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Alma M. García-Moreno, María D. Carbonero-Muñoz, María Serrano-Moral, Pilar Fernández-Rebollo. Grazing affects shoot growth, nutrient and water status of *Quercus ilex* L. in Mediterranean open woodlands. *Annals of Forest Science*, 2014, 71 (8), pp.917-926. 10.1007/s13595-014-0397-x . hal-01102966

HAL Id: hal-01102966

<https://hal.science/hal-01102966>

Submitted on 13 Jan 2015

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Grazing affects shoot growth, nutrient and water status of *Quercus ilex* L. in Mediterranean open woodlands

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Received: 2 April 2014 / Accepted: 9 June 2014 / Published online: 27 June 2014
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Abstract

• **Context** Mediterranean open woodlands (dehesa) have faced a dual process of intensification and abandonment of grazing which has resulted in alteration of the understory vegetation.
• **Aims** We analysed the effects of land use changes on the physiological status of holm oak in different open woodlands (dehesa) in southern Iberian Peninsula.
• **Methods** In an area of extensive grazing, we selected six paired plots (one grazed, one abandoned) and grouped them by habitat types according to understory composition (nearly all monospecific *Cistus ladanifer* L. shrub or mixed shrub). Six plots of moderate and heavy grazing intensity were chosen within a settled area of livestock use. Shoot growth, macro-nutrient concentrations and water content were assessed in samples of holm oak leaves.

• **Results** Abandonment of grazing affected some nutrient concentrations and water content of holm oak leaves, but the effects were different according to habitat type. *C. ladanifer* shrub reduced N and P concentrations and water content while mixed shrub increased P concentration and water content. High grazing intensity improved shoot growth and leaf N and Mg concentrations.
• **Conclusion** Extensive grazing could be a useful management tool to enhance growth, nutritional and water status of holm oak in a habitat with limited resources such as Mediterranean open woodlands (dehesa).

Keywords Holm oak · Leaf nutrient concentrations · Water content · Shoot length · Dehesa

Handling Editor: Gilbert Aussenac

Contribution of the co-authors P. Fernández-Rebollo conceived the idea. A. García-Moreno, M.D. Carbonero-Muñoz and M. Serrano-Moral performed the field samplings and laboratory measurements. A. García-Moreno and P. Fernández-Rebollo analysed the data and wrote the paper.

Executive summary The abandonment of grazing in Mediterranean open woodland enhances or makes worse the habitat for trees, depending on shrub species involved in encroachment process. In areas with ancient livestock use, tree growth and leaf N concentration increase with grazing intensity.

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1 Introduction

Quercus trees are widespread in many types of woodland in the Northern Hemisphere. In the Mediterranean basin, the sclerophyllous evergreen holm oak (*Quercus ilex* L.) is a common species which is found over an area extending from Portugal to Syria and from Morocco and Algeria to France. The holm oak is widespread in the Iberian Peninsula and is the dominant species in open woodlands (known as dehesa in Spain and montado in Portugal).

Like other *savanna* ecosystems in the world (McPherson 1997), the Mediterranean open woodland in the Iberian Peninsula is the result of human intervention in denser natural woodlands, by eliminating trees and shrubs to facilitate grazing, acorn production and occasional cereal and legume crops. Hence, the vegetation in this ecosystem consists of two distinct layers: a tree layer and a pasture or crop understory. The main land use is for livestock (sheep, cattle and Iberian pigs), which are mainly fed on the pasture and crops. These woodlands also provide forest products, such as firewood and cork

(where *Quercus suber* L. is present), as well as game for hunting (Moreno and Pulido 2009). In order to prevent shrub encroachment, Mediterranean open woodland requires constant human intervention. Although periodic ploughing and cropping are common practices to avoid shrub encroachment, livestock are the main tool used for preventing shrubs from colonizing the pasture.

Over the last few decades, Mediterranean open woodlands have faced a dual process of intensification and abandonment, due to the socioeconomic changes occurring in most European countries. For example, cattle have gradually replaced sheep as the main livestock in open woodlands in the Iberian Peninsula, mainly as a consequence of the higher labour demand required for sheep farming together with the drastic fall in the price of wool. Nowadays, this change is reflected in the livestock census, where sheep flocks have fallen by over 20 % in the last 10 years, while cattle herds have increased (Gaspar et al. 2007). Furthermore, as a result of reforms in the European Common Agricultural Policy, a noticeable increase in the stocking rate has taken place in many areas. On the other hand, open woodlands located in marginal areas have been abandoned, and these areas are now grazed by wild animals instead of livestock. This dual process of intensification and abandonment of grazing, which can even coexist on a local scale, has resulted in a change in the structure, composition and production of the vegetation.

Trees, the key element of the Mediterranean open woodland, have been affected by these changes in land use, in addition to the problems they face from climate change. Several studies have analysed the effect of land use changes on different areas of oak open woodland, focusing mainly on vegetation structure (Ramírez and Díaz 2008; Strandberg et al. 2005), floristic composition of pasture (Peco et al. 2006; Tárrega et al. 2009), tree regeneration (Pulido et al. 2010) and soil quality (Gómez-Rey et al. 2013; Seddaiu et al. 2013; Strandberg et al. 2005). However, less information is available about the effects of land use changes on the status of mature holm oaks.

The abandonment of grazing encourages the invasion of shrubs, which eventually replace the pasture. In areas where marginal shrub patches are dominated by *Cistus* species, a decrease in grazing leads to a rapid encroachment of shrubs (Ramírez and Díaz 2008; Tárrega et al. 2009), thus reducing the diversity of vegetation (Peco et al. 2006). Nevertheless, this encroachment process may occur slowly if more shrub species are present. The introduction of a new layer of woody vegetation in open woodlands can alter the physiological status of mature holm oak and boost its chances of its survival. Moreover, when widespread encroachment occurs, the persistence of adult trees in these ecosystems can be threatened, in spite of the beneficial effects of shrubs in helping seedling and sapling survival through nursing effects (Pulido et al. 2010). Several authors have described how shrub-tree interactions can reduce the opportunities for existing trees (Silva and Rego

2003; Cubera and Moreno 2007), due to competition for soil nutrients and water in semiarid environments. Experimental evidence supports the assumption that water limitations affect tree nutrient levels (Sardans et al. 2008). Other studies emphasize the ability of shrub species to alter soil environment directly through the production of toxin or allelopathic compounds (Chaves and Escudero 1997; Dias et al. 2010) or by indirectly affecting microclimatic conditions (Pulido et al. 2010). Nevertheless, there is a general consensus over the fact that the nature and degree of shrub-tree interactions depend largely on the species (Rolo et al. 2012).

The increase in grazing intensity and the intensification of livestock systems in open woodlands prevent shrub invasion and may improve soil fertility and the production and quality of pasture, as occurs in other pastoral systems (Augustine and McNaughton 2006). With better soils and a separate rooting-niche for both functional groups—pasture and tree (Moreno and Pulido 2009)—holm oaks may also improve their nutritional, physiological and productive status. Nevertheless, soil degradation due to overgrazing has been widely reported in temperate and semiarid pastures (Greenwood and McKenzie 2001; Drewry et al. 2008), and this degradation may lead to decreased holm oak growth and production. Therefore, the status of the holm oak in this situation depends on the net result of multiple interactions which rely mainly on farming practices.

In order to clarify the effects of these land use changes on trees, we analysed the shoot growth, nutrient and water status of holm oak leaves in different areas of open woodland in the southern Iberian Peninsula. We chose two areas of open woodland: the first area, stretching across north-western Andalusia, is a good example of the process of abandonment, whereby patches of open woodland subject to low-intensity grazing over a long period of time are interspersed with areas which are rarely grazed and hence have a dense shrub understory. We expected shrub-tree interaction to be dependent on shrub type (Rolo et al. 2012), and so we selected two types of habitats according to the shrub composition: nearly monospecific *Cistus ladanifer* L. or mixed shrubland. The second area, a smaller area located in the north of Andalusia, represents intensified open woodland whose pasture understory has been continuously grazed by livestock at different intensities over a long period of time. Using this framework, we hypothesized that moderate grazing increases soil nutrient availability, which could enrich the nutrient status and tree growth, but that heavy grazing may have an adverse effect. We therefore posed the following specific questions: (i) what impact shrub encroachment, through the abandonment of grazing, has on leaf-level macronutrient concentrations and water content of holm oak and whether this tree response is mediated by shrub type and (ii) what the impact of grazing intensity is on shoot growth and leaf macronutrient concentrations of holm oak.

2 Materials and methods

2.1 Study area and experimental layout

The study was conducted on different *dehesa* farms located in Andalusia (South-western Spain, 37° 72'–38° 25' N, 04° 18'–07° 11' W). The climate of the area is Mediterranean with hot, dry summers and mild, rainy winters. The soils are slightly thick, oligotrophic and acidic (IUSS Working Group 2006). Some features of the soils, climate and vegetation of the area studied are shown in Table 1. The vegetation of these farms is characterized by scattered adult trees at the top layer, where holm oak (*Quercus ilex* L.) is the dominant species. The understory consists of natural pasture of herbaceous annuals or shrubs.

Two samplings were carried out. For the first one, we evaluated the effect of the abandonment of grazing on water and nutrient concentrations of holm oak leaves. Six *dehesa* farms (A–F) located in the provinces of Cordoba, Huelva and Seville were selected. On each farm, two adjacent plots with similar soil, slope and tree coverage but with different land use were selected: grazed areas (native pasture+holm oak) and abandoned areas (shrub species+holm oak). Farms were grouped into two habitat types according to the shrub composition of the abandoned area: *Cistus* shrub, consisting of nearly all monospecific *C. ladanifer* L. shrub, found on farms A, B and C; and mixed shrub, composed mainly of *Quercus coccifera* L. and *Pistacia lentiscus* L., with presence of *Rosmarinus officinalis* L. and *Cistus* spp. found on farms D, E and F (Table 1). In the second sampling, we evaluated the effect of grazing intensity on the nutrient status of the holm oak leaves and shoot growth. An area of open woodland (named G in Table 1) was selected in the district of Los Pedroches (northern Andalusia, Spain). This site covers an area of about 840 km² with similar climatology. The soils are shallow and slightly acidic with a sandy texture (with abundant granite and quartz rocks). Twelve plots (paddocks) used for cattle, pig and sheep rearing were selected in this area: six with high intensity and six with moderate intensity of grazing. The allocation of grazing intensity tallied with the farm stocking rate data: around 1.2 livestock unit (LU) per ha in the first group and 0.4 LU per ha in the second group.

2.2 Sampling protocol

In the first sampling, 10 holm oaks were selected in each plot. A sample of leaves was collected from each tree in July (six farms×two types of land use×10 trees=120 leaf samples). Each sample consisted of 30 fully expanded mature leaves, without impurities or symptoms of pathogens or defoliators. Several branches were cut from the south-facing side of the tree at the middle section of the crown. The leaves were collected from the middle section of the current season's shoot

growth. The leaf samples were stored in plastic containers (100 ml), sealed with Parafilm and placed in a portable cooler ready for processing in the laboratory.

In the second sampling, seven holm oaks were selected in each plot, and a sample of leaves was collected from each tree in October (12 plots×seven trees=84 leaf samples), following the same methodology described above. The length of 10 current-year shoots was measured in each tree as an indicator of tree growth. In addition, one composite soil sample was collected per plot to a depth of 0–15 cm in open spaces (10 subsamples per sample). Soil penetration resistance (cone Index, hereafter CI) was evaluated using a cone penetrometer with a fine tip (cone diameter 12.6 mm, tip angle 30° and rod diameter 9.5 mm) following the recommendations established by standard ASAE S313.2 for soils with high mechanical impedance. Twenty CI measurements per plot were taken in the open spaces, to a depth of 5 cm at intervals of 0.5 cm. The CI measurements were then averaged to produce a single mean value per plot.

2.3 Analytical procedures

Leaf samples collected in both samplings were air-dried at 65 °C until the constant weight was reached, and then were ground in a stainless steel grinder to determine their total contents of N, P, Ca, Mg and K. N content was determined by the Kjeldahl method after the dry-ashing digestion method, P by the yellow colour method using vanadomolybdophosphoric acid, Ca and Mg by atomic absorption spectrometry and K by flame emission spectrometry. Leaf water content (hereafter, WC) was determined in the leaf samples collected in the first sampling according to the expression $WC = ((FW - DW) / DW) \times 100$, where FW is the fresh weight and DW is the dry weight, obtained after air-drying at 65 °C until the constant weight was reached. The soil samples were air-dried, sieved (2 mm) and analysed: soil texture percentage (clay, sand and silt), pH, soil organic matter (SOM) (by Walkley and Black method), available P (by Olsen), organic N (by Kjeldahl), cation exchange capacity (CEC) (1.0 M ammonium acetate, pH 7.0), and exchangeable base cations (1.0 M ammonium acetate extraction and flame emission spectrometry for Na and K, atomic absorption spectrometry for Ca and Mg). Percent base saturation (%BS) was calculated by multiplying the sum of the extractable bases by 100 and dividing it by the CEC.

2.4 Statistical analysis

In the first sampling, the mean values of leaf nutrient concentrations (N, P, K, Ca and Mg) and WC were compared in each habitat type by a factorial ANOVA with land use and farm as fixed and random factors, respectively. In addition, a principal components analysis (PCA) was performed to extract the

Table 1 Characteristics of the areas studied which include identifying letters for each farm, location, soil classification, topography of sampling area, annual rainfall (mm) and mean annual temperature (°C) of the nearest weather station (Red RIA, IFAPA), understory type according with land use (grazed areas/abandoned areas) and shrub composition (*Cistus* shrub/mixed shrub), shrub cover (%) and tree density (tree per hectare)

Farm	Site	Soil type	Topography	Annual rainfall	Mean annual temperature	Understory type	Shrub cover	Tree density
A	38° 7' N, 4° 31' W (Córdoba)	Regosol, Lithosol	Level	575	17	Grazed area: pasture (annual herbaceous species) Abandoned area: <i>Cistus</i> shrub (<i>Cistus ladanifer</i> , <i>C. albidus</i> , <i>C. crispus</i>)	–	30
B	37° 42' N, 7° 11' W (Huelva)	Cambisol, Eutric Regosol	Level	380	16	Grazed area: pasture (annual herbaceous species) Abandoned area: <i>Cistus</i> shrub (<i>Cistus ladanifer</i> , <i>C. monspeliensis</i>)	–	26
C	37° 57' N, 6° 31' W (Huelva)	Regosol, Lithosol	Undulating	420	16	Grazed area: pasture (annual herbaceous species) Abandoned area: <i>Cistus</i> shrub (<i>Cistus ladanifer</i>)	–	21
D	37° 52' N, 5° 12' W (Córdoba)	Cambisol, Eutric Regosol	Undulating	468	18	Grazed area: pasture (annual herbaceous species) Abandoned area: mixed shrub (<i>Pistacia lentiscus</i> L., <i>Phillyrea angustifolia</i> L., <i>Quercus coccifera</i> L., <i>Cistus</i> spp., <i>Rosmarinus officinalis</i> L.)	75	25
E	37° 57' N, 5° 32' W (Sevilla)	Cambisol, Eutric Regosol	Undulating	610	17	Grazed area: pasture (annual herbaceous species) Abandoned area: mixed shrub (<i>Quercus coccifera</i> L., <i>Pistacia lentiscus</i> L., <i>Lavandula stoechas</i> , <i>Rosmarinus officinalis</i> L., <i>Cistus</i> spp.)	–	31
F	37° 59' N, 5° 43' W (Sevilla)	Cambisol, Eutric Regosol	Undulating	646	17	Grazed area: pasture (annual herbaceous species) Abandoned area: mixed shrub (<i>Cistus</i> spp., <i>Quercus coccifera</i> L., <i>Pistacia lentiscus</i> L., <i>Lavandula stoechas</i> L.)	65	33
G (12 plots)	38° 15'–38° 25' N, 4° 18'–4° 41' W (Córdoba)	Eutric Cambisol	Level	756	15	Grazed area: pasture (annual herbaceous species)	–	28
							85	29
							–	26/43 ^a

^a Minimum/maximum tree density in sampling in 12 plots

main variables involved in the dissimilarity between habitats and land uses. Average leaf concentrations of N, P, K, Ca and Mg and WC per plot were included in the PCA.

In the second sampling, the effects of grazing intensity and plot on leaf nutrient concentrations and shoot length were assessed through a nested ANOVA, in which the plot was a random factor nested in grazing intensity. Moreover, the effects of grazing intensity on soil properties were assessed by a one-way ANOVA. Normality was checked by the Shapiro-Wilk test and homoscedasticity by the Levene test. When these conditions were not fulfilled, the values were transformed logarithmically [$\ln(x+1)$]. Fisher's test was applied for post hoc comparisons when ANOVA was significant ($p \leq 0.05$). Finally, the relationships between nutrients in leaves and soil were analysed by Pearson's correlation coefficient. All statistical analyses were performed using the STATISTICA v 6.0 software.

3 Results

3.1 Effects of land use and types of shrub understory on leaf nutrient concentrations and water status

Significant differences were found in leaf N concentration and WC between land uses in *Cistus* shrub habitat (Table 2). Trees in abandoned areas showed lower leaf N concentration and WC than trees in grazed areas (Fig. 1). Foliar K, Ca and Mg concentrations were not affected by land use. Foliar P concentration decreased in abandoned areas, although differences were only found on one farm, where the interaction between farm and land use factors was significant. As regards the mixed shrub habitat, significant differences were found in leaf

P concentration and WC between land uses, but unlike the former case, the lowest values were found in grazed areas. Foliar K, Ca, Mg and N concentrations were not affected by land use, and interactions between factors were not found.

The PCA extracted two principal components representing 69 % of the variances in the nutrient and water status of the leaves. Variables with significant loadings on PC1 were WC ($R^2=0.80$), Ca ($R^2=0.78$) and Mg ($R^2=-0.71$), while N ($R^2=-0.78$) had a negative loading on PC2 (Fig. 2). P and K leaf concentrations also contributed to the PC1 and PC2 definitions, although these were only marginally significant. The plot scores in PC1 (Fig. 2) showed that negative values were obtained for farms A, B and C, included in the *Cistus* shrub habitat, while positive values were obtained for farms D, E and F included in the mixed shrub habitat. Differences were observed in PC2 in plots of the *Cistus* shrub habitat according to land use, where abandoned plots were separated from grazed plots. However, plots in the mixed shrub habitat did not show any differences in land use.

3.2 Effect of grazing intensity on leaf nutrient concentrations and shoot length

The analysis of the variances revealed that CEC, SOM content, available P, organic N, exchangeable base cations K^+ and Ca^{2+} and CI were significantly different according to grazing intensity (Table 3). Also, the pH showed a marginally significant difference. Soil texture and exchangeable base cations Mg^{2+} and Na^+ were similar for both groups.

Pearson's correlations between leaves and topsoil nutrients were not significant in any cases (data not shown). Grazing intensity had an effect on the concentrations of some leaf macronutrients (Fig. 3, Table 4). N

Table 2 Results from a factorial ANOVA testing the effect of land use (grazed areas/abandoned areas), as fixed factor, and farm, as random factor, on foliar nutrient concentrations and water content (WC) of holm oak in two habitat types (*Cistus* shrub/mixed shrub)

	d.f.	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	WC
<i>Cistus</i> shrub							
Farm	2	2.08	2.83	3.68	6.40**	4.85*	2.13
Land use	1	40.87**	6.92*	0.02	0.25	3.19	6.57*
Farm×land use	2	0.05	4.49*	1.22	5.72	2.70	1.17
Mixed shrub							
Farm	2	0.91	4.95*	6.00**	2.11	19.06**	2.67
Land use	1	0.95	4.52*	0.16	1.32	0.02	10.08**
Farm×land use	2	0.91	1.39	2.41	0.75	0.27	2.69

F values are shown

* $p < 0.05$, significant difference

** $p < 0.01$, significant difference

Fig. 1 Mean values (\pm SE) of nutrient concentrations and water content in leaves of holm oak comparing land use (grazed areas/abandoned areas) in two habitat types (*Cistus* shrub/mixed shrub)

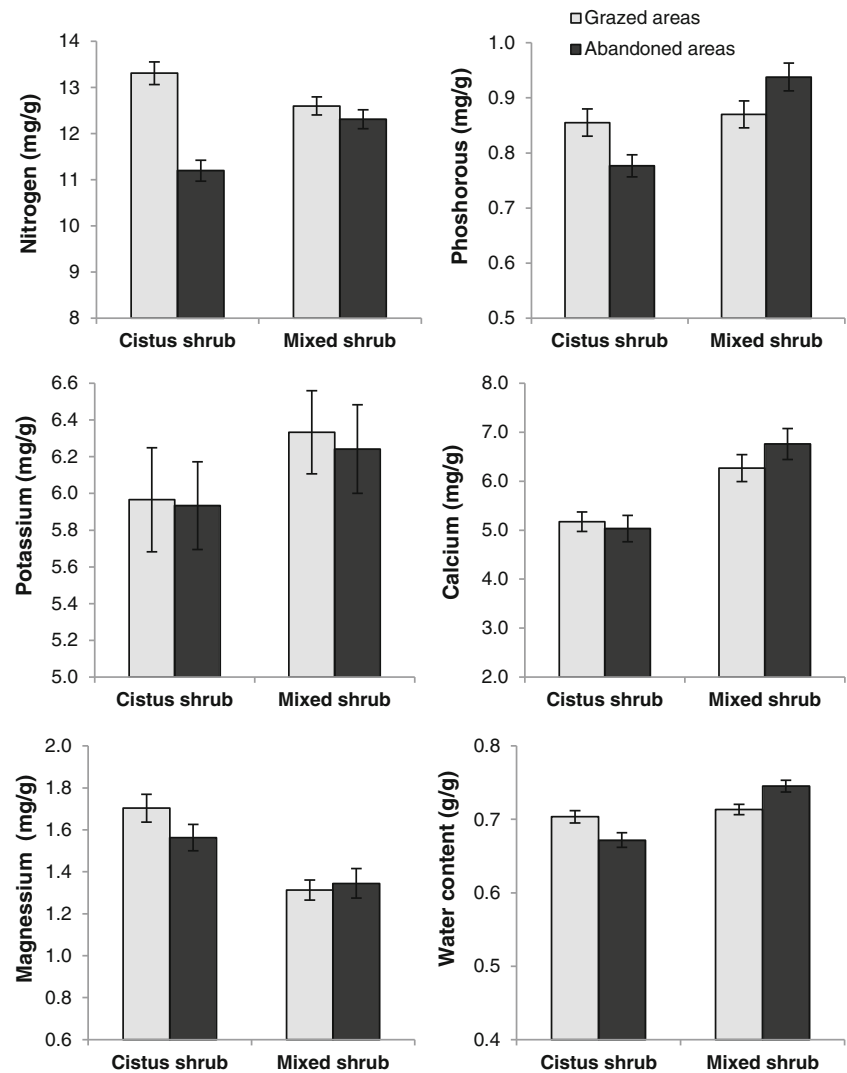


Fig. 2 Loading and score plots of principal components analysis performed with foliar nutrient concentrations (N, P, K, Ca and Mg) and foliar water content (WC) of holm oak in 12 plots within two habitat types (*Cistus* shrub/mixed shrub) and with different land use (grazed areas/abandoned areas)

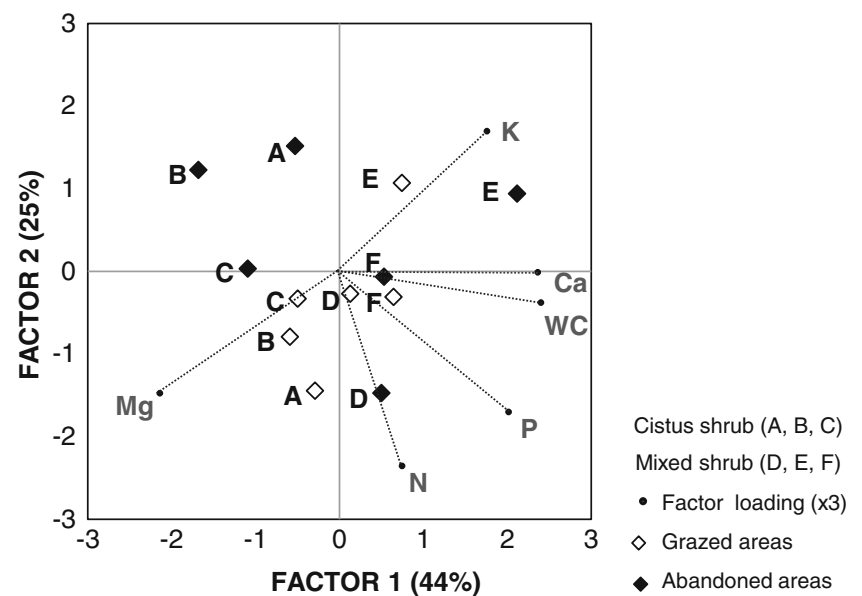


Table 3 Mean values (\pm SE) of soil properties according to grazing intensity (moderate/high) and results of one way ANOVA testing the effect of grazing intensity on soil properties in open woodlands with a long history of livestock use

	Grazing intensity				<i>F</i>	<i>p</i>
	Moderate		High			
CI (MPa)	2.15	± 0.18	2.82	± 0.10	10.59	<0.01
% Clay	5.4	± 0.4	6.1	± 0.4	1.51	0.24
% Sand	80.1	± 1.4	78.3	± 1.1	1.05	0.32
% Silt	14.4	± 1.3	15.6	± 1.2	0.44	0.52
pH	5.50	± 0.11	5.85	± 0.13	4.10	0.07
SOM (g/kg)	19.26	± 1.92	31.18	± 3.53	8.71	<0.01
Available P (mg/kg)	6.9	± 1.1	20.2	± 4.16	11.08	<0.01
CEC (meq/kg)	74.9	± 3.8	104.7	± 5.3	20.59	<0.01
K ⁺ (meq/kg)	2.9	± 0.2	5.2	± 0.6	10.48	<0.01
Ca ²⁺ (meq/kg)	31.7	± 2.5	45.2	± 3.5	9.83	<0.01
Mg ²⁺ (meq/kg)	23.0	± 2.6	20.3	± 2.7	0.51	0.48
Na ⁺ (meq/kg)	3.1	± 0.3	3.5	± 0.3	1.39	0.26
Organic N (g/kg)	0.75	± 0.05	1.20	± 0.18	5.76	0.04
% BS	81	± 5.69	71	± 2.55	2.79	0.12

Exchangeable cations: K, Ca, Mg and Na

CI cone index, SOM soil organic matter, CEC cation exchange capacity, BS base saturation percentage

and Mg concentrations in leaves were significantly higher in trees growing in heavily grazed plots. Mg concentrations showed significant differences between plots with similar grazing intensity, which were less significant than between the different groups of grazing intensity. However, Ca, K and P concentrations were not affected by grazing intensity, but there were differences in foliar P concentrations between plots within the same grazing intensity. Shoot length was significantly lower in trees from plots with moderate grazing, in spite

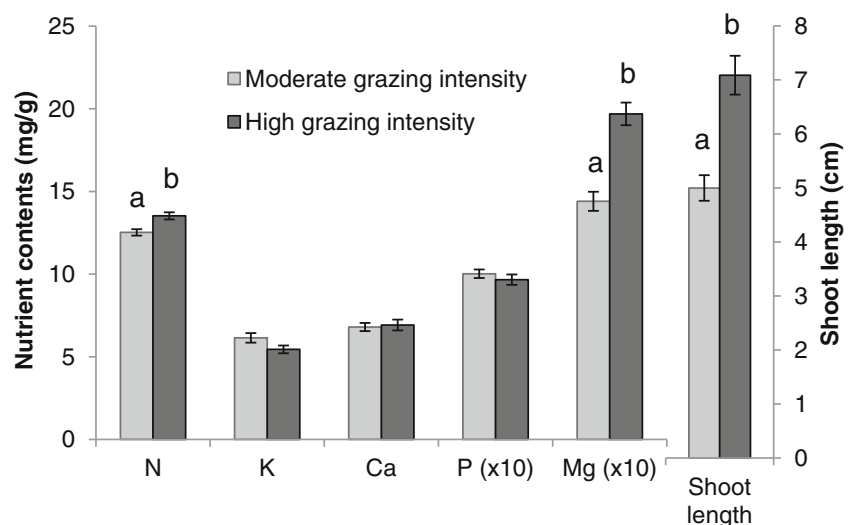
Table 4 Results from a nested ANOVA design testing the effect of grazing intensity (moderate/high), as fixed factor, and plot, as random nested factor, on foliar nutrient concentrations and shoot length of holm oak in open woodlands with a long history of livestock use

Nutrients	Grazing intensity		Plots (grazing intensity)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
N	12.89	<0.01	1.82	0.07
P	1.28	0.26	2.64	<0.01
K	3.01	0.08	1.47	0.17
Ca	0.13	0.71	1.41	0.19
Mg	40.09	<0.01	1.99	0.04
Shoot length	31.88	<0.01	3.03	<0.01

of the fact that shoot length showed significant differences between plots with a similar grazing intensity.

4 Discussion

The functioning of the holm oak in Mediterranean open woodlands is dictated by the environment in which the trees are established, where climate and soil are the main forces that determine its growth pattern. In our study, the first PCA axis performed on all the leaf nutrients and water content seems to reflect the environmental conditions of the farm, distinguishing trees that grow in different types of habitat. Farms with a mixed shrub habitat showed higher rainfall (average value 574 mm) and more fertile soils (Cambisols and Eutric Regosols) than farms with a *Cistus* shrub habitat, which had less rainfall (average value 458 mm) and more restrictive soils (Lithosols). Therefore, trees are expected to perform better in the first habitat. Better environmental

Fig. 3 Mean values (\pm SE) of foliar nutrient concentrations and shoot length of holm oak according to grazing intensities (moderate/high) in open woodlands with a long history of livestock use

conditions were linked to leaf Ca concentration and water content. Because the movement of Ca in plants is mainly driven by transpiration flow and is seldom redistributed after its deposition in tissues, Ca concentration must consequently be high in tissues with a high transpiration rate and a long growth period (Yang and Jie 2005). However, more restrictive environments seem to be associated with Mg concentration at leaf level. According with this, in an experiment carried out in a holm oak forest, Sardans et al. (2008) reported a difference in Mg leaf concentration after a period of induced drought. Nevertheless, these authors argued that it was difficult to discern whether the increase in Mg concentration was a plant response to drought or a result of decreased soil fertility.

Nevertheless, within an environment, land use may affect the availability of nutrients for trees through the changes in the structure and composition of vegetation and in soil fertility. In this regard, the second PCA axis seems to discriminate trees according to land use, but only in the *Cistus* shrub habitat. The concentration of foliar N was the main nutrient which reflected the holm oak's response to the abandonment of grazing in this habitat. There are several possible explanations for this outcome. Firstly, *C. ladanifer*, in this case the dominant species in abandoned areas, has a strong ability to transform its surrounding environment through allelopathic compounds, which reduces the density and diversity of plant species in the communities where it grows (Chaves and Escudero 1997). Several studies have reported a negative effect of polyphenols included in allelopathic substances on net nitrification (Erickson et al. 2000) and N mobilization (Schimel et al. 1996), and this reduces N availability for vegetation. Hence, the effects of *C. ladanifer* on the dynamics of soil N could explain the lower leaf N concentration found in holm oaks in plots without grazing. In this regard, Dias et al. (2010) showed that the increase in soil N makes the encroachment of *C. ladanifer* more difficult. Secondly, grazing may accelerate the cycle of N, increasing the size of the inorganic N pool available to plants at the onset of the growing season (Peco et al. 2006; Augustine and McNaughton 2006), which explains the results found in grazed areas on farms belonging to the *Cistus* shrub habitat. However, no differences were found in leaf N concentration owing to land use in a mixed shrub habitat, which suggests that grazing may have little effect on soil N availability in some sites or, alternatively, that mixed shrubs may have a positive effect on the soil N pool. As regards the effect of the grazer, Ritchie et al. (1998) found that herbivores may decrease the rate of N cycling, depending on the type of resources that limits plant growth. If plant growth is limited by N and dominant species have low N-tissues, herbivores may slow the cycle of this nutrient, while may accelerate it when the dominant species have tissues with high level of N that allows good efficiency in the use of other resources. Additionally, Augustine and McNaughton (2006) found that herbivores also decreased the rates of N

mineralization, suggesting that the combined effects of grazers on inorganic N and N mineralization rates may result in a net increase or decrease in N availability. A positive effect of shrubs on soil N was found by Moreno and Obrador (2007). They showed that the presence of shrubs in holm oak open woodlands due to low-level grazing increases the content of organic matter, total N and exchangeable cations in the soil due to the long-term integration of fallen leaves into the soil. In *Quercus pyrenaica* open woodlands, the level of soil N in a grazing site was similar to abandoned sites (Tárrega et al. 2009). Therefore, the effects of grazing/shrub encroachment on soil N dynamics seem to be complex and must be understood in the context of each habitat.

In both habitats, land use did not have any effect on the K concentration in leaves. The high mobility of this cation in plants at all levels (between cells and tissues and also in the distribution through the xylem and phloem) and its role in osmoregulation processes (Benlloch-González et al. 2008) could explain these results. According to Milla et al. (2005), an important remobilization of K from older to newer branches occurs in holm oaks in mid-summer as a response to water stress and the need for a better osmotic adjustment which could allow these new branches to survive.

With regard to P leaf concentration compared with trees in grazed areas, our results demonstrate a degree of competition among holm oak and *Cistus* spp. shrubs and a mutualism between holm oak and mixed shrubs. These results are consistent with other studies which found that P absorption by holm oaks can be encouraged by the presence of high shrub diversity (Moreno and Obrador 2007) or discouraged by monospecific shrubs (Rolo et al. 2012). Arbuscular mycorrhizal fungi appear to be directly linked to the increased capacity of trees to exploit the soil and particularly to use the less prevalent forms of phosphates (Barea et al. 2011). The simplification of vegetation structure and composition reduces the diversity of hosts and hence has a negative effect on the density, richness and diversity of these soil fungi.

The leaf water content of holm oak trees was dependent on land use, and the same pattern of P leaf concentration was found. In the *Cistus* shrub habitat, holm oaks in abandoned areas showed lower leaf water content than trees in pasture. This finding was expected and suggests that differences in root architecture between trees and herbaceous species and similarities between trees and shrubs (Silva and Rego 2003) result in less competition between trees and pasture for water (Moreno et al. 2007). However, Rolo and Moreno (2012) have shown that *Cistus* spp. roots are nearly all concentrated at surface level, which indicates that *Cistus*-holm oak competition can be as great as the competition between pasture and holm oak. In addition, the differences in life history between trees and pasture and between trees and shrubs might be another possible explanation, in that plant competition may also be reduced by shortening periods of joint water demand.

Mediterranean pastures in grazing areas are largely comprised of annual herbaceous species which complete their growth cycle, and hence their soil water demand, at the end of spring when the seeds are produced. Thereafter, during the summer, the little soil water available may be used by holm oak without interference from the pasture. In abandoned areas, the soil water demands of holm oak and *C. ladanifer* overlap throughout the year, including the dry summer, and thus, competition is sustained for longer and may result in a higher degree of exploitation of water resources. In contrast with our findings in the *Cistus* shrub habitat, the leaf water content of trees was favoured by the encroachment of mixed shrubs. Therefore, it seems that earlier arguments which focused on the hypothesis of divided resources through rooting-niche separation and life history do not provide a convincing explanation for plant interaction in open woodlands. However, these findings agreed with those of Rolo and Moreno (2011), who found that the shrub *Retama sphaerocarpa* slightly affected the water status of the holm oak and that there was fierce competition between *C. ladanifer* and the tree, which seriously affected its functional status. In addition, the holm oak can adapt its root depth by itself by achieving a balance between the cost of water and nutrient acquisition and the cost of developing and maintaining a root system; thus, to a degree, the soil use by tree and shrub may sometimes be complementary (Rolo and Moreno 2012). On the other hand, it has been suggested that arbuscular mycorrhizas are able to increase the tolerance of their host to water stress (Augé 2004), which may provide a possible explanation of our results. Several mechanisms have been proposed to explain this effect, including increased root hydraulic conductivity, improved stomatal regulation and improved contact with soil particles through the binding effect of hyphae, which enable water to be extracted from smaller pores. Consequently, the water status of holm oaks is linked not only to the understory type—pasture or shrub—but also to its composition, especially in case of the shrub understory.

Grazing intensity affects the growth pattern and nutrient status of holm oaks. In areas where pastures have been stabilized by livestock use, we have found an increase in shoot length with grazing intensity. A large growth could result in similar or even less nutrient concentration of leaves, due to dilution effect. However, leaf concentration of N also increased with grazing intensity. These results support the idea that in Mediterranean open woodland, grazing increases the size of the inorganic N pool available in the soil (Augustine and McNaughton 2006), stimulating primary productivity not only of pasture but also of trees. Herbivory can also favour the presence of annual legumes in Mediterranean pasture (Rochon et al. 2004), which act as nitrogen fixers increasing the quantity of this nutrient in soils and its availability for other species. Given that holm oaks in nutrient-poor environments have a low competitive capacity for soil N compared to pasture because of their dense, shallow root system (Rolo and

Moreno 2011), our results suggest that this tree may significantly benefit from soil N in nutrient-enriched environments, as occurs on farms with high grazing intensity. On the other hand, the foliar concentration of Mg increases with grazing intensity, even though no differences were found in the soil. Mg absorption tends to increase in those environments and seasons in which plants experience water stress (Sardans et al. 2008). Accordingly, mean values of leaf Mg concentration were higher in the second sampling, due to the fact that the sampling was conducted later in the year (in early and late summer, respectively). Given that most minerals are passively accumulated in tissues by the transpiration stream, higher leaf Mg concentration also implies higher transpiration rates and metabolic activity for trees in plots with heavy grazing (Zhu et al. 2010). However, grazing modifies water flow through the soil, and hence the nutrient uptake. Livestock trampling may reduce the water infiltration rate due to an increase in soil bulk density (Drewry et al. 2008). As a result, less water may accumulate at deeper layers, increasing drought stress in plots with heavy grazing and hence stimulating the absorption of Mg.

In conclusion, land use affects Holm oak performance in Mediterranean open woodland through changes in the structure and composition of the vegetation and changes in soil fertility. The abandonment of grazing encourages shrub encroachment but its effect is different according to the habitat type. In cases where *C. ladanifer* is the main species involved in this encroachment process, the resulting habitat becomes more stressful for the tree, reducing its opportunities in terms of N and water acquisition. When mixed shrub species are involved in the encroachment process following abandonment, the resulting habitat may be enhanced, with increased P nutrition and water status of the tree. Although there are social and environmental reasons for maintaining pastoral systems in marginal areas, according to our results, extensive grazing could be a useful management tool to enhance nutritional tree status in poor-nutrient habitats where *Cistus* species may be dominant, thus contributing to the maintenance of Mediterranean open woodland in the face of climate change. In those open woodlands with a well-developed pasture strata and a scarce shrub understory with a long history of livestock use, the increase of grazing intensity has resulted in an increase of tree growth and leaf N concentration. A higher growth rate implies higher water consumption, thus extending the season of water stress for these trees. Further research is needed to clarify the effect of grazing and grazing management on soil N dynamics in Mediterranean open woodlands, linking this with holm oak productivity and its resilience to drought.

Funding This study was sponsored by the Department of Innovation, Science and Business of the Regional Government of Andalusia, Spain (project P10-AGR6501), and the Spanish Ministry of Science (project AGL2009-00530).

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