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The seasonal impact of *Cytisus striatus* on soil fertility and the herbaceous understory

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Abstract

Cytisus striatus is an endemic shrubby legume from western Spain that grows on acidic and rocky soils forming extent shrublands. The shrub's effect on soil fertility and herbaceous species diversity and growth was studied in a natural population from central-western Spain. The concentrations of soil organic matter, nitrogen and phosphorus were higher under *Cytisus striatus* canopy. Herbaceous species in the understorey had higher nitrogen content than those growing in between shrubs. Isotopic nitrogen analyses did not show a direct relationship between symbiotic nitrogen fixation on *C. striatus* and the nitrogen content of herbaceous species. The presence of shrubs had a negative effect on herbaceous richness and diversity in its understorey. However, herbaceous diversity in the ecosystem was increased due to the spatial heterogeneity created by the shrubs. The biomass produced by herbaceous species was lower under a dense shrub canopy than in areas without shrubs. It is proposed that intense competition could be responsible for these results, with Poaceae and Asteraceae outcompeting other species under a dense *C. striatus* canopy.

Introduction

Shrublands dominated by Fabaceae species are one of the most important ecosystems under Mediterranean-type climate. Shrubs are key components in these ecosystems as they influence both biotic and abiotic conditions. Woody species may create 'islands of fertility' either by improving availability of water and nutrients (Richards & Caldwell, 1987; Joffre & Rambal, 1993; Moro *et al.*, 1997a), or by protecting against direct irradiance and overheating (Moro *et al.*, 1997b; López-Pintor *et al.*, 2000). Plant growth is, therefore, enhanced in the understorey because of the amelioration of the environmental conditions. It has been shown that herbaceous richness and diversity increase under the canopy of woody species in some arid and semi-arid environments, although this facilitation effect has not been demonstrated for more mesic ecosystems (Pugnaire *et al.*, 1996; Pugnaire & Luque, 2001; Rodríguez-Echeverría & Pérez-Fernández, 2003). Plant interactions change depending on both biotic and abiotic conditions (Brooker & Callaghan, 1998; Pugnaire & Luque, 2001). Facilitation mechanisms seem to be more important in extreme environments whereas competition processes are favoured in mild rich habitats (Callaway & Walker, 1997; Brooker & Callaghan, 1998).

Leguminous species can use atmospheric nitrogen through the symbiotic association with rhizobia. This process accounts for the ability of legumes to colonise soils with a low nitrogen concentration. Additionally, legumes can increase the fertility of soils due to nitrogen-enriched litter deposition or direct release of nitrogen from the roots (Haystead *et al.*, 1989; Dart, 1998). In the last two decades researchers have become interested in woody legumes because of their ecological importance and their prospective use in revegetation projects (Faria *et al.*, 1987; Ndiaye & Ganry, 1997; Dart, 1998). As in most areas under Mediterranean climate, desertification is a serious threat for ecosystems in the Iberian Peninsula. However, the effect of shrubby legumes native to the Iberian Peninsula on the herbaceous understorey has only been studied for species growing in neutral or high pH soils (Herrera *et al.*, 1993; Pugnaire *et al.*, 1996; Moro *et al.*, 1997a;

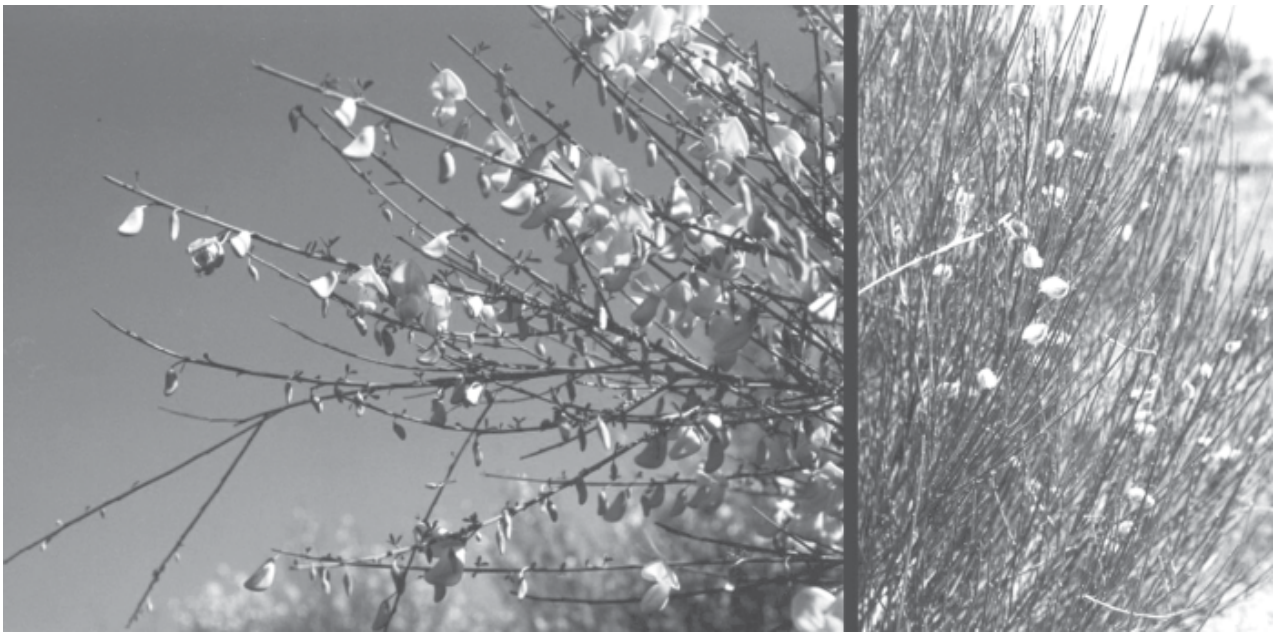

Fig. 1. Detail of flowers and fruits of *Cytisus striatus* (Hill) Rothm.

Requena *et al.*, 2001). Further research in acidic soils is essential to develop revegetation methodologies for western Spain. A low soil pH prevents the establishment of a high diversity of plant species. Acid soils have a reduced availability of some nutrients such as calcium, molibdenum and phosphorus. Furthermore, aluminium and proton concentrations can reach toxic levels and alter root growth (Blamey *et al.*, 1993).

Cytisus striatus (Hill) Rothm is a leguminous shrub endemic to central-western Iberian Peninsula (Fig. 1) that grows in acidic rocky soils at altitudes between 30 and 1400 metres. This work aims to determine the effect of *C. striatus* on the herbaceous community growing in its understorey as well as on soil fertility. The ^{15}N natural abundance technique is used to track nitrogen transfers between the woody legume and neighbouring plants (Handley & Scrimgeour, 1997).

Materials and Methods

Field study site

The study site is located in San Vicente de Alcántara (Badajoz), central-western Spain (39º 21' N, 8º 51' W, 504 m altitude) (Fig. 2). The average annual precipitation is 600-1000 mm, and mean annual temperature is 13-16ºC. The precipitation regime is characterised by dry summers and rain falling mainly during winter and spring. Over the study period (March 2000 to December 2000) the monthly average temperature ranged between 7.6ºC and 23.9ºC. Total rainfall was 1425 mm, with the maximum in March 2001 and the minimum in August 2000 (Fig. 3). The bedrock is siliceous and the soil in this location has a high sand content (87%) and low pH (3.8-4.6).

The vegetation is composed by shrublands dominated by either *C. striatus* or *Cytisus multiflorus* and by

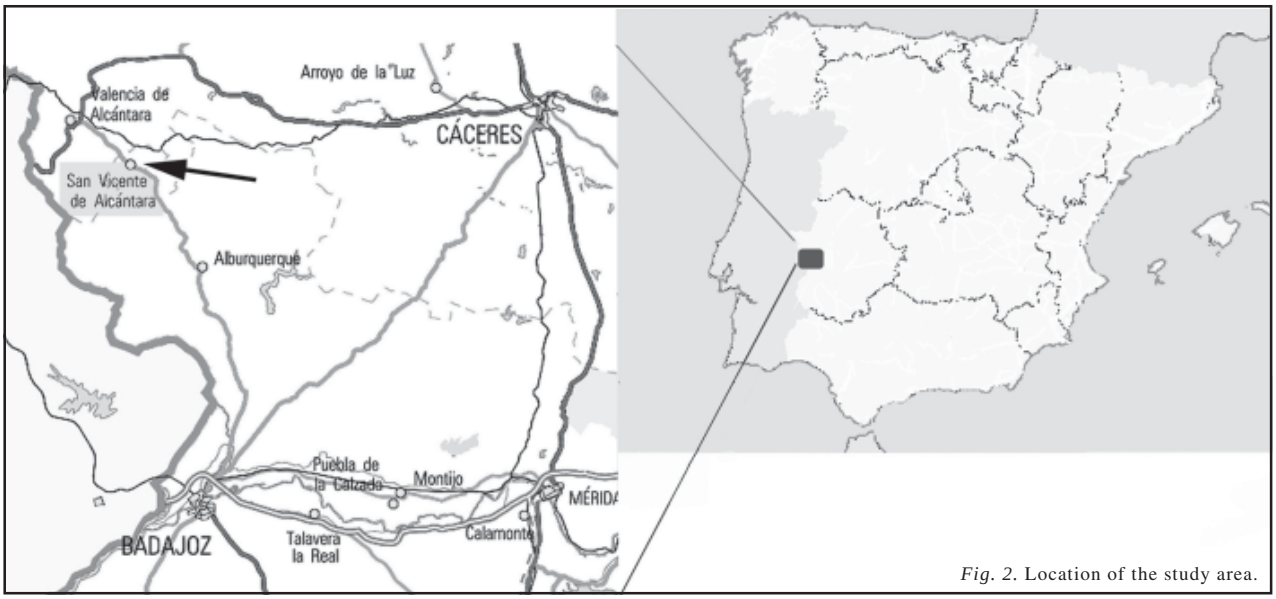

Fig. 2. Location of the study area.

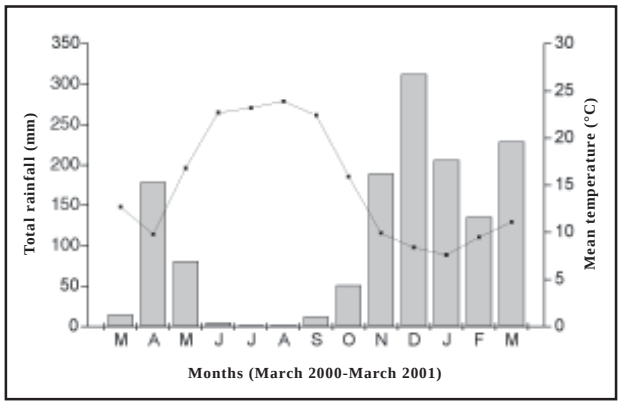

Fig. 3. Monthly values of total rainfall (bars) and mean temperature (line) in San Vicente de Alcántara (Badajoz, Spain) from March 2000 to March 2001.

woodlands of *Quercus suber*. The selected shrubland, dominated by *C. striatus*, is more than 20 years old with shrubs as high as two metres. The herbaceous layer is a mixture of annual and perennial monocotyledonous and dicotyledonous species.

Experimental design

Eight sampling plots (3x3 m) corresponding to two replicates of the following four plot types were established in March 2000.

1. A dense shrub canopy with underlying herbaceous vegetation (DE)
2. A single shrub with surrounding herbaceous vegetation (E)
3. Herbaceous vegetation only (V)
4. No vegetation (S).

Monthly soil samples were taken from each of the eight plots between March 2000 and March 2001. Samples were collected from the soil surface to 5-cm deep. For the first three kinds of experimental plots, herbaceous vegetation richness, diversity and cover were recorded during the spring of 2000; data were taken using 0.25 m^2 sampling squares. In addition, vegetation samples of two replicates of 0.25 m^2 in each type of experimental plot were taken to estimate the biomass of herbs and to analyse for N and ^{15}N content.

Chemical analyses

Soil samples were air-dried and sieved with a 2 mm sieve. Analysis for pH, nitrogen, phosphorus and organic matter were performed following the procedures described by Reed & Cumings (1945), Allen (1989) and Walkley & Black (1934).

For isotopic analysis of N, soil samples were ground using an agate ball mill Pulverisette 0 (Fritsch, Germany) and sieved (0.5 mm). The N_2 gas released during the combustion was purified and analysed for ^{15}N isotope composition with an Elemental Analyser Carlo Erba EA 1108 (Carlo Erba, Italy) coupled to a Finningan MAT DELTA^{plus} Mass Spectrometer (Finningan, Germany).

Caryophyllaceae, Plantaginaceae and Poaceae herbaceous species were used for N and ^{15}N analysis. The selection of those families was based on their high biomass production and on the availability of these families in all the experimental plots.

Collected plant material was classified and separated into botanical families and oven-dried at 75ºC for 48 hours. Total biomass was calculated by weighing each group in a laboratory precision balance (SARTORIUS analytic, Germany). For N analysis, shoots and leaves of plant samples were ground using a mechanical mill (Retsch MM2000). Total N content was determined using a Carlo Erba Instruments EA 1108 CHNS/O analyser (Carbo Erba, Italy). Samples were combusted at 1020ºC in sealed quartz tubes with a Cr_2O_3 catalyst. N_2 gas was purified and analysed for isotopic composition with a Finnigan MAT DELTA^{plus} mass spectrometer (Finningan, Germany).

Data analysis

Data from vegetation sampling were used to calculate: a) richness as the total number of species, b) diversity as the Shannon-Wiener Index (Shannon & Weaver, 1949) using the richness and frequency of each species. Cover was estimated as the percentage of soil covered by a particular species in a sampling square and data were processed to obtain the cover per botanical family. Biomass was calculated using the dry weight of the collected plant material and expressed as g/m^2 for each botanical family.

Prior to statistical analyses, all soil and plant data were tested for normality (Cochran, 1941; David *et al.*, 1954) and when necessary transformed using natural logarithms. Data were analysed using either one-way ANOVA and Tukey post-hoc test for overall comparisons or Student's t-test.

Results

Soil data

The analysis of soil pH showed values between 3.8 and 4.6 with minimum values in summer and maximum in spring (Fig. 4). Those plots with vegetation had similar patterns of pH values along the study ranging between 4.1 and 4.6. The greatest variation was observed in plots without vegetation (S) where soil pH dropped in September to 3.8. Significant differences ($p<0.05$) were obtained between S plots and the remaining ones for that month.

Organic matter values ranged between 4.8 and 10.8 % during the year with maximum values in summer and minimum values at the end of winter (Fig. 4). Significant differences ($p<0.05$) were detected between E and S plots in May 2000 (Table 1).

Soil phosphorus content was highly variable during the study with values between 0.01 mg/g and 0.12 mg/g (Fig. 4). Phosphorus content was higher in E and V plots. Significant differences ($p<0.05$) were detected between V and S plots for June, DE plots and the other three plots for July and between plots with (DE, E) and without shrubs (V, S) for January (Table 1).

Nitrogen concentration varied between 2.64 and 6.91 mg/g (Fig. 4). Maximum values were observed in plots with a single shrub and minimum values were obtained in plots with only herbaceous vegetation. Significant differences ($p<0.05$) were detected between V plots and

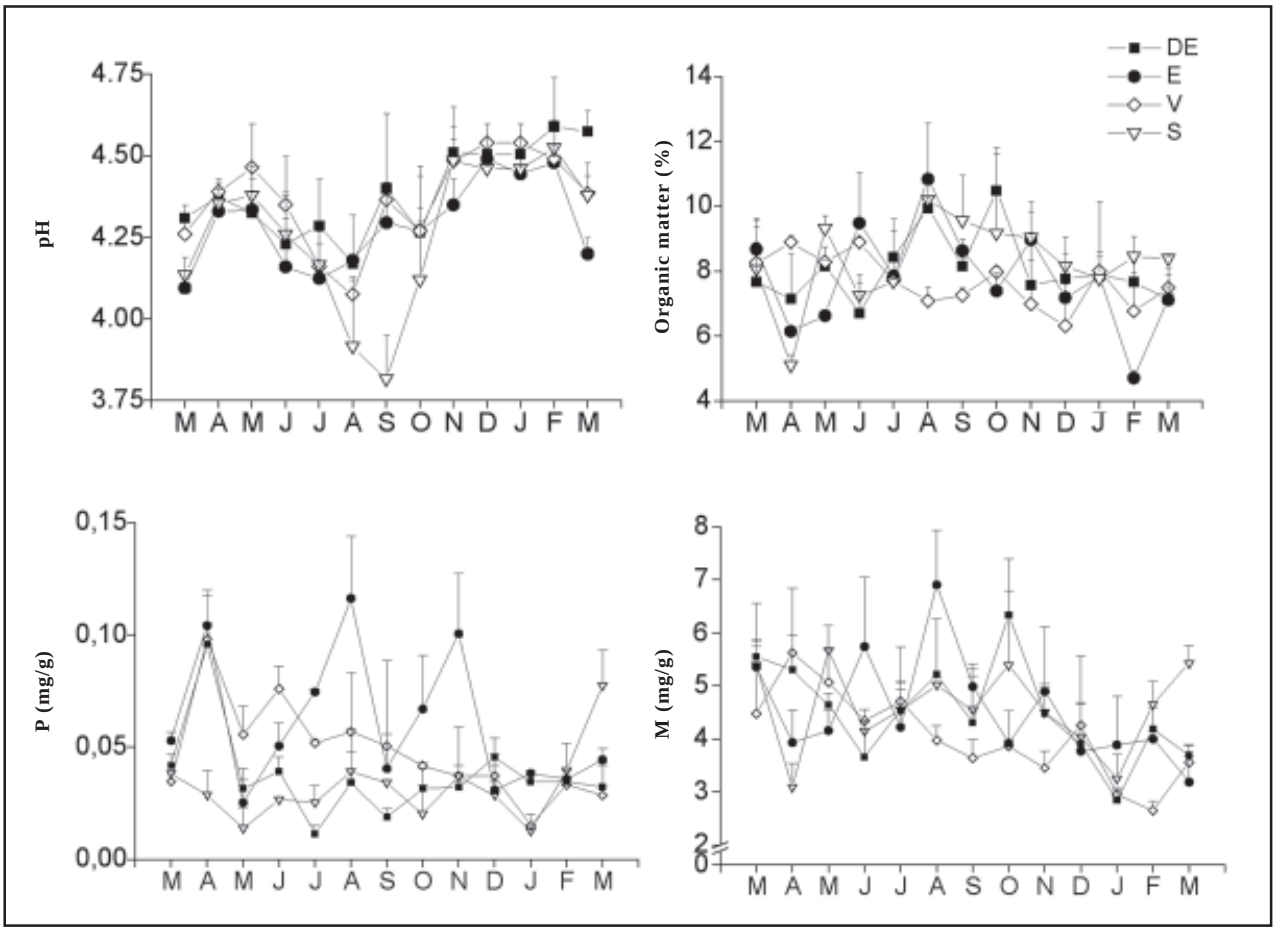

Fig. 4. Soil pH, organic matter, phosphorus and nitrogen concentrations in each experimental plot from March 2000 to March 2001. Values are mean ± standard error.

the other three plots in February and between S and V plots for March 2001 (Table 1).

$\delta^{15}N$ values ranged between 5 and 7 ‰ for DE and E plots, 3 and 4.7 ‰ for V plots and 5.5 and 7.5 ‰ for S plots (Fig. 5). Statistically significant differences ($p<0.001$) were detected between the four plots for all the analysed months except March, for which no significant differences ($p>0.05$) were found between E and S plots (Fig. 5, Table 1).

Plant data

Thirty-two herbaceous species belonging to thirteen different botanical families were identified in the shrubland (Appendix I). Some of these species were

Table 1. F and *p* values after one-way ANOVA comparing soil pH, organic matter (O.M.), phosphorus (P), nitrogen (N) and $\delta^{15}N$ between the four experimental plots for each month.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
F													
pH	4.444	0.299	0.260	0.294	0.294	0.892	3.500	0.206	0.513	0.178	0.442	0.249	4.755
O.M.	0.123	1.703	13.109	1.885	0.050	3.327	0.490	0.613	0.642	0.207	0.009	4.967	1.215
P	3.769	4.171	2.660	7.634	25.991	2.328	0.367	1.988	3.154	0.628	14.310	0.125	3.853
N	0.208	1.380	2.034	1.403	0.067	1.814	0.408	0.437	0.352	0.052	0.781	15.447	7.779
$\delta^{15}N$	188.9		2708.5			392.8			2793.4		573.3		
p													
pH	0.092	0.826	0.851	0.829	0.829	0.518	0.039	0.887	0.695	0.906	0.736	0.859	0.083
O.M.	0.942	0.303	0.015	0.273	0.983	0.138	0.708	0.642	0.627	0.887	0.999	0.078	0.412
P	0.116	0.101	0.184	0.039	0.004	0.216	0.782	0.258	0.148	0.634	0.013	0.941	0.113
N	0.886	0.370	0.252	0.364	0.974	0.284	0.756	0.739	0.791	0.982	0.563	0.012	0.038
$\delta^{15}N$	<0.001		<0.001			<0.001			<0.001		<0.001		

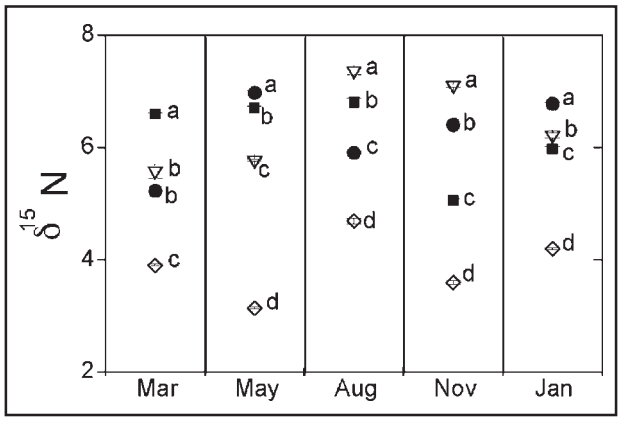

Fig. 5. Soil $\delta^{15}N$ values (mean – S.E.) for each experimental plot: DE (Dense shrub canopy); E (Single shrub); V (only herbs); S (no vegetation). Mar: March 2000, May: May 2000; Aug: August 2000; Nov: November 2000; Jan: January 2000. Different letters indicate significant differences ($p<0.001$) between plots for each month.

associated with different plots: *Rumex angiocarpus* L., *Polygonum aviculare* L. and *Muscari comosum* (L.) Miller were identified only in DE plots; *Sedum arenarium* Brot. in plots without a dense canopy (E and V plots); and *Trifolium* sp. only in V plots. Herbaceous specific richness and diversity varied between different experimental plots and months (Fig. 6). In March, no herbaceous vegetation was present in E plots. Richness ranged between 8.6 and 12.2 for DE plots, zero and 10.2 species for E plots and 12.2 and 12.8 species for V plots. Diversity values varied between 2.6 and 2.7 for DE plots, zero and 2.9 for E plots and 2.7 and 3.3 for V plots. Richness and diversity were higher in V plots than in the other experimental plots for March 2000 and February 2001. Significant differences ($p<0.05$) were detected between DE and V plots for both months but not for May 2000 (Fig. 6, Table 2).

Maximum herbaceous cover (164.8 %) was observed for DE plots in March 2000 (Fig. 7). Herbaceous cover was lowest in May 2000 for all three plots (40-41.6 %). Cover values in February ranged between 77.1 % and 105.5 %. No significant differences ($p>0.05$) were detected between experimental plots in the three studied months (Fig. 7, Table 2).

Herbaceous biomass was higher in March than in May. The highest value was for V plots with 135.5 g/m^2, which was statistically different ($p<0.05$) from that in DE plots (69.4 g/m^2) (Fig. 7, Table 2). Biomass values in May were also higher in V plots (93.4 g/m^2) than in plots with shrubs (37.2 g/m^2 for DE plots and 28.8 g/m^2 for E plots), but no significant differences were detected within this month. When biomass production by Poaceae, Asteraceae, Caryophyllaceae and Plantaginaceae was analysed, significant differences ($p<0.05$) between the three experimental plots were observed (Table 3, Table 4). In March, the biomass of Poaceae species in DE plots (54.4 g/m^2) corresponded to the 77.9 % of total biomass in this plot. Asteraceae species were the main biomass producers in V plots with 48.4 g/m^2 (35.7 % of the total biomass). In May, biomass production was dominated by Asteraceae species in DE plots (42.0 % of total biomass), by Caryophyllaceae (43.9 %) in E plots, and by Plantaginaceae (56.7 %) in V plots.

Plant nitrogen content ranged between 0.9% and 1.9%

Appendix I. Herbaceous species identified in the *Cytisus striatus* shrubland in San Vicente de Alcántara (Badajoz, Spain).

Asteraceae
Chamaemelum fuscatum (Brot.)Vasc.
Leontodon taraxacoides (Vill.)Mérat
Sonchus oleraceus L.
Tolpis barbata (L.)Gaertner
Brassicaceae
Cardaria draba (L.)Desv.
Teesdalia coronopifolia (J. P. Bergeret) Thell.
Caryophyllaceae
Silene gallica L.
Spergula arvensis L.
Spergularia rubra subsp. *longipes* (Lange)Briq
Cistaceae
Xolantha tuberaria (L.)Gallego, Muñoz Garm. & C.Navarro
Crassulaceae
Crassula tillaea L.
Sedum arenarium Brot.
Fabaceae
Ornithopus compressus L.
Ornithopus perspusillus L.
Trifolium angustifolium L.
Trifolium subterraneum L.
Geraniaceae
Erodium cicutarium (L.)L'Hér.
Erodium moschatum (l.)L'Hér.
Iridaceae
Romulea bulbocodium (L.)Sebastiani & Mauri
Liliaceae
Muscari comosum (L.) Miller, Gard. Dict.
Scrophulariaceae
Linaria spartea (L.)Chaz.
Plantaginaceae
Plantago coronopus L.
Plantago lagopus L.
Plantago lanceolata L.
Poaceae
Agrostis pourretii Willd.
Anthoxanthum odoratum L.
Briza maxima L.
Festuca elegans Boiss.
Molineriella laevis (Brot.) Rouy
Vulpia ciliata Dumort.
Polygonaceae
Polygonum aviculare L.
Rumex angiocarpus Murb.

Table 2. F and *p* values after one-way ANOVA or Student's t-test (for March) comparing the data from the three sampling plots in the *Cytisus striatus* shrubland in San Vicente de Alcántara (Badajoz, Spain).

	March	May		February	
	p (t-test)	F	p	F	p
Richness	0.024	5.734	0.018	5.346	0.022
Diversity	0.012	6.754	0.011	7.635	0.007
Cover	0.116	0.010	0.990	0.568	0.581
Biomass	0.022	0.431	0.684	----	----

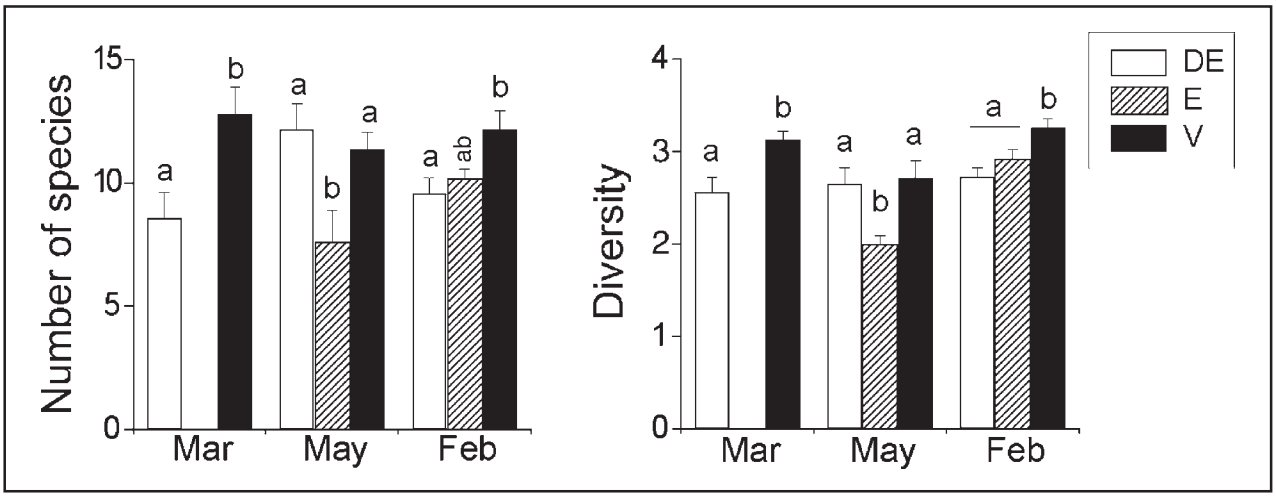

Fig. 6. Species richness and diversity (mean ± S.E.) for herbaceous vegetation. Mar: March 2000, May: May 2000; Feb: February 2001. Different letters indicate significant differences ($p<0.05$) between plots after one-way ANOVA and Tukey test (after Student's t-test for March data).

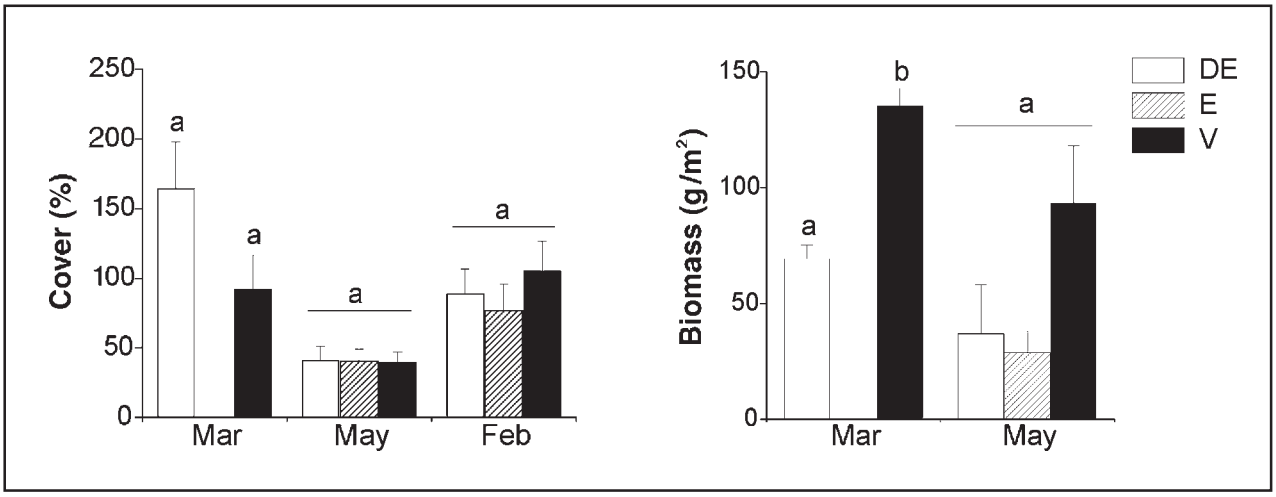

Fig. 7. Cover and biomass production (mean ± S.E.) for herbaceous vegetation. Mar: March 2000, May: May 2000; Feb: February 2001. Different letters indicate significant differences ($p<0.05$) between plots after one-way ANOVA and Tukey test (after Student's t-test for March data).

for the studied families (Fig. 8). Caryophyllaceae species had the highest nitrogen content ranging between 1.5 % and 1.9 %. Total nitrogen content was significantly higher ($p<0.001$) for the families Poaceae, Plantaginaceae and Caryophyllaceae in those plots with a dense canopy of *C. striatus*, with the exception of Poaceae in March (Fig. 8, Table 4).

The isotopic analysis showed values of $\delta^{15}N$ between –0.9 and 3.9 ‰ (Fig. 9). Significant differences ($p<0.001$) were detected for the three families growing in different

Table 3. Biomass production in g/m² (mean ± S.E.) for herbaceous species from Asteraceae, Caryophyllaceae, Plantaginaceae and Poaceae families in each sampling plot. Different letters indicate significant differences ($p<0.05$) between plots within each month, after Student's t-test for March data, and one-way ANOVA and Tukey test for May data. Percentages of total biomass production for each plot type corresponding to these plant families are indicated in brackets.

	March		May		
	ED	**V**	**ED**	**E**	**V**
Asteraceae	3.14 ± 2.0[a]	48.44 ± 12.1[b]	15.62 ± 11.1[a]	0.04 ± 0.04[a]	19.16 ± 9.8[a]
	(4.5 %)	**(35.7 %)**	**(42.0 %)**	(0.1 %)	(20.5 %)
Caryophyllaceae	0.78 ± 0.7[a]	3.02 ± 1.2[a]	0.64 ± 0.4[a]	12.62 ± 9.3[b]	6.44 ± 2.2[b]
	(1.1 %)	(2.2 %)	(1.7 %)	**(43.9 %)**	(6.9 %)
Plantaginaceae	4.96 ± 0.2[a]	35.11 ± 8.5[b]	4.90 ± 1.9[a]	3.00 ± 0.8[a]	52.94 ± 2.3[b]
	(7.1 %)	**(25.9 %)**	(13.2 %)	(10.4 %)	**(56.7 %)**
Poaceae	54.10 ± 4.0[a]	28.84 ± 16.5[a]	7.78 ± 3.1[a]	2.00 ± 1.7[a]	5.28 ± 2.5[a]
	(77.9 %)	(21.3 %)	(20.9 %)	(6.9 %)	(5.7 %)

Table 4. F and *p* values after Student's t-test (March) and one-way ANOVA (May) comparing data from the botanical families grown in different sampling plots in the *Cytisus striatus* shrubland in San Vicente de Alcántara (Badajoz, Spain).

		March	May	
Biomass		***p* (t-Student)**	**F**	***p***
	Asteraceae	0.046	3.199	0.180
	Caryophyllaceae	0.293	2.598	0.221
	Plantaginaceae	0.036	1.452	0.037
	Poaceae	0.425	0.084	0.922
N content				
	Caryophyllaceae	0.002	2613.8	<0.001
	Plantaginaceae	<0.001	1000.9	<0.001
	Poaceae	0.022	2187.0	<0.001
$\delta^{15}N$				
	Caryophyllaceae	<0.001	2602.5	<0.001
	Plantaginaceae	<0.001	933.7	<0.001
	Poaceae	<0.001	2121.6	<0.001

plots (Fig. 9, Table 4). Values for herbaceous species grown in V plots were close to zero, ranging from –0.9 to 0.4 ‰. $\delta^{15}N$ values in DE and E plots were between 1.5 and 3.9 ‰, with the lowest values for Poaceae species and the highest for Plantaginaceae.

Discussion

Soil covered by any kind of vegetation showed a smaller monthly variation on pH values. Only plots without vegetation reached pH values lower than four. Soil acidity limits plant growth through nutrient deficiencies (P, Ca and Mg) and accumulation of phytotoxic substances such as soluble Al and Mn (Awad *et al.*, 1976). The buffer effect of vegetation is, therefore, positive for soil fertility and for the establishment of new plant species.

Soil content in phosphorus and nitrogen was higher for plots with shrubs, although significant differences were not always detected. These results suggest that *C. striatus* accumulates nutrients under its canopy. This increase was not as high as the reported for other woody species (Pugnaire *et al.*, 1996; Cross & Schlesinger, 1999)

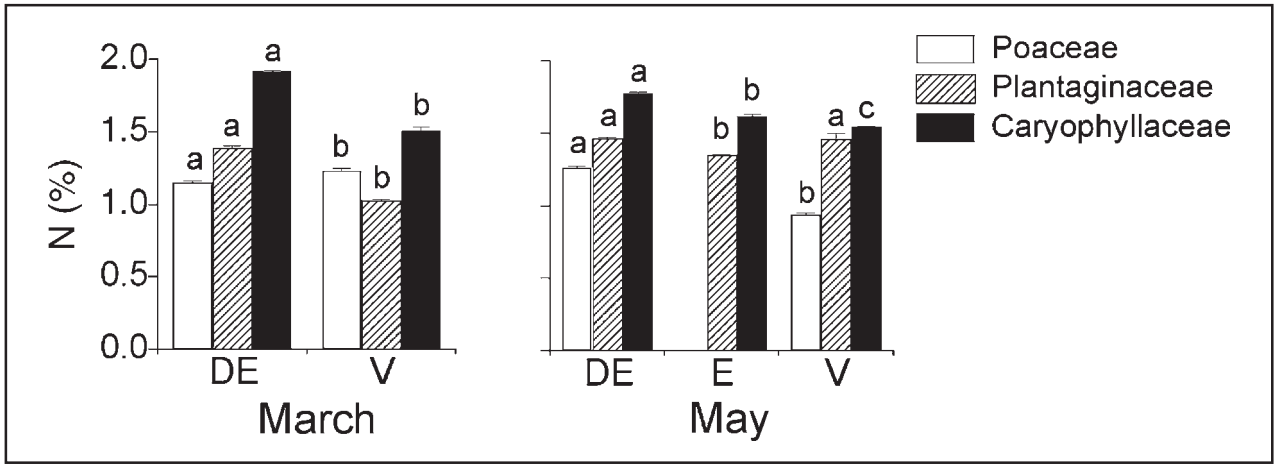

Fig. 8. N content of shoots and leaves from herbaceous species belonging to three plant families harvested in the *C. striatus* shrubland. Different letters above the bars mean significant differences (p<0.001) between families within each plot and month, after one-way ANOVA and Tukey test (after Student's t-test for E plots in May).

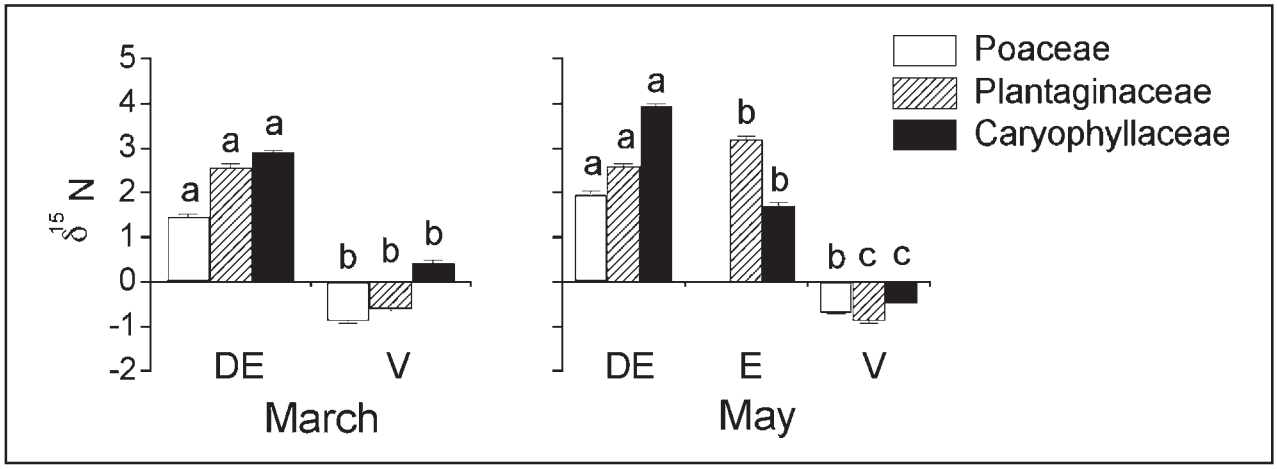

Fig. 9. Values of $\delta^{15}N$ (mean ± S.E.) for shoots and leaves of herbs from three botanical families harvested in the *C. striatus* shrubland. Different letters above the bars mean significant differences (p<0.001) between families within each plot and month after analysis by one-way ANOVA and Tukey test for overall comparisons (after Student's t-test for E plots in May).

indicating a smaller effect of *C. striatus* on soil nutrient distribution in the studied ecosystem.

Methods based on natural abundance of nitrogen stable isotopes are useful to identify and quantify the contributions of N-fixation to ecosystem nitrogen pools (Handley & Scrimgeour, 1997; Pate et al., 1993). The atmospheric $\delta^{15}N$ value is zero; soil $\delta^{15}N$ values are usually higher as a result of the deposition of organic matter enriched in ^{15}N (Ehleringer & Rundel, 1989). In our study, soil $\delta^{15}N$ values did not indicate the existence of important pools of nitrogen from biological fixation in plots with shrubs. Since significant differences were observed between the four plots in ^{15}N soil content, alterations in the ^{15}N content of litter and in the microbial activity due to the presence of shrubs and herbaceous vegetation may be expected. Changes in microbial processes such us nitrification and denitrification affect the soil nitrogen isotopic composition because nitrate is usually enriched in ^{15}N in contrast to ammonia (Pate *et al.*, 1993).

Plants living on soil nitrogen have a ^{15}N content higher than plants using biologically fixed nitrogen (Handley & Scrimgeour, 1997). The lowest $\delta^{15}N$ values were obtained in plots with only herbaceous vegetation, both for soil and plant samples. This result points out that there is not a direct transfer of fixed nitrogen between *C. striatus* and herbaceous species as has been shown for other leguminous species (Unkovich *et al.*, 1994). In contrast, $\delta^{15}N$ values observed for herbs growing in plots without shrubs indicate that they could be using the nitrogen fixed by free-living microorganisms. Poaceae and Plantaginaceae species showed consistent differences in $\delta^{15}N$ values that could be explained by differences in root architecture. The isotopic values indicate that the soil nitrogen used by Plantaginaceae is enriched in ^{15}N, which may be related to vertical differences in ^{15}N content or with the predominant use of soil nitrate instead of ammonia (Koba *et al.*, 1997). Plantaginaceae species develop deeper roots than Poaceae, thus, they could exploit different soil nitrogen sources.

Plant nitrogen content was higher in herbs growing in plots with a dense *C. striatus* canopy. Although no direct transfer was found between the shrub and the herbs, the enrichment in nitrogen could be explained by higher nitrogen content in the shrub litter that can be exploited by the herbs.

Species richness and diversity were diminished in the presence of *C. striatus*. Woody species can either increase or reduce the establishment of plant species in the understorey (Pugnaire *et al.*, 1996; Pugnaire & Lázaro, 2000; Rodríguez-Echeverría & Pérez-Fernández, 2003). Positive interactions, like facilitation, are more important in stressful environments; and negative interactions, such as competition, predominate in mesic ecosystems (Callaway & Walker, 1997). Under the climatic conditions in the study area the increased soil fertility in the understorey of *C. striatus* could lead to a greater competition between herbs, thereby, decreasing species richness and diversity (Wilson & Tilman, 1991; Foster & Gross, 1998). Other factors that can restrict herbaceous establishment are limitation in light availability imposed by the dense *C. striatus* canopy (Facelli & Picket, 1991) and phytotoxic effect of compounds released from legume litter (Frutos *et al.*, 2002). However, the presence of shrubs in this ecosystem results in diverse microenvironments that can be exploited by different plant species. The occurrence of new species associated to those microenvironments increases total richness and diversity in the ecosystem.

Herbaceous biomass in March was higher in plots without shrubs than in the other two plots. Limiting light conditions in the understorey could explain the inferior growth observed in plots with a dense shrub canopy (Grubb, 1998; Valladares, 2001). The herbaceous growth period was limited between March and May due to the poor soil quality. Apart from the problems derived from acidity, the soil has a very low capacity to store water (soil is less than 10-cm deep). Water availability decreases very quickly after rain, thereby shortening the growing season.

Competition is the most plausible explanation for the differences in herbaceous biomass observed in different plots. Although 13 botanical families were identified, Caryophyllaceae, Plantaginaceae and Poaceae account for more than 60% of the herbaceous biomass production in the ecosystem. The Plantaginaceae was the predominant group in plots without shrubs in May. This botanical family endures drought, high temperatures and direct irradiation. Asteraceae and Poaceae are better competitors in the understorey, which has more mesic conditions, higher soil fertility and reduced light. Higher water availability, as a result of higher precipitation in April, enabled Asteraceae species to displace Poaceae from the understorey of *C. striatus* in May. Plots with only one shrub displayed different vegetation patterns. No herbaceous vegetation was found in March and Caryophyllaceae species were predominant in May. Different soil physical properties in the plots where only one shrub was found must account for those divergences.

In conclusion, the presence of *C. striatus* has a negative effect on herbaceous richness and diversity in the understorey. However, patchiness due to the presence of shrubs resulted in the appearance of new species in the ecosystem. Shrubs in this ecosystem do not have a facilitation effect on plant growth in their understorey, although nitrogen content is higher for plants growing under a dense shrub canopy. The isotopic analysis indicates that herbaceous vegetation could benefit from nitrogen fixation processes not related to the legume-rhizobia symbioses.

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