2003). Such positive interactions have been proposed as a tool to improve restoration success in degraded arid and semi-arid ecosystems (Maestre et al. 2001, 2002b; Gasque & García-Fayos 2004) as well as in Mediterranean mountains (Castro et al. 2002; Gómez-Aparicio et al. 2004). However, *S. tenacissima* also may compete for water with other species (Maestre et al. 2003; Armas & Pugnaire 2005), or soil fertility beneath *S. tenacissima* tussocks may have a weak positive effect on understorey plants (Maestre et al. 2003). Thus, research is needed to determine the balance of competition and facilitation in *S. tenacissima* interactions with other species.

Facilitation and conservation biology

Facilitation among plants has been an item in conservation because of its role in structuring plant communities and promoting biodiversity (Hacker & Gaines 1997; Tewksbury & Lloyd 2001). A few studies have considered facilitation in the conservation biology of endemic and threatened species. García et al. (2000) and García & Obeso (2003) examined positive interactions of holly (*Ilex aquifolium*) and other fleshy-fruited shrubs on a threatened yew (*Taxus baccata*). They suggested the use of ungulate exclosures, cattle rotation, or selective hunting in populations lacking nurse plants to improve yew regeneration. Suzán et al. (1994) detected a strong association between the Sonoran night-blooming cereus cactus (*Peniocereus striatus*) and its nurse plants. Nurse plants harvesting for charcoal and scarcity of sphingid moths (which pollinate the cactus), have increased the natural rarity of this specie. Tewksbury et al. (1999) found over 75 % of wild chilli plants (*Capsicum annuum* var. *aviculare*) under the canopies of fleshy-fruited shrubs that collectively made up less than 25% of the cover. The distribution of chillies appeared to be a function of interactions between consumers, nurse plants, and secondary chemicals in the chillies themselves.

In all examples of facilitation of threatened species involved, the scarcity of nurse plants was the decisive factor of the rarity of the target species.

Aims

Our *a priori* hypothesis is that *S. tenacissima* is a nurse plant of the rare, endemic, and threatened *Haplophyllum bastetanum* F.B. Navarro, V.N. Suárez-Santiago & Blanca (*Rutaceae*). *H. bastetanum*, was recently discovered (Navarro et al. 2004) in the Guadix-Baza Basin (SE Spain). This plant forms part of the low woody shrublands and *S. tenacissima* grasslands, where this species is often found inside adult tussocks. Navarro et al. (2004) reported that only two *H. bastetanum* populations are known, with a total of roughly 100 scattered reproductive individuals. The degree of threat, according to IUCN categories (Anon. 2001a) was Critically Endangered (CR). Recently, new individuals have been discovered in one of the populations, and thus the conservation status of this species should be updated.

Our aim is to determine the current conservation status of *H. bastetanum*, to evaluate the role of *S. tenacissima* as a nurse plant of the rare, endangered, and endemic species *H. bastetanum*, and to analyse the causes for facilitation of *S. tenacissima* on this species.

Material and Methods

Characteristics of Haplophyllum bastetanum

H. bastetanum is a perennial herbaceous plant (10-50 cm), with dark-green actinomorphic flowers (1-15). The flowering period spans May to June, and presents hermaphroditic and pentamerous flowers with insect-mediated pollination. Fruits appear from June to July (sometimes August) located in a corymbose infructescence, with 1-10 fruits forming a 5-lobed, dehiscent capsule, often with 5 seeds that may remain inside of capsules until the next flowering season. The seed-dispersal mechanism is unknown, but it is possibly autochorous, since no obvious adaptation can be discerned (pers. obs.).

In the Iberian Peninsula, in addition to *H. bastetanum* ($2n = 18$), another two species ($2n = 36$): *H. linifolium* and *H. rosmarinifolium* occur; all three constitute a geographically isolated group towards the rest of the genus *Haplophyllum*. Navarro et al. (2004) suggested that *H. bastetanum* or an ancestor ($2n = 18$) could have arrived from North Africa during the Messinian (around 5 million years ago), following the model proposed in other groups of vascular plant species, originating from a tetraploid-by-autopolyploidy species, with the consequent diversification as an adaptation to different environmental conditions.

Study sites

The two known *H. bastetanum* populations are located in the district of Guadix (Granada province, SE Spain). The first of these is in the locality of Hernán Valle (S1), at 1135 m a.s.l. (37º23'28'' N and 3º02'25'' W), where the soil is mostly a lithosolic Regosol (Pérez-Pujalte 1997). The climate is dry (according to Rivas-Martínez & Loidi 1999), with an annual precipitation of 397 mm. The average annual air temperature is 11.4 ºC, the hottest and coldest months being August (21.3 ºC) and January (2.7 ºC), respectively. The annual precipitation of the period October 2004-September 2005 (study period) was 219 mm.

The second population is located at Baños de Alicún (S2), situated at 800 m a.s.l. (37º30'26'' N and 3º06'03'' W). The predominant soil of the area, classified as calcaric Regosol (Pérez-Pujalte 1997), develops over marls and conglomerates of Pliocene limestone cement (Anon. 1979). The climate is semi-arid (according to Rivas-Martínez & Loidi 1999), with an annual precipitation of 336 mm; however, the annual precipitation of the period October 2004-September 2005 (study period) was 185 mm. The average annual air temperature is 14.0 ºC, the hottest and coldest months being August (24.4 ºC) and January (5.3 ºC), respectively.

Threat assessment

In order to assign the conservation status of the species, we estimated its population size. For this purpose, a concentric sampling was made, beginning in the centre of the known populations and extending the sampling to the potential neighbouring zones. Individuals of the species were located with GPS (± 5 m error). The large patch size, in some cases, and the low detectability advised against direct counting of individuals. Therefore, 15 transects of 50 m × 1 m were established. In these transects, all the individuals intercepted were counted and classified as potentially reproductive or vegetative individuals. The definition of the threats followed the recommendations of IUCN/SSC (Anon. 2001b), and for the assignment of the endangered status, the categories of IUCN (Anon. 2001a) were used with the help of software RAMAS-Red list v2.0 (Akçakaya & Ferson 2001), which takes into account the uncertainty concept (Akçakaya et al. 2000).

Microhabitat effects

A total sample of 487 *H. bastetanum* individuals was randomly assigned to the analysis of microhabitat effects during June-July 2005. Of these, 227 corresponded to Hernán Valle (S1), and 260 to Alicún (S2). For each individual, the microhabitat with respect to the *S. tenacissima* tussock or other shrubs were noted (see App. 1 for more details) together with its life stage (vegetative or reproductive), the aspect (N, S, E, W and flat), and damage from insects or other herbivores (presence or absence).

Height (cm) was measured for all individuals from samples ($n = 487$), but the number of flowers ($n = 272$) and capsules ($n = 233$) were measured only in the reproductive individuals, when possible. Not more than a single individual of *H. bastetanum* per tussock was sampled in order to maintain spatial independence of the data. The *S. tenacissima* tussocks were, in general, adult/reproductive with a compact canopy of living tillers, but also with a large amount of dead leaves inside. Only in some cases the *S. tenacissima* tussocks consisted of senescent plants with few or no living tillers.

Soil analysis

Soil properties affected by individual plants of *S. tenacissima* were determined at the three different microhabitats described, consistently where *H. bastetanum* appeared. Three soil replicates per microhabitat were taken at each site (3 × 3 × 2 = 18 samples). The soil samples were taken in the uppermost 15 cm of the soil, the zone where most of the roots of *H. bastetanum* grow. In the same bore holes, soil samples were taken with soil-sample ring kits (Eijkelkamp) to determine bulk density (Blake & Hartge 1986). The samples 'inside' and 'below' were not collected in the same tussocks in order to maintain spatial independence of the data.

The soil texture was analysed with air-dried, screened soil samples (< 2 mm) by the pipette method of Robinson (Anon. 1972). The available water content was calculated by the difference between the moisture content at field capacity extracted in a pressure plate at 33 kPa and the moisture at the withering point, measured at 1500 kPa (Cassel & Nielsen 1986). The exchange bases (Ca^{2+}, Mg^{2+}, Na^+ and K^+) were extracted with NH_4OAc 1M, and the cation-exchange capacity was determined by saturation in sodium and, prior to washing with alcohol and extraction of the sodium adsorbed with NH_4OAc 1M (Anon. 1972). The pH was measured with a Crison model 2002® pH-meter in a soil suspension in distilled water (1:2.5). For the determination of the organic carbon and N^+ content of the soil, the samples were ground and screened again (0.125 mm grid size). The organic carbon was determined using the method of Walkley & Black (1934) modified by Tyurin (1951). For total N^+, the Kjeldahl method was used (Bremner 1965).

In addition, direct measurements of soil moisture (%) were taken during the flowering and fruiting periods of *H. bastetanum* (May, June 2006), in the three selected microhabitats, at the two sites and at six different times (3 × 2 × 6 times × 7 replicates = 252 measurements). These measurements were taken with the soil-moisture probe Theta Probe® type ML2x (Delta-T Devices, Cambridge, UK) in the uppermost six cm of the soil and were collected from the same points at the different sampling times.

Statistical analysis

The search for a relationship between pairs of nominal categorical variables was made by the non-parametric χ^2-test, comparing the observed distribution with the expected distribution. The influence of the site, microhabitat, and life stage on the metric variables measured (height, number of flowers, and number of capsules) was analysed by two and three-way ANOVAs, except for the soil moisture measurements that were analysed by a three-way (site, microhabitat, and time) ANOVA with repeated measures of the factor time. The Tukey HSD test of all-pairwise comparisons was run in all cases. Normality was checked by the Shapiro-Wilk test, and homogeneity by the Bartlett test. Simple regression analyses were used to determine the relationship between edaphic variables (independent variables) and biological variables (dependent variables). We chose the models that explained the most variability (%) of the dependent variables among different linear and non-linear functions without any specific criteria. All statistical analyses were performed using the STATISTIX 8 (Analytical Software, Tallahassee, Florida, USA) and STATGRAPHICS Plus 4.0 (Manugistics, Rockville, USA). Data are presented as ± 1 SE throughout.

Results

Threat assessment and conservation status

The two *H. bastetanum* populations – subpopulations *sensu* IUCN (Anon. 2001a) are 12.73 km apart. The population at S1 was smaller (1465 m^2) and divided into two patches, while the population at S2, was larger (24 948 m^2) and was fragmented, presenting 14 patches of variable size (from 4280 to 109 m^2; see App. 2 for details). The total area occupied by the species was approximately 2.6 ha and the total number of individuals was an estimated 3135 (Table 1).

The species has been classified as Critically Endangered (CR) according to IUCN categories, under the following items: criteria B2ab (i,ii,iii,iv,v), (Anon. 2001a) for a further explanation about threat criteria.

Effect of nurse plants on plant performance

There was the same proportion of vegetative and reproductive individuals of *H. bastetanum* at both sites (Table 2A). However, the proportion of individuals in the microhabitats did depend on the site. All together, in the S1 sample, 39.6% of the plants occurred in the open areas as opposed to 60.4% associated with the nurse plants, both below (20.26%), as well as inside the *S. tenacissima* tussocks (37.9%) or beneath the canopy of other species (2.2%). This fact was even more pronounced in the S2 sample, where only 16.2% of the plants were found in the open areas, against 83.8% associated with the nurse plants, both below (12.3%), as well as inside the *S. tenacissima* tussocks (67.3%) or in patches of other species (4.8%). Regarding aspect, 100% of the plants

Table 1. Number of *H. bastetanum* individuals in the two known populations (S1=Hernán Valle, S2= Alicún). Area = area of the populations in m^2, Density = number of individuals/100 m^2 ± 1SE, veg. = vegetative, rep. = reproductive, ind. = individuals. *Numbers in parentheses indicate the confidence interval of the mean of 95 %.

	Area (m^2)	Density		No. of individuals*		Ratio rep./veg.	Total ind.
		rep.	veg.	rep.	veg.		
S 1	1465	29.0±5.3	23.2±10.7	425 (390-564)	340 (183-497)	1.25	765
S 2	24 948	5.3±2.1	4.2±2.8	1322 (798-1846)	1048 (349-1746)	1.26	2370
Total	**26 413**			**1747**	**1388**		**3135**

Table 2. Analysis of the relationship between the samples taken of the two known *H. bastetanum* localities (**A**) and their life stage (**B**), with respect to the microhabitat, the aspect and the existence of damage caused by insects or other herbivores, made by non-parametric χ^2 test (n = 487). S1 = sample at Hernán Valle, S2 = sample at Alicún, open = open areas in the inter-tussocks spaces, below = below *S. tenacissima* canopy, Ins *Stipa* = inside *S. tenacissima* tussocks, Ins others = inside other species.

A

Site		Life stage		Microhabitat				Aspect				Damage	
	Frequency	Vegetative	Reproductive	Open	Below	Ins Stipa	Ins others	Flat	North	West	South	No	Yes
S1	Observed	106	121	90	46	86	5	227	0	0	0	188	39
	Expected	98.82	128.18	61.53	36.36	121.66	7.46	107.21	94.16	18.64	6.99	192.04	34.96
	Cell χ	0.52	0.40	13.18	2.56	10.45	0.81	133.86	94.16	18.64	6.99	0.09	0.47
S2	Observed	106	154	42	32	175	11	3	202	40	15	224	36
	Expected	113.18	146.82	70.47	41.64	139.34	8.54	122.79	107.84	21.36	8.01	219.96	40.04
	Cell χ^2	0.46	0.35	11.50	2.23	9.12	0.71	116.87	82.21	16.28	6.10	0.07	0.41
		χ^2 = 1.73, df = 1, P = 0.1882		χ^2 = 50.56, df = 3, P = 0.0000				χ^2 = 475.10, df = 3, P = 0.0000				χ^2=1.03, df = 1, P= 0.3092	

B

Life stage		Microhabitat				Aspect				Damage	
	Frequency	Open	Below	Ins *Stipa*	Ins others	Flat	North	West	South	No	Yes
Vegetative	Observed	77	40	89	6	106	91	12	3	204	8
	Expected	57.46	33.95	113.62	6.97	100.12	87.93	17.41	6.53	179.35	32.65
	Cell χ^2	6.64	1.08	5.33	0.13	0.34	0.11	1.68	1.91	3.39	18.61
Reproductive	Observed	55	38	172	10	124	111	28	12	208	67
	Expected	74.54	44.05	1447.38	9.03	129.88	114.07	22.59	8.47	232.65	42.35
	Cell χ^2	5.12	0.83	4.11	0.10	0.27	0.27	1.30	1.47	2.61	14.35
		χ^2 = 23.35, df = 3, P = 0.0000				χ^2 = 7.16, df= 3, P = 0.0670				χ^2 = 38.95.73, df = 1, P= 0.0000	

sampled at S1 were found in flat areas, while most of the plants sampled at S2 were found on northern aspects (Table 2A). There were no differences in damage from insects or other herbivores between the samples at the two sites.

In terms of life stage, there were significantly more reproductive individuals within the tussocks than expected (Table 2B). Overall, 80% of the reproductive individuals were associated with nurse plants, both inside the *S. tenacissima* tussocks (62.6%) and below (13.8%), as well as in thickets of other species (3.6%). No differences were found in aspect, but there was herbivore damage, which was higher than expected in reproductive individuals. This damage was independent of the microhabitat of the individuals in relation to the tussocks (χ^2 = 2.37, df = 3, P = 0.4994, n = 487).

The reproductive individuals were taller (21.9 cm ± 0.65, n = 276) than vegetative ones (7.7 cm ± 0.74, n = 211), although this depended on the microhabitat with respect to the tussocks (see App. 3A). The individuals that grew inside the tussocks were taller than the others, although this also depended on site and life stage (Fig. 1; App. 3A). In general, individuals of the S2 sample were taller (20.5 cm ± 0.73, n = 260) than those of S1 (10.3 cm ± 0.78, n = 227), although a positive interaction was found with the microsite factor (P = 0.0178, see App. 3A).

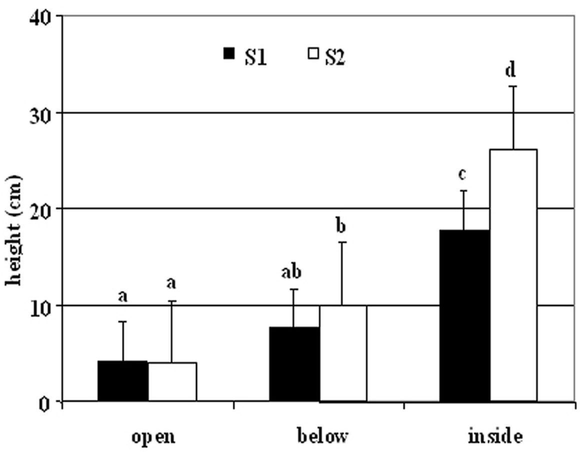


Fig. 1. Differences in height (± 1 SE, n = 487) of the *H. bastetanum* individuals at the three microhabitats studied, with respect to the sites (S1 = Hernán Valle; S2 = Alicún). Different letters indicate significant differences at P < 0.05 (Tukey test).

The reproductive individuals found within the tussocks had a higher number of flowers and produced a greater number of capsules than did the individuals that

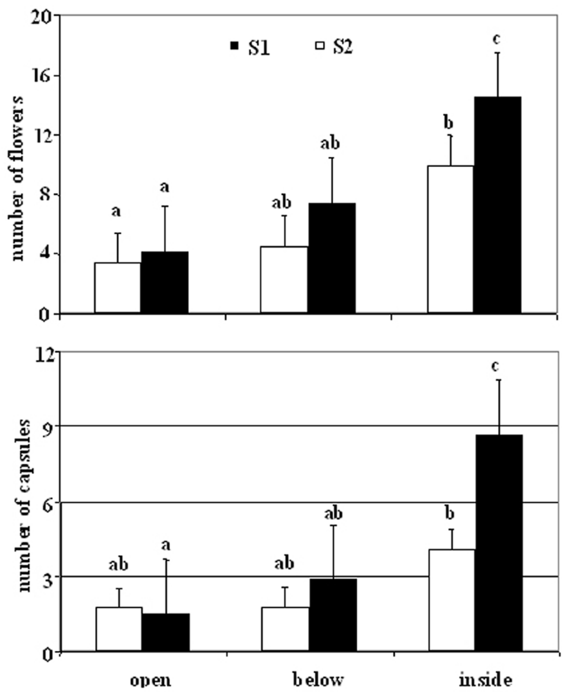


Fig. 2. Differences in the mean number of flowers ($n = 272$) and capsules ($n = 233$) (± 1SE) of the reproductive *H. bastetanum* individuals at the three microhabitats studied, with respect to the sites (S1 = Hernán Valle; S2 = Alicún). Different letters indicate significant differences at $P < 0.05$ (Tukey test).

grew below the tussocks or in open areas (Fig. 2), regardless of site (App. 3B, C). Flower and capsule production of reproductive individuals within the tussocks was significantly greater in the S1 than in the S2 sample (Fig. 2).

Effect of S. tenacissima on soils

The edaphic characteristics of the two localities studied had notable differences (Table 3). The differences in texture (loamy sandy in S1 and loamy clayey in S2) resulted in a greater water-retention capacity at 33 and 1500 kPa in S2 as than in S1. In addition, the organic carbon and K^+, as well as the cation-exchange capacity were markedly higher in S1.

However, regardless of site, values were higher in K^+, organic carbon, carbon:nitrogen ratio and available water content inside and below the tussocks than open microhabitats, but lower in bulk density. No significant differences were found between the cation-exchange capacity and moisture at 33 kPa in open areas or below the tussocks. The percentage in N^+ was significantly higher inside the tussocks than open areas.

In terms of the direct measurements of soil moisture, a significant and gradual decline was found (RM-ANOVA: $F_{microhabitat} = 45.92$, df = 2, $P = 0.0000$, $n = 126$) from the inside of the tussock (15.87 ± 0.19 %, $n = 84$) towards the periphery (13.14 ± 0.19 %, $n = 84$) and the open areas (11.73 ± 0.19 %, $n = 84$), clearly independent of site (RM-ANOVA: $F_{microhabitat\ x\ site} = 1.17$, df = 2, $P = 0.3486$). The moisture on 01.06.2006 (23.18 ± 0.26 %, $n = 42$) was greater than on other dates, due to a prior storm at both sites (Fig. 3). The pattern of dryness found indicated that the water was lost with greater speed in the open microhabitat than in the interior of the tussocks. In general, greater moisture was found in S2 (15.89 ± 0.15 %, $n = 126$) than in S1 (11.28 ± 0.15 %, $n = 126$), according to the RM-ANOVA ($F_{site} = 8.92$, df = 1, $P = 0.0306$).

Table 3. Mean values (± 1SE, $n = 3$) found in the soil analysis by site and microhabitat of *H. bastetanum*. CEC = Cation-Exchange Capacity, AW = Available Water content, RC = Retention Capacity, C:N = carbon:nitrogen ratio, OC = Organic Carbon, H 33 kPa = Moisture measured at 33 kPa, H 1500 kPa = Moisture measured at 1500 kPa.

Edaphic variables	Site		Microhabitat		
	S1	S2	Open	Below	Inside
Clay (%)	16.36 ± 0.69	29.19 ± 1.36	24.30 ± 3.16	22.73 ± 3.67	21.28 ± 2.45
Sand (%)	66.81 ± 1.91	32.61 ± 2.24	47.38 ± 8.73	51.27 ± 8.25	50.48 ± 7.08
Fine silt (%)	11.43 ± 0.79	31.64 ± 0.97	22.25 ± 5.06	20.35 ± 4.30	22.02 ± 4.52
Coarse silt (%)	5.37 ± 0.74	6.57 ± 0.51	6.07 ± 0.80	5.63 ± 0.70	6.20 ± 1.00
Gravel (%)	43.38 ± 7.19	40.17 ± 2.18	50.40 ± 6.05	39.07 ± 7.01	35.85 ± 5.30
Bulk density ($g\ m^{-3}$)	1.14 ± 0.10	1.08 ± 0.03	1.26 ± 0.09	1.15 ± 0.05	0.92 ± 0.06
pH	7.74 ± 0.05	8.07 ± 0.04	8.05 ± 0.07	7.85 ± 0.07	7.82 ± 0.09
Ca^{2+} ($Cmol_c kg^{-1}$)	4.96 ± 0.03	5.17 ± 0.01	5.09 ± 0.06	5.09 ± 0.05	5.03 ± 0.05
K^+ ($Cmol_c kg^{-1}$)	0.41 ± 0.02	0.52 ± 0.02	0.42 ± 0.04	0.47 ± 0.02	0.51 ± 0.03
N^+ (%)	0.20 ± 0.02	0.23 ± 0.01	0.18 ± 0.02	0.22 ± 0.01	0.25 ± 0.02
Mg^{2+} ($Cmol_c kg^{-1}$)	0.45 ± 0.00	0.47 ± 0.00	0.45 ± 0.00	0.46 ± 0.00	0.47 ± 0.00
Na^+ ($Cmol_c kg^{-1}$)	0.08 ± 0.00	0.10 ± 0.00	0.09 ± 0.00	0.08 ± 0.00	0.10 ± 0.01
C/N	8.36 ± 0.52	10.58 ± 1.29	7.13 ± 0.77	10.34 ± 1.13	10.93 ± 1.36
OC (%)	1.69 ± 0.16	2.39 ± 0.32	1.25 ± 0.15	2.21 ± 0.27	2.67 ± 0.28
CEC ($Cmol_c kg^{-1}$)	15.96 ± 1.17	23.67 ± 1.33	16.87 ± 2.27	19.15 ± 1.27	23.41 ± 2.29
H 33 kPa (%)	16.57 ± 1.08	22.08 ± 1.04	17.00 ± 3.15	18.47 ± 1.60	22.50 ± 1.58
H 1500 kPa (%)	9.68 ± 0.55	12.86 ± 0.87	10.05 ± 0.74	10.97 ± 1.11	12.78 ± 1.22
AW	6.89 ± 0.66	9.22 ± 0.30	6.94 ± 0.76	7.48 ± 0.68	9.74 ± 0.40
RC (mm)	106.75 ± 10.47	154.88 ± 6.60	113.84 ± 16.37	129.00 ± 11.35	149.60 ± 13.7

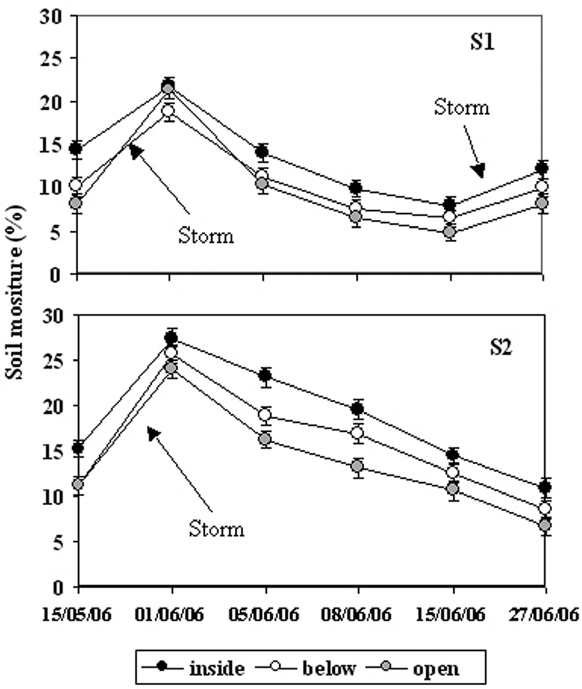


Fig. 3. Temporal development of soil moisture (%) at the two sites and in the three microhabitats considered (mean values ± 1 SE, $n = 252$).

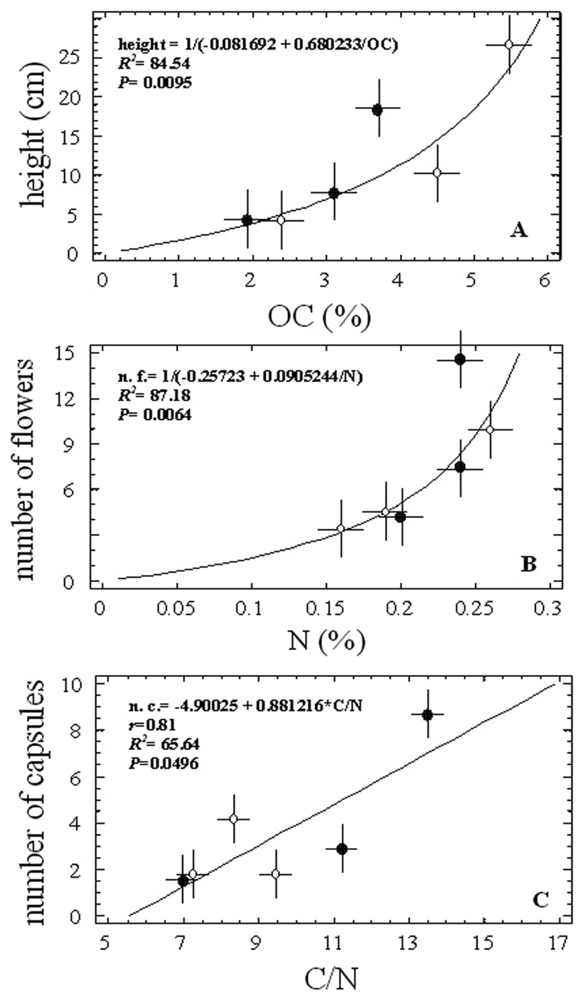
Effect of soil conditions on plant performance

A significant and strong relationship was found among the parameters of soil fertility and the height and number of *H. bastetanum* flowers and capsules (Fig. 4), although a non-linear relation was found in the case of height and number of flowers.

Discussion

H. bastetanum continues to be Critically Endangered (CR), in agreement with previous evaluations (Navarro et al. 2004; Cabezudo et al. 2005). Although the number of individuals was higher than estimated in these works, the criterion of occupation area (reduction of small and fragmented patches) led us to maintain this category.

S. tenacissima had a general positive effect on the distribution of *H. bastetanum*, and this effect was more pronounced in the S2 than in the S1 sample, where 83.8% of the plants were associated to nurse plants. Also, there were more individuals that became reproductive inside the *S. tenacissima* tussocks than in the open areas, and these individuals had greater flower and fruit production, especially in the S1 sample. The *H. bastetanum* plants were also found higher inside of *S. tenacissima* tussocks than at the other microsites, although this depended on site and life stage. The causes for this positive interaction on these plants appear to be due to the effects of *S. tenacissima* on soil water and fertility, as pointed out by other authors (Cerdà 1997; Bochet et al. 1999; Maestre et al. 2001, 2003; García-Fayos & Gasque 2002). In fact, the nutrient supply and changes induced in the physical properties and water-holding capacity of the soil have been the advantages cited as the facilitative effects of *S. tenacissima* and other species on seedlings in semiarid environments (Sánchez 1995; Maestre et al. 2003; Pugnaire et al. 2004; Armas & Pugnaire 2005). In this



[**Fig. 4.** Simple regression analysis between: (A) mean height of the *H. bastetanum* individuals and the mean content in organic carbon (OC) in the soil, (B) mean number of flowers per *H. bastetanum* individual and the mean N^+content in the soil, (C) mean number of capsules per *H. bastetanum* individual and the carbon:nitrogen ratio of the soil (n.f. = number of flowers, n.c. = number of capsules, error bars are ± 1 SE, r = correlation coefficient, R^2 = coefficient of determination; black circles = samples at S1, empty circles = samples at S2).]

work, organic carbon, N^+, and carbon:nitrogen ratio were related with the height and number of *H. bastetanum* flowers and capsules (plant productivity), but height and number of flowers lost linearity with high organic carbon and N^+ contents, probably due to interaction of other factors such as available water content. Although direct measurements of soil moisture were taken one year after the taking of the general data (2006), the results clearly show that the moisture is maintained better inside the *S. tenacissima* tussock than in open areas, regardless of the site (see Fig. 3).

However, we have found no other experimental studies that directly correlate the effects of such factors on plant fitness or plant productivity in semi-arid environments. Only Moro et al. (1997b) found a greater germination rate, dry mass production, individual mass production, height, N^+ uptake and N^+ concentration of barley plants grown in soil from central and intermediate positions in the understorey of *Retama sphaerocarpa* shrubs than in soil of outer positions, where organic matter and total N^+ contents were lower than in the inner positions. Franco-Piñaza et al. (1996) also found a greater root mass, stem mass, leaf mass, and seedling mass of *Celtis pallida* and *Acacia smallii* seedlings grown in soil from beneath *Prosopis glandulosa* canopies than seedlings grown in soil from interspaces.

In this work, almost all the edaphic parameters studied decreased from the canopy centre of *S. tenacissima* outwards, regardless of locality. Therefore, distance from the nurse plant appears to be an important factor to ameliorate negative conditions and boost the availability of resources (Moro et al. 1997b; Dickie et al. 2005). In this way, the application of facilitation to restoration projects may improve the establishment of target plants, mimicking a natural process. Padilla & Pugnaire (2006) showed the role of the nurse plants in the restoration of degraded environments. These authors reviewed restoration experiments in which seeds or seedlings of restored species were placed both near adults plants that acted as nurses and in control gaps (see Castro et al. 2002, 2006; Maestre et al. 2001, 2002 b; Egerova et al. 2003; Gasque & García-Fayos 2004; Gómez-Aparicio et al. 2004; Sánchez-Velásquez et al. 2004; Bignaut and Milton 2005; Huber-Sannwald & Pyke 2005), and showed that the nurse plants improve seedlings establishment in some systems, and that they may have potential for use in restoration projects. However, restoration experiments of threatened or endemic species using facilitation have never been carried out.

Our results support the hypothesis of the facilitation effect of *S. tenacissima* on the rare endemic *Haplophyllum bastetanum*. Facilitation by nurse plants of species of interest in conservation is an aspect that has not previously been clearly reported and this study expands our knowledge on the topic. However, contrary to the examples of facilitation on threatened species commented upon in the Introduction (see García et al. 2000; García & Obeso 2003; Suzán et al. 1994; Tewksbury et al. 1999), where the scarcity of nurse plants was a decisive factor of the rarity of the target species, in the Guadix-Baza basin the *S. tenacissima* steppes have a wide range of distribution and they are the dominant habitat. In this sense, it becomes necessary to increase knowledge related to the natural rarity and low recruitment rates of *H. bastetanum*, and therefore further observations and experiments of reproductive biology need to be conducted. In any case, the conservation and adequate management of *S. tenacissima* tussocks are necessary for the recovery of the *H. bastetanum* populations, which, according to our evaluation, are critically endangered by changes related to agriculture (change in soil use, management, ploughing, etc.) and probably by natural causes including drought, wild or human-mediated fire, limited dispersal, poor recruitment/reproduction/regeneration, high juvenile mortality, low densities and restricted range.

Finally, we may emphasize that *ex situ* propagation strategies with the targets of reinforcing the remaining populations or of establishing new populations in a suitable habitat with low human pressure should be promoted and the seedlings should always be placed inside the adult *S. tenacissima* tussocks. We propound facilitation as a valuable tool for rehabilitation of populations of threatened plant species into conservation biology projects.

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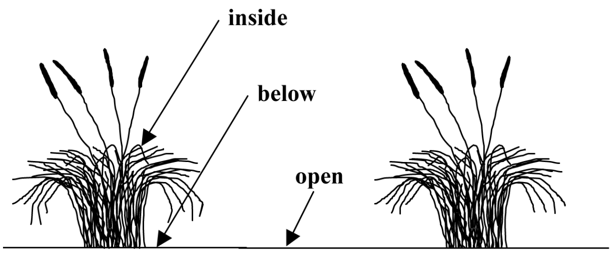

App. 1. Three different microhabitats selected: open (open areas in the inter-tussocks spaces), below (nearby of *Stipa tenacissima* tussocks and under the influence of its canopy), and inside (inside the tussocks).

App. 2. Area of the different patches of the two *H. bastetanum* populations. S1 = population at Hernán Valle, S2 = population at Alicún.

	Patches	Area (m^2)
S1	1	1430.6
	2	34.7
S2	1	3685.9
	2	3845.1
	3	1157.2
	4	4279.8
	5	178.2
	6	324.6
	7	2227.1
	8	3043.3
	9	1147.0
	10	109.0
	11	2510.7
	12	1656.6
	13	148.8
	14	635.2

App. 3. Two- and three-way ANOVA results.

A Dependent variable: **height**

Source	DF	SS	MS	F	P
Site (S)	1	1143.1	1143.1	22.90	**0.0000**
Life Stage (LS)	1	7428.9	7428.9	148.82	**0.0000**
Microhabitat (M)	2	18301.7	9150.84	183.32	**0.0005**
S × LS	1	176.3	176.27	3.53	0.0608
S × M	2	405.4	202.68	4.06	**0.0178**
LS × M	2	1321.2	660.62	13.23	**0.0000**
Error	477	23810.6	49.92		
Total	486				

B Dependent variable: **number of flowers**

Source	DF	SS	MS	F	P
Site	1	265.6	265.59	2.58	0.1095
Microhabitat	2	2670.4	1335.18	12.97	**0.0000**
S × M	2	109.7	54.84	0.53	0.5877
Error	266	27392.0	102.98		
Total	271				

C Dependent variable: **number of capsules**

Source	DF	SS	MS	F	P
Site	1	97.37	97.365	2.75	0.0986
Microhabitat	2	738.88	369.442	10.44	**0.0000**
S × M	2	168.24	84.120	2.38	0.0952
Error	227	8034.75	35.395		
Total	232				

App. 1-3. Internet supplement to:
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