Nutr Cycl Agroecosyst (2011) 90:347–354
DOI 10.1007/s10705-011-9436-2

Belowground competition for nutrients in shrub-encroached Mediterranean dehesas

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Received: 21 February 2011 / Accepted: 28 April 2011 / Published online: 12 May 2011

Abstract Managing multilayered silvopastoral systems such as Mediterranean dehesas requires the study of nutrient resource partitioning among coexisting species and determination to what extent soil nutrients are limiting plant growth. We determined the effects of NPK fertilisation maintained over two consecutive years on dry matter production and nutritional status of pasture (herbaceous) species, two shrub species and *Quercus ilex* L. in two silvopastoral sites with different shrub-layer species. We selected two prominent Mediterranean shrub species that vary in their specific ecological strategies: a N_2-fixing and sparse deep-rooting shrub (*Retama sphaerocarpa* (L.) Boiss, *Retama* site), and a dense shallow-rooting shrub (*Cistus ladanifer* L., *Cistus* site). Fertilisation significantly ($P \leq 0.05$) increased pasture dry mass by 460% and 1,090% in the *Retama* and *Cistus* sites, respectively. Nitrogen uptake by pasture species was most stimulated in both sites, and was the major limiting nutrient for this group. At the *Cistus* site, fertilisation significantly increased leaf dry mass of *Q. ilex* by 53%, but no significant effect was found at the *Retama* site. There were no significant effects of fertilisation treatments on dry mass and nutrient status of *Retama* cladodes and *Cistus* leaves. Vector analysis revealed that the magnitude of relative changes in nutrient uptake and dry matter production of pasture in response to fertilisation was markedly higher than that of *Q. ilex*, *R. sphaerocarpa* and *C. ladanifer*, suggesting high competitive ability of pasture species for soil nutrients. Results suggest that patterns of soil nutrient partitioning are site-specific and, thus, likely depend on the dominant species in the shrub layer.

Keywords *Cistus ladanifer* · Dry matter production · Native pasture · Nutrient uptake · *Quercus ilex* · *Retama sphaerocarpa* · Silvopastoral systems

Introduction

Mixing plant species in agroecosystems may result in “niche complementarity”, that is increased resource exploitation, as well as spatial and temporal partitioning of resource use by coexisting species (Hector et al. 1999). For example, Kahmen et al. (2006) showed that plant species from different functional groups may be complementary in their specific N-uptake strategies, suggesting a potentially beneficial effect of functional group diversity on ecosystem functioning. Ecological and economic benefits of

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multispecies systems relative to homogeneous pure cropping systems depend, however, on the net effects of facilitative and competitive interactions on resources use between coexisting species (Malézieux et al. 2009). To develop ecologically and economically profitable agroecosystems, it is therefore necessary to consider resource limitations, species competition for nutrients and other resources, and nutrition partitioning as affected by mobility and other nutrient properties (see reviews by Schroth 1998, and García-Barrios and Ong 2004). Here, we focused on multilayered Mediterranean dehesas as a suitable model for the study of differences in nutrient partitioning among plants belonging to different functional groups.

Dehesas are silvopastoral systems that are used by cattle, sheep, goats, pigs and horses, and are limited in their agricultural potential, owing to dry climatic conditions and low soil fertility (Gómez-Gutierrez and Pérez-Fernández 1996). Dehesas are among the most important and widespread agroforestry land-use systems in Europe (Eichhorn et al. 2006). These agroecosystems consist of scattered oaks, chiefly holm oak (*Quercus ilex* L. ssp. *ballota*), within a mosaic of grasslands, croplands and shrublands, where livestock is extensively raised. Livestock is undoubtedly the most important output of the dehesas, and its diet depends largely on pasture production. As a foundation tree species (*sensu* Ellison et al. 2005) in the dehesas, *Q. ilex* can drive vegetation dynamics and influence the distribution and abundance of many dependent community members. Shrub species develop in dehesas as a natural process resulting from the reduction in grazing pressure. These shrubs offer “safe-sites” that may promote tree regeneration (Pulido et al. 2010).

This study aimed to discern the ability of different vegetation layers to compete for different soil nutrients. We compared dry matter production and nutritional status of pasture, shrubs and trees under a no fertilisation regime and under NPK fertilisation in two farmer-designed silvopastoral sites. These study sites differed in the species that formed the shrub layer. We selected two prominent Mediterranean shrub species that vary in their specific ecological strategies and niches: a N_2-fixing and sparse deep-rooting shrub (*Retama sphaerocarpa* (L.) Boiss, hereafter *Retama*), versus a dense shallow-rooting shrub (*Cistus ladanifer* L, hereafter *Cistus*). We used vector analysis to explore the competitive ability of each vegetation layer and to speculate on long-term maintenance of pasture and tree nutrition in shrub encroached-dehesas, where low soil N availability is limiting plant growth. We hypothesised that pasture species would be more responsive to fertilisation than shrubs (*Retama* and *Cistus*) and *Q. ilex* because of the conservative nutrient-use strategies of evergreen Mediterranean trees and shrubs (Aerts 1995; Valladares et al. 2000). Based on our previous studies (Rivest et al. 2011; Rolo and Moreno 2011), we also hypothesised that the magnitude of pasture and *Q. ilex* response to fertilisation would be higher in the site encroached by the shrub “competitor” *Cistus* (i.e., contributes to increased limiting soil nutrients) than that encroached by the shrub “facilitator” *Retama* (i.e., contributes to increased N, usually the most limiting of soil nutrients).

Materials and methods

Study sites and experimental design

The study was conducted at Retortillo (39°57′ N, 6°6′ W) and San Esteban (39°56′ N, 6°11′ W) in the north of the Extremadura region of central western Spain. The climate is Mediterranean, with dry and hot summers, and cool and rainy winters. The region is characterised by an annual average temperature of 15.7°C, and 568 mm of annual precipitation (Aldehuela del Jerte station, 40°00′ N, 6°13′ W, 2000–2010 records). Monthly average air temperature and precipitation during the study (from January 2009 to July 2010) are shown in Fig. 1. Soils are loam or sandy loam Distric Cambisols (IUSS Working Group WRB 2006). Both study sites included a *Q. ilex* overstorey, a shrub layer, and a pasture understorey dominated by annual native Mediterranean herbaceous species (Fernández-Moya et al. 2010) with a weak presence of legumes. The shrub layer was composed of *Retama* at Retortillo, hereafter called the *Retama* site, and *Cistus* at San Esteban, hereafter called the *Cistus* site. Most annual species germinate in autumn, develop in early spring, and desiccate in late spring, when soil water becomes limiting. In Iberian dehesas, the mature sclerophyll *Q. ilex* typically grows in pure and low-density stands (15–45 trees ha^{-1}) and develops deep (i.e., mostly beneath roots of herbaceous species) and laterally extended root systems (Moreno et al. 2005). *Retama* is a leafless N_2-fixing shrub with photosynthetic stems (i.e., cladodes) that develops a deep-root system and grows in scattered patches (Haase et al. 1996). *Cistus* is an evergreen semi-deciduous shrub that forms dense populations, and develops shallow, dense-root systems (Silva and Rego 2004). Relevant vegetation and soil characteristics for each site are summarised in Table 1.

In each site, the experimental design compared two fertilisation treatments (unfertilised vs. fertilised) that were introduced in January 2009 and which were maintained over the next two years. The two treatments were applied in a completely randomised design. Each treatment was applied in eight plots, corresponding to a total of 16 plots in each site. Each circular plot measured ca. 315 m^2 (radius of 10 m), with a single *Q. ilex* at its centre, and a mosaic of pasture and shrub patches around. Plots were separated by buffer bands of 20–30 m width. In each year, fertilised plots received hand-applied inorganic fertiliser in January (25 kg N ha^{-1}, 21.8 kg P ha^{-1}, 62.3 kg K ha^{-1}), and March (55 kg N ha^{-1}). These fertiliser rates were chosen according to Moreno et al. (2007). All plots had not been cropped, fertilised, or tree-pruned during the 10-y period prior to this study.

Foliar sampling and analysis

Pasture was manually harvested (cut at ground level) in early June, corresponding to the peak in green biomass of 2010, to determine the effect of fertilisation on nutrient concentration and pasture dry mass. In each plot, a sample was collected in a 0.5 m × 0.5 m quadrat that was protected from livestock grazing by an exclusion cage (1 m × 1 m at the base × 0.5 m in height). Each protected quadrat was located in the subcanopy area of a randomly selected shrub, which was itself positioned in the tree canopy periphery (ca. 5 m east of the tree base). Pasture samples were oven-dried (at 65°C for 48 h) to determine dry mass.

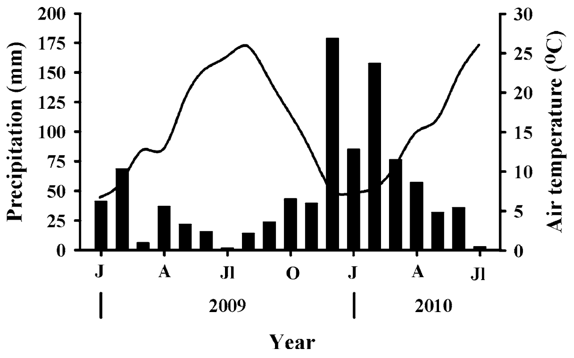

Fig. 1 Monthly average precipitation (*filled bars*) and air temperature (*line*) at the Aldehuela del Jerte station (40°00′ N, 6°13′ W) in central-western Spain. *O*, *J*, *A*, *Jl*, October, January, April, July

Current-year shrub and tree shoot samples were collected at the end of July 2010, after shoot elongation and leaf expansion had been completed, to determine the effect of fertilisation on leaf (*Q. ilex* and *Cistus*) and cladode (*Retama;* one cladode = one shoot) dry mass and nutrient concentrations. Ten shrub shoots were collected from each of four randomly selected shrub plants per plot (one per cardinal direction, totalling 40 shoots per plot). *Cistus* leaves that had been removed from twigs and *Retama* cladodes were bulked into one composite sample per plot. Forty *Q. ilex* shoots (10 per cardinal direction) were collected from the mid-crown of each sampled tree (i.e., one per plot), after which leaves were removed from twigs and bulked into one composite sample per plot. *Q. ilex* and *Cistus* foliar samples and *Retama* cladode samples were oven-dried (at 65°C for 48 h) to determine leaf dry mass per shoot and unit cladode dry mass.

Dried pasture, shrub and tree material was ground to pass a 250 µm mesh, and 0.5 g subsamples were wet-digested with H_2SO_4/H_2O_2. Nitrogen, P and K concentrations in the digest were measured by the Kjeldahl method, vanadomolybdophosphoric acid yellow method, and atomic absorption spectrometry, respectively.

Data analyses

The two sites (*Retama* and *Cistus*) were analysed independently. The effects of fertilisation treatments on dry mass, nutrient concentration and nutrient content of pasture, *Q. ilex* and *Cistus* leaves and *Retama* cladodes were tested by one-way ANOVA. When necessary, data were log-transformed to meet assumptions of normality and homoscedasticity. A P value ≤ 0.05 was considered statistically significant. All tests were performed using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA).

Table 1 Main characteristics of the Retortillo and San Esteban experimental sites in central-western Spain

	Retortillo (*Retama* site)	San Esteban (*Cistus* site)
Tree density (tree ha^{-1})	28	37
Tree canopy cover (%)[a]	20.3	18.7
Tree DBH[b]	38	39.5
Shrub species	*Retama sphaerocarpa*	*Cistus ladanifer*
Shrub height (m)	2.0	2.7
Shrub canopy cover (%)[c]	30	80
Soil texture[d]	Sandy loam (58% sand and 7% clay)	Loam (48% sand and 9% clay)
Soil pH (H_2O)	5.3	5.1
Soil organic matter (g kg^{-1})	2.0	2.5
Mineral N (g kg^{-1})	35.3	13
P-Olsen (mg kg^{-1})	8.9	12.5
K-exchangeable (meq kg^{-1})	2.4	1.8

[a] Cover estimated as the percentage of land covered by tree canopy

[b] Diameter at 130 cm height

[c] Cover estimated as the percentage of land covered by shrub canopy

[d] Soil characteristics were assessed in the 0–30 cm depth

Vector analysis was performed to diagnose the nutritional responses to fertilisation, and to identify possible nutrient conditions such as deficiency, sufficiency, dilution and antagonism. Detailed description regarding the development and use of the technique can be found in Haase and Rose (1995) and Isaac and Kimaro (2010). Briefly, the vector diagrams reflect the function that nutrient content in a plant (bottom horizontal axis) is the product of its nutrient concentration (vertical axis) multiplied by its dry mass (top horizontal axis). Changes in these variables relate to two key processes driving plant growth: nutrient uptake and dry matter production that depict differing treatment responses. Responses are expressed relative to the control (here, the unfertilised treatment) that is normalised to 100 to simplify comparisons between treatments and nutrients. Individual responses are integrated into a vector defined by its orientation and magnitude. Vector length represents response magnitude and vector direction identifies diagnostic interpretations and possible nutrient disorders (see Haase and Rose 1995).

Results

Fertilisation significantly increased pasture dry mass by 460% and 1,090% in the *Retama* and *Cistus* sites, respectively (Table 2). Fertilisation also induced a significant increase in pasture concentrations of N at both sites, P at *Retama* site and K at *Cistus* site, and increased pasture N, P, and K contents at both sites. There were no significant effects of fertilisation treatments on dry mass and nutrient status of *Retama* cladodes and *Cistus* leaves (Table 3). At the *Retama* site, fertilisation significantly decreased K concentration and content of *Q. ilex* (Table 4). Leaf dry mass and P content of *Q. ilex* also tended to be lower with fertiliser application ($P = 0.06$). At the *Cistus* site, leaf dry mass, N concentration and N content of *Q. ilex* were higher in the fertilised than in unfertilised treatment. Potassium concentration decreased in the fertilisation treatment and P concentration tended to increase ($P = 0.051$).

Vector analysis (Fig. 2; Table 2) indicated that pasture species had a N and P deficiency in the unfertilised treatment (*shift A*, positive shift in dry mass, nutrient concentration and content) at the *Retama* site ($P \leq 0.04$) and N and K deficiency at the *Cistus* site ($P \leq 0.01$). At the *Retama* and *Cistus* sites, plant uptake of N, P, and K in fertilised plots was 868–1,840%, 778–1,450%, 732–1,617% higher than in unfertilised plots, respectively (Fig. 2). This ranking and the comparison of vector length indicated that N uptake was most greatly stimulated by fertilizer application at both sites, and was probably the major pasture limiting nutrient. At the *Retama* site, K concentration and content of *Q. ilex* decreased (*shift B*, $P \leq 0.04$), which reflects a likely antagonism with another nutrient, most probably N. At the *Cistus* site, K concentration of *Q. ilex* also decreased but this occurred with gains in dry mass without significant increases in nutrient uptake, depicting dilution effects (*shift C*, $P \leq 0.003$). Nitrogen dynamics in *Q. ilex* at the *Cistus* site followed a *shift A* vector ($P \leq 0.003$), indicating an enrichment response to a nutrient deficiency. *Retama* and *Cistus* had N, P and K

Table 2 Dry mass, nutrient concentration, and nutrient content of pasture species as influenced by N, P, and K application in central-western Spain

Site	Fertilisation treatment	Pasture dry mass (g m^{-2})	Concentration (mg g^{-1})			Content (g m^{-2})		
			N	P	K	N	P	K
Retama	Fertilised	892 ± 118	27.6 ± 1.2	3.5 ± 0.5	25.5 ± 3.8	24.3 ± 3.2	3.11 ± 0.61	22.7 ± 4.7
	Unfertilised	160 ± 23	16.9 ± 0.4	2.3 ± 0.3	18.1 ± 1.9	2.8 ± 0.5	0.40 ± 0.10	3.1 ± 0.8
	P value	<0.001	<0.001	0.04	0.105	<0.001	<0.001	<0.001
Cistus	Fertilised	310 ± 91	29.5 ± 1.6	3.8 ± 0.2	32.6 ± 1.6	9.2 ± 2.2	1.16 ± 0.33	9.7 ± 2.5
	Unfertilised	26 ± 5	19.3 ± 0.5	3.1 ± 0.3	23.5 ± 2.7	0.5 ± 0.1	0.08 ± 0.01	0.6 ± 0.1
	P value	<0.001	<0.001	0.057	0.012	<0.001	0.002	<0.001

Means are followed by ± 1 SE. In each site, $n = 8$ per site and treatment

Table 3 Dry mass, nutrient concentration, and nutrient content of *Retama sphaerocarpa* cladodes and *Cistus ladanifer* leaves as influenced by N, P, and K application in central-western Spain

Site	Fertilisation treatment	Dry mass (g shoot^{-1})	Concentration (mg g^{-1})			Content (mg shoot^{-1})		
			N	P	K	N	P	K
Retama	Fertilised	2.38 ± 0.17	19.0 ± 0.4	1.15 ± 0.02	5.6 ± 0.2	45.5 ± 3.6	2.77 ± 0.23	13.4 ± 1.2
	Unfertilised	2.45 ± 0.16	17.9 ± 1.2	1.11 ± 0.05	5.3 ± 0.2	44.1 ± 4.5	2.79 ± 0.23	13.0 ± 0.9
	P value	0.764	0.39	0.748	0.333	0.812	0.936	0.776
Cistus	Fertilised	1.80 ± 0.09	11.4 ± 0.6	1.70 ± 0.08	6.1 ± 0.3	20.6 ± 1.9	3.07 ± 0.24	11.0 ± 0.8
	Unfertilised	1.72 ± 0.05	10.7 ± 0.3	1.62 ± 0.05	5.9 ± 0.1	18.4 ± 0.9	2.79 ± 0.12	10.2 ± 0.3
	P value	0.477	0.359	0.415	0.576	0.314	0.315	0.338

Means are followed by ± 1 SE. In each site, $n = 8$ per site and treatment

Table 4 Leaf dry mass, nutrient concentration, and nutrient content of *Quercus ilex* leaves as influenced by N, P, and K application in central-western Spain

Site	Fertilisation treatment	Leaf dry mass (g shoot^{-1})	Concentration (mg g^{-1})			Content (mg shoot^{-1})		
			N	P	K	N	P	K
Retama	Fertilised	0.54 ± 0.05	10.9 ± 0.4	0.80 ± 0.02	3.5 ± 0.2	5.9 ± 0.6	0.43 ± 0.05	1.9 ± 0.2
	Unfertilised	0.66 ± 0.04	10.4 ± 0.4	0.84 ± 0.04	4.2 ± 0.2	7.0 ± 0.5	0.56 ± 0.04	2.8 ± 0.2
	P value	0.056	0.384	0.297	0.025	0.195	0.058	0.011
Cistus	Fertilised	0.53	12.3 ± 0.3	0.97 ± 0.05	5.3 ± 0.2	6.4 ± 0.5	0.52 ± 0.07	2.8 ± 0.3
	Unfertilised	0.35	10.7 ± 0.4	1.16 ± 0.07	6.5 ± 0.3	3.7 ± 0.3	0.39 ± 0.03	2.3 ± 0.2
	P value	0.003	0.007	0.051	0.003	<0.001	0.097	0.111

Means are followed by ± 1 SE. In each site, $n = 8$ per site and treatment

sufficiency (i.e., no marked differences in dry mass, nutrient concentration and content, $P > 0.3$). Overall, our results revealed that the magnitude of relative changes in nutrient uptake and dry matter production of pasture species in response to fertilisation was markedly higher than those of *Q. ilex*, *Retama* and *Cistus*.

Discussion

Dehesas typically have limited growth potential because of low soil fertility (Moreno and Obrador 2007). This assumption was revealed in our study by the fact that leaf nutrient concentrations of *Q. ilex* in the unfertilised treatment were relatively low.

For instance, foliar N concentrations (10.4–10.7 mg g^{-1}) were near the lower values of the range reported by Stephan et al. (1997) for *Q. ilex* all over Europe: 9.9–21.6 mg N g^{-1}. The oaks studied here also showed low foliar P and K concentrations following ranges reported by these same authors. Our results further showed that fertilisation dramatically increased dry matter production and nutrient uptake (especially N, Fig. 2) of pasture. However, shrub species were not affected by fertilisation, and *Q. ilex* responded weakly to this treatment, with slight increases in leaf N concentrations and decreases in leaf P and K concentrations. This finding is likely the result of a higher nutrient-use plasticity potential of pasture that may enhance its nutrient competitive ability (Casper and Jackson 1997). This conjecture is supported by results from Aerts et al. (1991), who found that the deciduous grass *Molinia caerulea* had higher competitive ability at high nutrient supply than the evergreen shrubs *Erica tetralix* and *Calluna vulgaris.* In contrast, the low responsiveness of *Q. ilex*, *Retama* and *Cistus* to fertilisation in our silvopastoral systems is probably the consequence of their conserving nutrient use strategy (i.e., growth characteristics of evergreens lead to a low responsiveness to environmental change), which seems to be adaptative for evergreen woody plants in Mediterranean-type ecosystems (Valladeres et al. 2000). The latter nutrient use strategy typically leads to a low potential growth rate and a low competitive ability in nutrient-enriched soils (Aerts 1995; Chapin 1980).

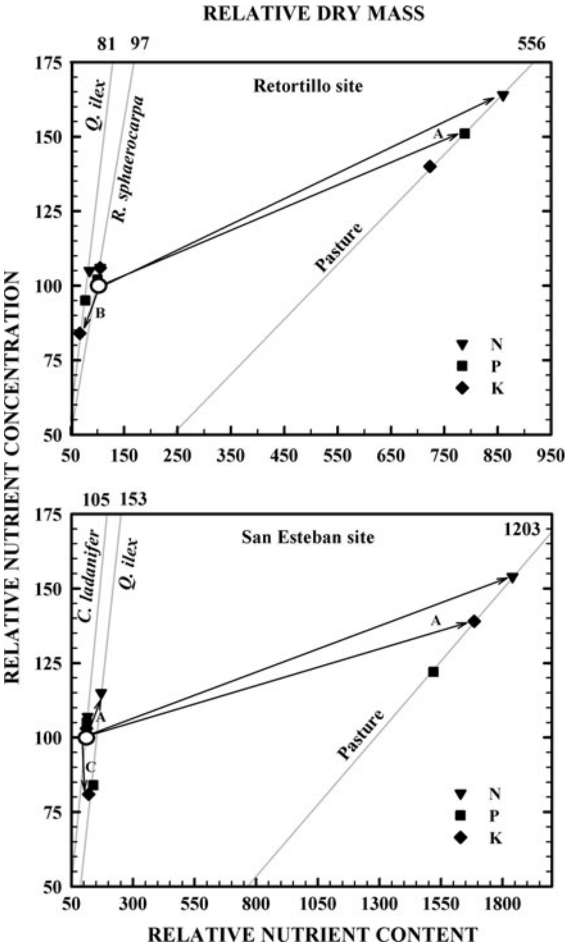

Fig. 2 Vector nutrient diagnosis of *Quercus ilex*, *Retama sphaerocarpa*, *Cistus ladanifer* and pasture species response to fertilisation at the Retortillo and San Esteban agroforestry sites in central-western Spain. All values are normalised with respect to unfertilised treatment values (set to 100), represented by the open circles. Only statistically significant vectors are depicted in each nomogram. *Shift A* vectors indicate nutrient deficiency; *shift B* vectors indicate nutrient antagonism; *shift C* vectors indicate nutrient dilution; all other points reflect nutrient sufficiency

Our previous studies offered presumptive evidence that the shallow-rooted *Cistus* may compete strongly with pasture and *Q. ilex* for belowground resources, whereas the sparse deep-rooting *Retama* may act as a plant “facilitator” (Rivest et al. 2011; Rolo and Moreno 2011). Likewise in the present study, the sign and magnitude of fertilisation effects on dry matter production of pasture and *Q. ilex* are site-specific and affected by the dominant shrub species. For example, vector analysis revealed that pasture N enrichment response to N limitation at the *Cistus* site was several orders of magnitude higher than that at the *Retama* site, where soil mineral N was higher (Table 1). The more nutrient-limited an individual is, the more its production increases in response to a large addition of the limiting nutrient (Chapin et al. 1986). Moreover, our results also highlighted that N was a major determinant of *Q. ilex* growth limitation in the unfertilised treatment at the *Cistus* site, but not at the *Retama* site. We believe this difference reflects a stronger soil N depletion potential of *Cistus* compared to the N_2-fixing *Retama*. For example, the two-year average accumulation of inorganic-N in *Retama* microsites was found to be 5.3 times higher than that in open areas lacking *Retama* (Delgado-Baquerizo et al. 2010). Foliar analyses further suggest that, of the nutrients made readily available through the addition of fertilisers (i.e., N, P and K), only N at the *Cistus* site had been taken up by *Q. ilex*. This may result from a higher mobility potential of N compared to P and K (Lehmann and Schroth 2003), combined with weak root length density of *Q. ilex* in the uppermost soil layer (i.e., low ability of *Q. ilex* to take up the less mobile P and K) (Moreno et al. 2005). *Q. ilex* had lower dry matter production (*Retama* site) and foliar K and P concentrations (both sites) in the fertilisation treatment, thereby suggesting that management practices oriented to improve soil chemical fertility may have positive effects on pasture understorey productivity and quality, but with potentially detrimental consequences for long-term productivity on tree overstorey.

A worldwide fundamental issue that currently faces extensive silvopastoral systems, including Iberian dehesas, is the progressive loss of tree cover resulting from the lack of natural tree regeneration (Gibbons et al. 2008). Shrub encroachment has been proposed as an effective means to resolve this issue and ensure the long-term persistence of dehesas (Pulido et al. 2010). Nevertheless, management of shrub-encroached silvopastoral systems remains crucial to soil nutrient dynamics and overall system productivity (i.e., sum of yields for both pasture and tree components). Our findings address this concern and suggest that a dense cover of *Cistus* may affect more severely and negatively the growth and nutrient uptake (especially N) of *Q. ilex* than scattered patches of *Retama*. Partial clearing of *Cistus* in dehesas (i.e., retaining only some patches) could be therefore a profitable means of minimising soil nutrient competition, but this approach needs further research. At the *Retama* site (richer in soil mineral-N), an important pasture limitation in N (and other nutrients) indicated a limited capacity of the N_2-fixing *Retama* to supply N to pasture understorey (Rodríguez-Echeverría and Pérez-Fernández 2003). Future research is needed to compare the effects of several fertilisers with varying solubility and composition on growth and nutrition of pasture and trees in dehesas that differ in soil fertility and shrub species understory composition. This would help our understanding of the nutrient foraging ability of different co-occurring plants in multilayered silvopastoral systems, and planning of fertilisation regimes that may optimise pasture and tree productivity.

Acknowledgments The project was supported financially by the Spanish Ministerio de Ciencia e Innovación (project MODE, AGL2006-09435/FOR) and the plan regional de Investigación de la Junta de Extremadura (III PRI+D+I, PRI07C044). David Rivest was awarded a postdoctoral research grant from the Fonds québécois de recherche sur la nature et les technologies (FQRNT). Víctor Rolo was supported by a doctoral grant funded by the Regional Government of Extremadura and the Fondo Social Europeo. We thank Antonio Garcia for technical assistance, and William F.J. Parsons and Miren Lorente for improving the language of this paper.

References

Aerts R (1995) The advantages of being evergreen. Trends Ecol Evol 10:402–407

Aerts R, Boot RGA, van der Aart PJM (1991) The relation between above- and belowground biomass allocation patterns and competitive ability. Oecologia 87:551–559

Casper BB, Jackson RB (1997) Plant competition underground. Ann Rev Ecol Syst 28:545–570

Chapin FS III (1980) The mineral nutrition of wild plants. Ann Rev Ecol Syst 11:233–260

Chapin FS III, Vitousek PM, Van Cleve K (1986) The nature of nutrient limitation in plant communities. Am Nat 127:48–58

Delgado-Baquerizo M, Castillo-Monroy AP, Maestre FT, Gallardo A (2010) Plants and biological soil crusts modulate the dominance of N forms in a semi-arid grassland. Soil Biol Biochem 42:376–378

Eichhorn MP, Paris P, Herzog F, Incoll LD, Liagre F, Mantzanas K, Mayus M, Moreno G, Papanastasis VP, Pilbeam DJ, Pisanelli A, Dupraz C (2006) Silvoarable systems in Europe -past, present and future prospects. Agrofor Syst 67:29–50

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 9:479–486

Fernández-Moya J, San Miguel-Ayanz A, Cañellas I, Gea-Izquierdo G (2010) Variability in Mediterranean annual grassland diversity driven by small-scale changes in fertility and radiation. Plant Ecol. doi:10.1007/s11258-010-9869-8

García-Barrios L, Ong CK (2004) Ecological interactions, management lessons and design tools in tropical agroforestry systems. Agrofor Syst 61:221–236

Gibbons P, Lindenmayer DB, Fisher J, Manning AD, Weinberg A, Seddon J, Ryan P, Barrett G (2008) The future of scattered trees in agricultural landscapes. Conserv Biol 22:1309–1319

Gómez-Gutierrez JM, Pérez-Fernández M (1996) The dehesas, silvopastoral systems in semiarid Mediterranean regions with poor soils, seasonal climate and extensive utilisation. In: Étienne M (ed) Western European silvopastoral systems. INRA Editions, Paris, pp 55–70

Haase DL, Rose R (1995) Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. For Sci 41:54–66

Haase P, Pugnaire FI, Fernández EM, Puigdefábregas J, Clark SC, Incoll LD (1996) An investigation of rooting depth of the semiarid shrub *Retama sphaerocarpa* (L.) Boiss. by labelling of ground water with a chemical tracer. J Hydrol 177:23–31

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras A-SD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127

Isaac ME, Kimaro AA (2010) Diagnosis of nutrient imbalances with vector analysis in agroforestry systems. J Environ Qual. doi:10.2134/jeq2010.0144

IUSS Working Group WRB (2006) World reference base for soil resources 2006, 2nd edn. World Soil Resources Reports No. 103. FAO, Rome

Kahmen A, Renker C, Unsicker S, Buchmann N (2006) Niche complementarity for nitrogen: an explanation for the biodiversity and ecosystem functioning relationship? Ecology 87:1244–1255

Lehmann J, Schroth G (2003) Nutrient leaching. In: Schroth G, Sinclair FL (eds) Trees, crops and soil fertility: concepts and research methods. CABI publishing, Wallingford, pp 151–166

Malézieux E, Crozat Y, Dupraz C, Laurans M, Makowski D, Ozier-Lafontaine H, Rapidel B, de Tourdonnet S, Valantin-Morison M (2009) Mixing plant species in cropping systems: concepts, tools and models. A review. Agron Sustain Dev 29:43–62

Moreno G, Obrador JJ (2007) Effects of trees and understorey management on soil fertility and nutritional status of holm oaks in Spanish dehesas. Nutr Cycl Agroecosyst 78:253–264

Moreno G, Obrador J, Cubera E, Dupraz C (2005) Fine root distribution in dehesas of Central-Western Spain. Plant Soil 277:153–162

Moreno G, Obrador JJ, García A (2007) Impact of evergreen oaks on soil fertility and crop production in intercropped dehesas. Agric Ecosyst Environ 119:270–280

Pulido F, García E, Obrador J, Moreno G (2010) Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. J Appl Ecol 47:1272–1281

Rivest D, Rolo V, López-Díaz L, Moreno G (2011). Shrub encroachment in Mediterranean silvopastoral systems: *Retama sphaerocarpa* and *Cistus ladanifer* induce contrasting effects on pasture and *Quercus ilex* production. Agric Ecosyst Environ (in press)

Rodríguez-Echeverría S, Pérez-Fernández MA (2003) Soil fertility and herb facilitation mediated by *Retama sphaerocarpa*. J Veg Sci 14:807–814

Rolo V, Moreno G (2011) Shrub species affect distinctively the functioning of scattered *Quercus ilex* trees in Mediterranean open woodlands. For Ecol Manag 261:1750–1759

Schroth G (1998) A review of belowground interactions in agroforestry, focusing on mechanisms and management options. Agrofor Syst 43:5–34

Silva JS, Rego FC (2004) Root to shoot relationships in Mediterranean woody plants from Central Portugal. Biologia 59:109–115

Stephan K, Fürst A, Hacker R, Bartels U (1997) Forest foliar conditions in Europe—results of large-scale foliar chemistry surveys, 1995. EC, UN/ECE, Brussels/Geneve

Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E, Manrique E (2000) Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol 148:79–91