

Changes in limiting resources determine spatio-temporal variability in tree–grass interactions

G. Gea-Izquierdo · G. Montero · I. Cañellas

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Abstract Changing biotic and abiotic stress mediate in plant–plant interactions resulting in positive to neutral or negative effects, and these effects can change with gradients of stress or through plant dynamics. Here we studied the variability in annual grass production and composition induced by gradients of intercepted light by trees in years of contrasting precipitation in Mediterranean holm oak open woodlands. Although trees reduce the light radiance received by the pasture community, the presence of trees generally had a positive effect on pasture production in average climatic years where soil fertility was low. However, the interaction changed with increasing abiotic water stress. In a dry year, the increase in fertility could not be utilized and the effect of the crown was neutral. The effect of shade turned out to be beneficial for growth, contrary to the situation in an average climatic year. Light insolation was positive for legume biomass. There was high variability in functional components over the course of the growing period and from 1 year to another. Under low levels of other biotic stresses such as livestock grazing or root competition, the limiting

factor among light, soil moisture or soil nutrients may determine whether facilitation or competition occurs.

Keywords Facilitation · Competition · Grass production · Mediterranean · Dehesa · Abiotic stress

Introduction

Plants compete within ecosystems for resources such as light, water and nutrients. Relationships between plants, whether positive (facilitation), neutral or negative (competition), have been the subject of much attention during recent decades. Formerly, it was believed that increasing abiotic stress favored facilitation [the so-called stress-gradient hypothesis (Bertness and Callaway 1994)], but recently this relationship has been questioned (Callaway and Walker 1997; Maestre et al. 2005), with current literature providing examples of variable interactions, for example in time or different levels of abiotic or biotic stress. Depending on different ecological factors, the balance of the interaction between the tree and the understory vegetation can sway from facilitation to competition. Within the same system, facilitation and competition can coexist both in time and space making prediction and modeling of plant–plant interactions somewhat complex (e.g., Callaway and Walker 1997; Brooker et al. 2008).

The tree–grass interaction has been studied chiefly: (a) from the perspective of grass production

G. Gea-Izquierdo (✉) · G. Montero · I. Cañellas
Departamento Sistemas y Recursos Forestales,
CIFOR-INIA, Crta. La Coruña km 7.5,
28040 Madrid, Spain
e-mail: guigeiz@inia.es

in livestock producing systems; (b) from an ecological point of view either analyzing the role played by the tree in the ecosystem nutrient cycle or tree interactions with other plants. The ecological role of trees in low density tree systems has been studied extensively in all kinds of ecosystems, from the tropics to temperate biomes (Mosquera et al. 2005). Agroforestry systems share the presence of a woody component, generally not in the form of complete canopy cover, which interacts with understory plants. The overall effect of trees on their understory is determined by the balance of both facilitation and competition (e.g., Belsky 1994; Callaway and Walker 1997), and the effect of trees is different depending on the species and stand density, among other factors. Trees increase the nutrient content below their canopies, directly through biomass and atmospheric deposition and leaching (throughfall/stemflow) and indirectly by attracting animals. The soil below canopies has lower bulk density, higher water holding capacity and nutrient content (e.g., Joffre and Rambal 1993; Rhoades 1997), and roots compete for water and nutrients with understory vegetation (Belsky 1994; Ludwig et al. 2004). Precipitation is redistributed by canopies (Bellot and Escarre 1998) trees reduce light availability and soften temperatures (Vetaas 1992). There is an increase in grassland β -diversity below trees (e.g., González Bernáldez et al. 1969; Marañón 1986).

The ‘dehesas’ in the western part of the Iberian peninsula are an example of an agroforestry system. These are savanna-like open woodlands dominated by perennial *Quercus* sp., such as *Quercus. ilex* L., *Quercus. suber* L., with crops, pastures and shrubland intermixed (Olea and San Miguel 2006). This system was created by humans with a pastoral objective; hence the presence of grazing animals, which play a major role in shaping the landscape. The silvopastoral, rather than agricultural nature of the system, is a consequence of the oligotrophy of its soils under the influence of a Mediterranean climate, with its characteristic summer drought. Water and nutrients are redistributed as a result of the hilly topography leading to a diversification of soils, which in turn creates a mosaic of ecologically different grassland communities (Puerto and Rico 1992; Pérez Corona et al. 1995). These grasslands are composed of different forms of plant-life with different phenologies, particularly annual and perennial species. Thus,

the understory vegetation can be summarized as (e.g., Luis Calabuig et al. 1980; Olea and San Miguel 2006): (a) crops in the best soils; (b) annual-perennial herbaceous species dominated by grasses in valley bottoms, more fertile and wet non-cultivated soil; (c) annual-perennial communities dominated by *Poa bulbosa* L. and *Trifolium subterraneum* L. established through redistribution of nutrients by livestock, mostly sheep; (d) annual herbaceous species in other non-cultivated soils (where there is no water compensation, as annuals are adapted to summer drought). This occurs in places where grazing is active and shrub encroaching is controlled, otherwise shrubs tend to colonize (Olea and San Miguel 2006). The previously described differences in soil nutrients and moisture availability in the different grasslands, make it unlikely that the interaction with trees will be the same in these understory groups. It might be supposed that they would respond differently as a consequence of the differences in their ecology and particularly, the different soils in which they grow. Facilitation of the herbaceous stratum might prevail particularly in low nutrient soils, which in the Mediterranean usually means annual communities in dry soils. Additionally, a reduction in precipitation could result in changes in the tree–grass interaction, and this is likely to differ depending on light radiation levels.

In this study, we try to respond to the following questions, focusing on annual grasslands: in the temporal scale (a) do changes in ecologically stressful factors such as very dry years affect the influence of trees on the understory biomass and composition within the same ecosystem?; (b) does the effect of the tree vary over the course of the year?; and in the spatial scale: (c) is the interaction of the tree symmetrical within and around its canopy?

Materials and methods

Study area and sampling design

Ten holm oak (*Quercus ilex* L.) trees were used as replicates at a site in West Central Spain (39°N 5°W) in a typical ‘dehesa’ ecosystem. Mean tree density was around 10 trees/ha, and always below 30 trees/ha. Trees had a mean diameter (standard deviation in brackets) of 63.5 (26.0) cm, height 8.8 (1.6) m and crown radius 4.9 (1.8) m. The climate is continental

Mediterranean, with mean precipitation of 573 mm (September–August period) and summer drought. The mean annual temperature is 15.1°C. During the period of the study (2004–2006) annual precipitation (precipitation for March–May in brackets) was 782.3 (214.1), 343.9 (96.5) and 583.0 (205.3) mm, respectively, with minimum precipitation registered during the summer period (June–September). This means that 2005 was an extremely dry year whereas 2004 can be considered wet and 2006 average. The top soil is acidic, sandy and has low nutrient and organic matter content (Table 1; Gea-Izquierdo 2008). Understory vegetation was composed of annual grassland both below and outside the canopy, dominated by species such as *Ornithopus compressus* L., *Ornithopus sativus* Brot. (these two species were dominant among legumes), *Trifolium campestre* Schreb. (among several other annual *Trifolium* species), *Lolium rigidum* Gaud., *Vulpia myuros* K (L.) C.C.Gmel., *Stipa barbata* Desf., *Bromus diandrus* Roth, *Bromus hordeaceus* L., *Holcus setiglumis* (L.) Gaertn., *Xolantha guttata* (L.) Raf., *Tolpis barbata* Boiss. & Reu, *Rumex bucephalophorus* L., *Echium plantagineum* L., *Raphanus raphanistrum* L. or *Plantago lagopus* L. Today, grazing is mainly associated with wild animals, especially deer, but traditionally the area was grazed by livestock (sheep and cattle).

An intensive sampling to study the small scale variability in the interaction between the tree and the understory vegetation was performed by analyzing the effect of two factors (independent variables) on the dependent variables herbage yield ('production') and grassland abundance (%) of functional groups (grasses, legumes and forbs). The two factors were: (a) distance from the tree (DT), to study the spatial extent of the influence (indirectly reflecting mostly a combination of shade, nutrients and root competition)

of the tree; (b) orientation (OR), to study the differential effect of light insolation and the asymmetry of the crown effect. In 2004 and 2005, 16 sampling points were displaced proportionally to the crown radius (R) within the influence of each tree (hence, DT ranged from 0.25 times R to 2.0 times R; hereafter 0.25R, 0.5R... and 2.0R) in the most and least shaded aspects (hence OR had two categories): eight sampling points in the North-East (NE) and eight South-West (SW). Proportional distances to the tree base were sampled to assure that the sample design is representative of any tree regardless of its size. In the third year of the study (2006) the sampling points were extended to 2.25R and 2.5R for both orientations, since in 2004 we found differences between orientations at 2.0R. Therefore, a total of 200 sampling points per collection date (mid April and late May, resulting in 400 samples in that year) were clipped in 2006 whereas 160 samples per collection date were collected in 2004 and 2005. Grazing was excluded by either fencing off the trees or using cages.

Data collection

The herbaceous material was collected in 20 × 50 cm rectangles in 2004, and 50 × 50 cm squares the other 2 years (2005–2006). We decided to change the rectangle size to ensure that enough biomass was collected for other analyzes not included in this study. They were separated into plant functional groups (grasses, legumes and forbs) and then dried for 48 h at 60°C to estimate the biomass of each group. Sampling points were displaced slightly each year to avoid the influence of previous clippings. Since we were interested in studying within year variability, biomass was collected in mid April and at the end of May to estimate annual yield (these dates

Table 1 Summary results of soil attributes (top 20 cm)

	pH	OM (%)	N (%)	C:N	P (ppm)	K (ppm)	Ca	Mg	CEC	Sand (%)	Clay (%)	Density (g/cm ³)
Mean	5.3	1.2	0.06	16.5	26.9	89.6	1.9	0.3	7.7	84.4	1.3	1.5
SD	0.5	0.4	0.03	7.6	15.1	42.3	1.1	0.1	2.6	4.2	0.3	0.2
Max	6.6	2.3	0.13	47.3	64.8	237.8	5.6	0.7	13.9	91.8	2.4	1.9
Min	4.5	0.4	0.01	8.3	0.0	41.5	0.5	0.1	2.3	70.1	0.8	1.1

SD Standard deviation, OM Organic matter, CEC Cation exchange capacity, Ca, Mg and CEC are in meq/100 g. Data comes from 72 sampling points corresponding to six trees, at six different distances and two orientations (see Gea-Izquierdo 2008 for more details)

were considered to be the middle and the end of the growing season, and growth is mostly concentrated between March and the beginning of June). Functional groups (hereafter ‘composition’) were separated in May 2004/2006, and April 2005/2006. In 2005 the growing season was much shorter and the grassland was almost dry when sampled in May. This was the reason why it was not separated into functional components.

Light, top soil moisture and temperature were characterized in the studied plots. Hemispherical photographs were taken from the same 200 sampling points used in 2006. Photographs were obtained in February 2006 and light transmitted was estimated using GLA 2.0 (Frazer et al. 1999). This software allows estimating light radiation for specific periods. Two periods of radiation were studied: (a) from 21st September to 21st June (although this varies between years, we considered this period as the ‘vegetative period’); (b) from 1st March to 21st June (‘spring’ or period of maximum growth). To estimate soil moisture, 18 × 0.5 m tubes were placed on the NE side of three trees at six different distances proportional to the crown radius, and moisture was estimated once a month using time domain reflectometry (TDR). Finally, we include temperatures measured around a tree close to our experimental plots. Temperature data were registered at eight probes, four placed below canopy and four beyond the canopy on the SW side. Data were recorded daily for the period 1996–1999. Probes were situated 30 cm above ground, at ground level, at a depth of 15 cm and at a depth of 30 cm both below and beyond the canopy.

Analysis

Data gathered included both spatial and temporal correlation; therefore, in order to test for differences between sample points and perform accurate tests, we used linear mixed models with random effects (Verbeke and Molenberghs 2000). All covariates, namely distance, orientation, year, month and their interactions, were treated as independent fixed effects, whereas we included a random intercept (grouping by sampling point) and the R matrix was modeled using a first order autoregressive structure [AR(1)], with submatrixes corresponding to observations within a tree. Wald tests were used to test for significance of variance–covariance parameters. Nested models were compared using likelihood ratio tests with likelihood estimated using maximum likelihood. The final model was fitted using restricted maximum likelihood (Verbeke and Molenberghs 2000). To test for differences within fixed effects we used contrasts compared to an F distribution, with degrees of freedom calculated following Kenward and Roger (1997). All tests were at $\alpha = 0.05$. An estimate of the percentage of variance explained by each covariate was calculated as the difference between the efficiency ($EF = 1 - \frac{\sum_{i=1}^n (est_i - obs_i)^2}{\sum_{i=1}^n (obs_i - \overline{obs})^2}$) estimated

for the full model containing all significant covariates and the reduced model removing one factor each time. Finally, the non-linear relationship (Fig. 1) of light interception and distance to the tree was modeled using the coefficients of the relative distance (i.e., 0.25, 0.5, ..., 2.5) as dependent variables. All analyzes were carried out in SAS 9.1. (SAS Institute Inc 2004).

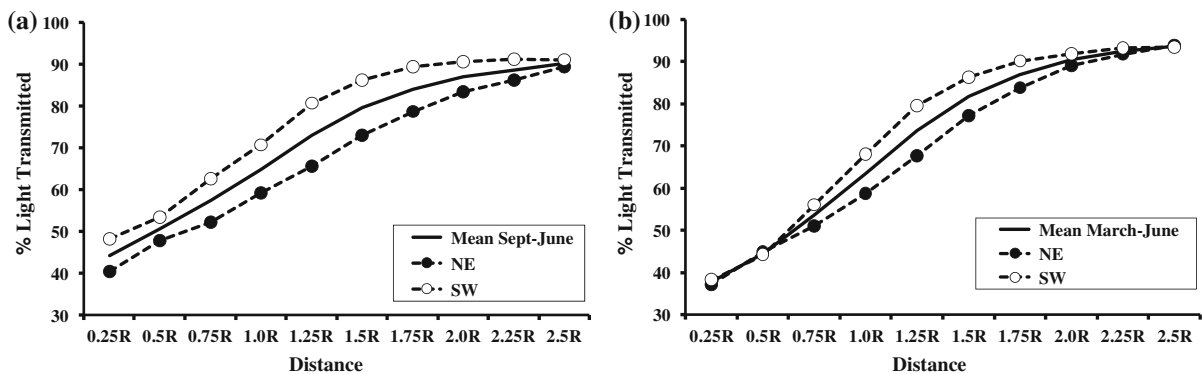


Fig. 1 Mean light transmitted under isolated holm oaks in relation to proportional distance to the tree base: (a) complete annual grassland phenological period (21 September–21 June,

see main text); (b) spring, main growth period (1 March–21 June, see main text)

Results

Small-scale spatial heterogeneity in light, temperature and moisture conditions

The SW locations received more transmitted light on average over the whole vegetative period, and none of the sampling points were totally exposed to sunlight either throughout the day or the year (Fig. 1a). Light intercepted over the whole growth period (September–June) on the NE side was significantly greater than on the SW side (t -value = 8.53; $P < 0.0001$), and the expression was:

$$\begin{aligned} \%light &= \exp((4.25182 - 0.108609 \cdot \text{NEdum}) \\ &\quad \cdot \text{Dist}^{0.08301}); \\ R^2 &= 0.851; \\ RMSE &= 6.828; \end{aligned}$$

with ‘NEdum’, a dummy variable for the NE orientation and ‘Dist’, relative distance to the tree. In spring, when most grassland growth occurs, the two sampling points closest to and farthest from the tree (0.25R–0.5R and 2.25R–2.5R) received the same light on both sides (Fig. 1b).

Soil water was only measured on the NE side, and although accurate estimation of soil water dynamics requires a more intense sampling, our results showed that moisture was greatest in the first 10 cm during winter, spring and fall. In summer the first 40 cm were almost dry, with moisture remaining only in the deepest profile measured (40 cm), particularly at the points farthest from the tree (Fig. 2). In general, the closer to the tree the lower the soil moisture was. Average soil surface temperatures were lower below the canopy, with less pronounced maximum and minimum peak values in summer and winter (Fig. 3). The annual mean of surface temperature was $14.5 \pm 5.8^\circ\text{C}$ below canopy (mean maximum temperature 17.0°C ; mean minimum monthly temperature 12.8°C) and $16.9 \pm 9.3^\circ\text{C}$ outside the canopy (mean monthly maximum, 24.8°C ; mean monthly minimum 11.9°C).

Effect of drought and light interception in grassland productivity

Average grassland production was higher throughout the vegetative period (in April and May) both below

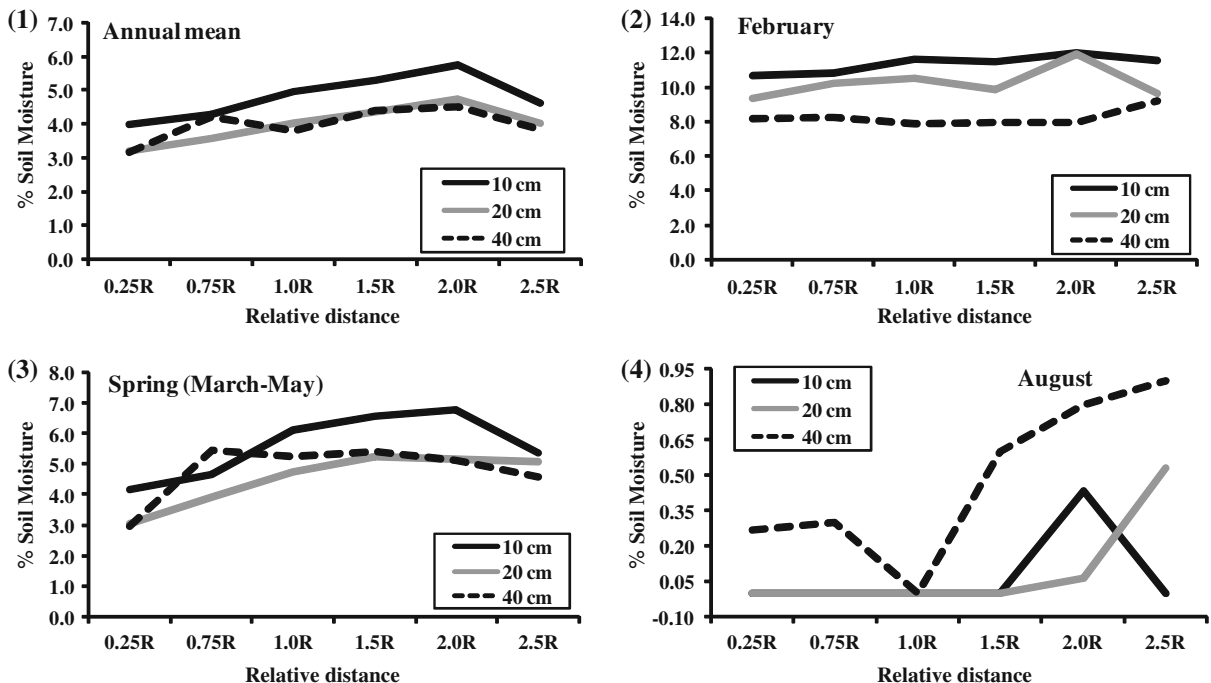


Fig. 2 Soil water content in relation to distance to the tree base (measurements from February 2006 to June 2007, in the NE orientation): (1) Annual mean; (2) maximum moisture

content (winter, February); (3) spring (March–May); (4) August (minimum moisture content)

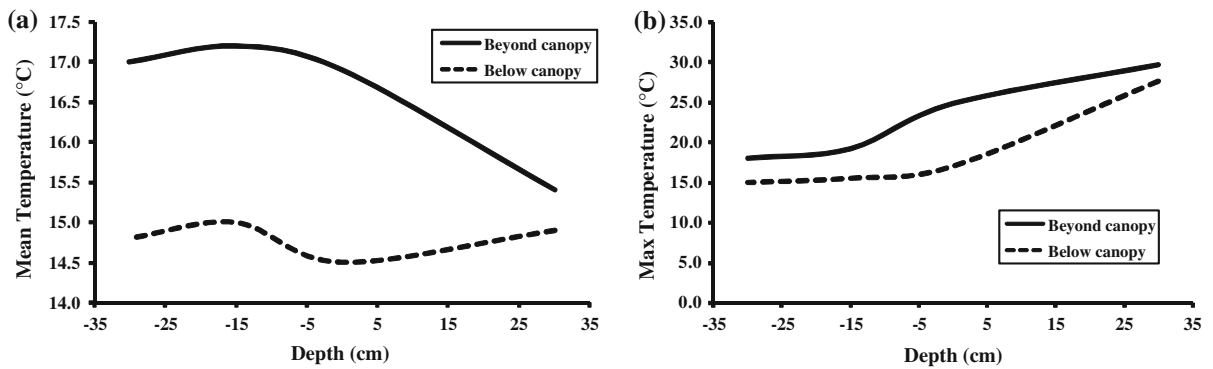


Fig. 3 (a) Mean and (b) maximum soil temperatures (see text for details). Negative values in the *x*-axis correspond to below ground measurements whereas positive values to above ground

the canopy ($F_{1,415} = 71.42$; $P < 0.0001$) and in the sunniest locations (SW) ($F_{1,259} = 22.91$; $P < 0.0001$; Fig. 4), except for the location closest to the tree base, where production was equal on both sides ($F_{1,228} = 0.03$; $P = 0.8703$). The average production was also similar for each orientation at the second closest location to the base of the tree ($F_{1,304} = 0.72$; $P = 0.3968$), although in Fig. 4 it can be appreciated

that the difference fluctuates depending on the year and month. As a rule in Mediterranean ecosystems, production varies greatly in climatically different years. The interaction between DT and year, and OR and year were significant (Table 3; Fig. 4), thus differences for each factor varied depending on the other factor categories in different years (hence different precipitation). This variability was produced

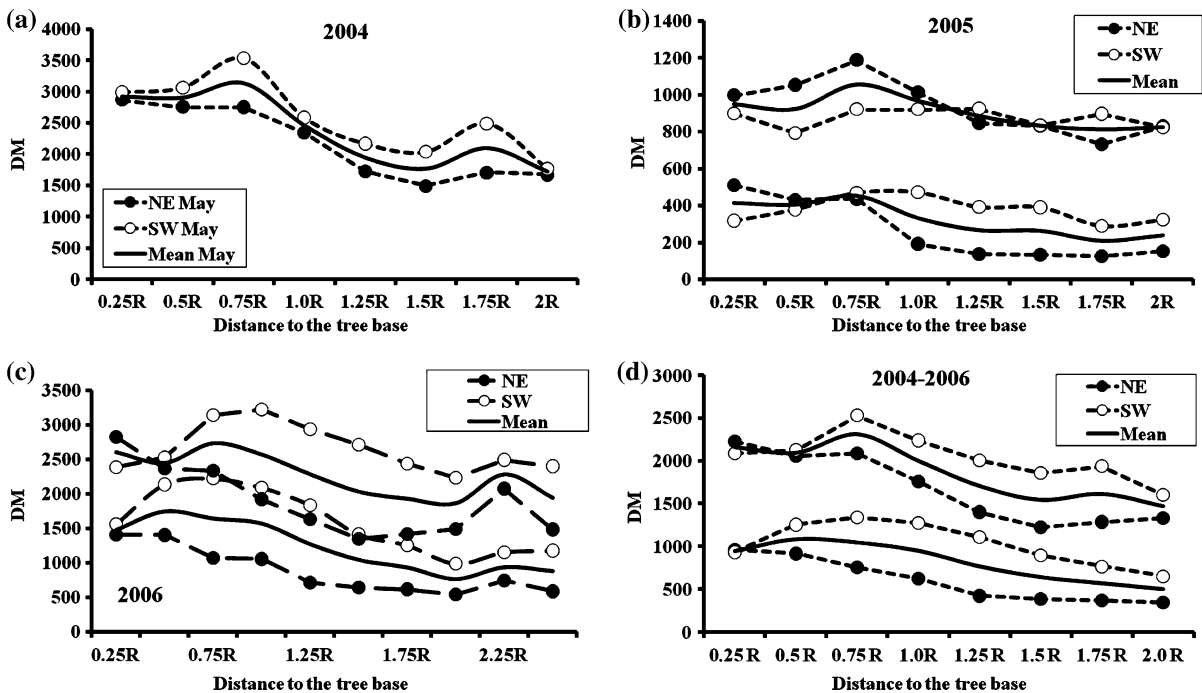


Fig. 4 Pasture production by distance and orientation in the three years of study. DM = Dry matter (kg/ha). (a) May production year 2004; (b) May (upper graphs) and April (lower graphs) production year 2005; (c) May and April production year 2006; (d) Average production (May and April)

2004–2006. Solid lines are means of NE and SW orientations for specific sampling dates (April or May); dashed lines with white circles are SW values while dashed lines with black circles NE values

by the difference results found in 2005, a very dry year (dry spring). That year, mean production was greater below the canopy only in NE locations ($F_{1,223} = 6.80$; $P = 0.0097$). The NE orientation was more productive over the whole season (except in April) whereas in the SW locations there was not a significant increase in pasture yield below the canopy ($F_{1,170} = 0.18$; $P = 0.6709$). Precipitation was the most important factor, as the effect of ‘year’ accounted for 49% of the variance explained by a model just containing the four fixed effects (EF = 62.3%), followed by month (28.8%), which reflects the logical growth increase over the life of annuals which occurs in spring. Since only one intercept random effect was introduced, the variance function is additive between the estimated residual and random effect variances; therefore, the calculation of the percentage of the residual variance explained by the random effect in the final model was straightforward, giving a result of 22.5%.

Effect of drought and light interception on grassland composition dynamics

As expected, on average, grasses and forbs were dominant in the grassland (Table 2), and tended to play complementary roles, with grasses being generally more abundant (on average 0.25R–1.0R) below canopy ($F_{1,396} = 39.9$; $P < 0.0001$) and forbs outside the canopy ($F_{1,322} = 11.93$; $P = 0.0006$). Legumes were the least abundant component of the grassland; although they exhibited the highest variability both in space and time (all fixed effects were significant; Table 3). Forbs seemed to be the main component at the beginning of the season, decreasing in importance (in terms of percentage of herbaceous biomass) towards the end of the vegetative season, with grasses and legumes increasing their abundance as the season

Table 2 Summary results of biomass production and grass composition

	DM	Grasses (%)	Legumes (%)	Forbs (%)
Mean	1,901.8	43.1	15.3	41.6
SD	1,122.6	27.6	18.9	24.7
Max	5,777.0	100.0	95.1	100.0
Min	111.6	0.0	0.0	0.0

SD Standard deviation, DM Dry matter (kg/ha-year) at the end of the vegetative period (May)

advances. As with the forbs, legumes were on average more abundant outside rather than below canopies ($F_{1,347} = 10.59$; $P = 0.0012$) and were also more abundant in SW locations compared to more shaded NE locations ($F_{1,83} = 51.7$; $P < 0.0001$), hence the effect of the tree was asymmetric. These results clearly show the preference of legumes for spots with high levels of irradiance.

Grassland composition also varied significantly from one year to another (Table 3). In 2005 there was an increase in grasses in all locations ($F_{1,74.7} = 40.9$; $P < 0.0001$) and the difference below canopy and beyond canopy was less evident, especially in the case of the NE locations (Fig. 5). Furthermore, although on average (2004–2006) there was no difference between the two orientations (Table 3), in 2006 there were more grasses to the NE than to the SW below the canopy ($F_{1,79} = 16.11$; $P < 0.0001$), whereas this difference was not significant beyond the canopy in that year ($F_{1,78} = 0.06$; $P = 0.8127$). For grasses and forbs, the respective decrease or increase in production with increasing distance to the tree appears to be continuous up to 2.5R in an average year (Fig. 5), particularly to the NE: thus, the influence of the crown goes beyond the crown border, probably due to the influence of shade (or some other factor indirectly influenced by shade) on the composition. The large increase in legumes recorded in 2006 ($F_{1,83} = 51.7$; $P < 0.0001$), directly following the dry year, is a noteworthy occurrence. In 2006, legumes increased from an average of 3.8% in 2005 to 26.7% [33.4% in May 2006, 40.1% to the SW in May 2006; 54.4% at 2.25R to the SW in May 2006. (Fig. 5)].

The percentage of variance explained by the random effect was 20.1% in grasses, 25.2% in legumes and 20.9% in forbs. In the case of grasses, the efficiency of the four fixed effects was 44.2%, of which 48.7% is explained by year. In legumes, the year comprised 75.4% (of a total of 46.6% explained by the four fixed effects) and 46.0% (of 22.7%) in forbs.

Discussion

Facilitation and competition coexist within the same system and can alternate depending on the ecological factor which most limits growth (Belsky 1994; Ludwig et al. 2001; Brooker et al. 2008). Von Liebig’s Law of the Minimum (Von Liebig 1840 cited in Koerselman

Table 3 Linear mixed model results

	Above-ground biomass(kg/ha)		Grasses(%)		Legumes(%)		Forbs(%)	
	F (df)	P-value	F (df)	P-value	F (df)	P-value	F (df)	P-value
DT	10.11 (9, 145)	<0.0001**	5.65 (9, 127)	<0.0001**	2.94 (9, 122)	0.0034**	1.53 (9, 98)	0.1493
OR	27.37 (1, 211)	<0.0001**	1.39 (1, 139)	0.2409	5.06 (1, 159)	0.0258**	0.10 (1, 172)	0.7465
Year	120.35 (2, 106)	<0.0001**	34.33 (2, 71)	<0.0001**	30.47 (2, 71)	<0.0001**	11.02 (2, 68)	<0.0001**
Month	98.85 (1, 104)	<0.0001**	0.05 (1, 67)	0.8311	25.09 (1, 66)	<0.0001**	12.12 (1, 64)	0.0009**
DT * OR	1.59 (9, 150)	0.1217	1.32 (9, 132)	0.2344	0.50 (9, 128)	0.8698	0.52 (9, 94)	0.8559
DT * Year	3.50 (14, 538)	<0.0001**	0.45 (14, 357)	0.9554	2.28 (14, 355)	0.0055**	0.88 (14, 341)	0.5756
DT * Month	0.78 (9, 540)	0.6388	1.47 (9, 336)	0.1591	1.54 (9, 335)	0.1310	0.78 (9, 319)	0.6352
OR * Year	11.04 (2, 148)	<0.0001**	0.78 (2, 105)	0.4628	1.65 (2, 99)	0.1966	0.16 (2, 117)	0.8564
OR * Month	0.02 (1, 149)	0.9019	0.86 (1, 96)	0.3568	1.77 (1, 92)	0.1863	0.02 (1, 96)	0.8989
Year * Month	7.90 (1, 107)	0.0059**	-	-	-	-	-	-
DT * Year * Month	0.45 (7, 526)	0.8695	-	-	-	-	-	-
OR * Year * Month	0.56 (1, 146)	0.4553	-	-	-	-	-	-
DT * OR * Year	1.15 (14, 541)	0.3143	0.77 (14, 361)	0.7035	1.50 (14, 356)	0.1068	0.98 (14, 329)	0.4733
DT * OR * Month	0.24 (9, 534)	0.9890	0.47 (9, 336)	0.8960	1.81 (9, 333)	0.0652*	0.30 (9, 317)	0.9740
DT * OR * Year * Month	0.39 (7, 522)	0.9098	-	-	-	-	-	-

	Z value	P-value	Z value	P-value	Z value	P-value
σ^2 (b)	2.82	0.0024**	2.06	0.0199**	3.07	0.0011**
ϕ (ρ)	15.92	<0.0001**	16.31	<0.0001**	14.73	<0.0001**

DT Distance to tree base, OR Orientation, σ^2 (b) = variance component estimate for the random effect, ϕ (ρ) = estimate for the autocorrelation parameter in variance-covariance residual matrix

** Test significant at $\alpha = 0.05$

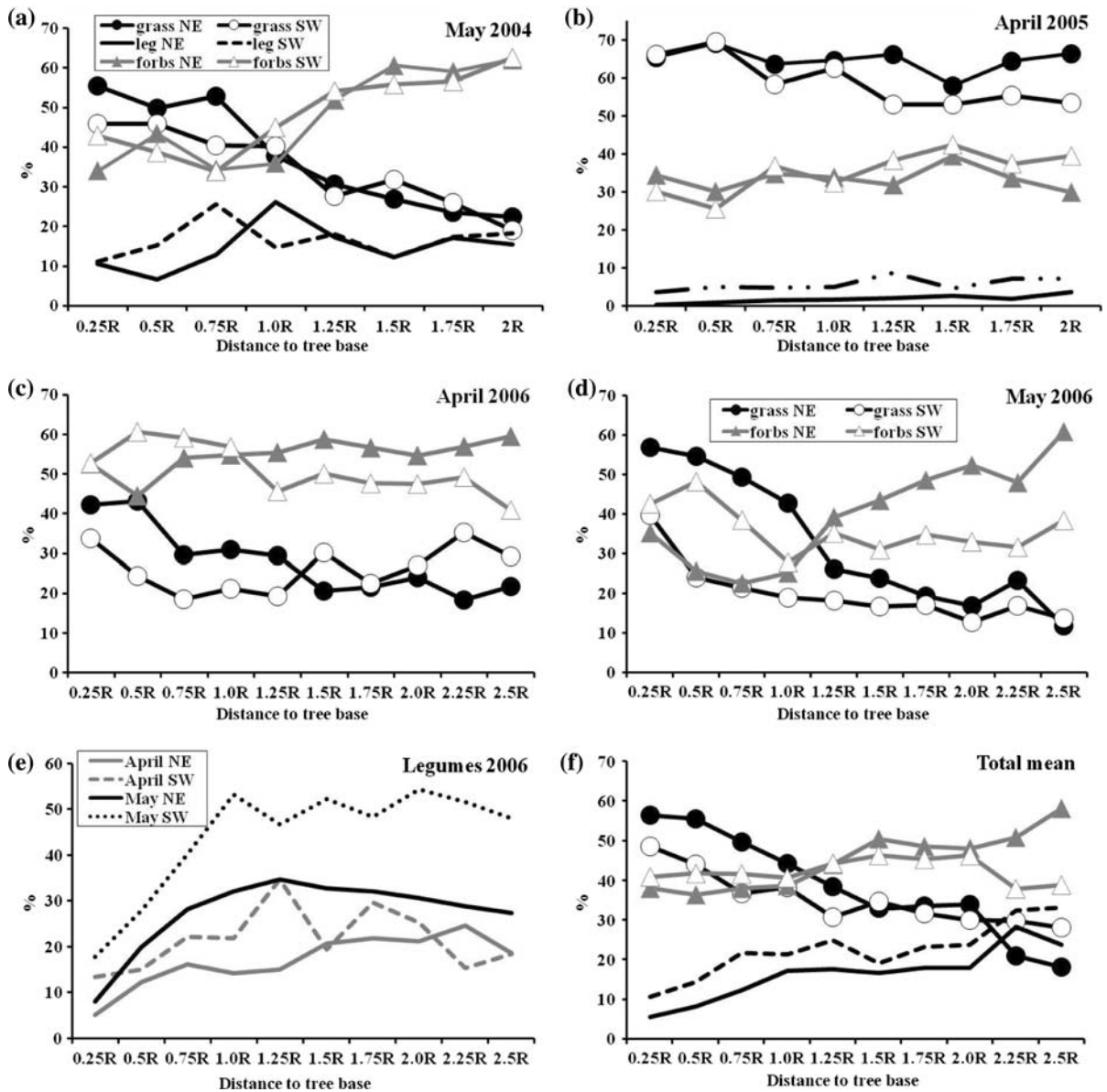


Fig. 5 Mean percentage pasture composition by distance and orientation in the three years of study. (a) May 2004; (b) April 2005; (c) grass and forbs April 2006; (d) grass and forbs May 2006; (e) legumes April and May 2006; (f) total mean April and May 2004–2006 Grasses are represented by black solid

line with circles (dark, NE; white, SW); Legumes by solid line in the NE and dashed line SW; forbs are represented by grey solid lines with triangles (dark, NE; white, SW). Legend in Fig. 1 also corresponds to (2), (3) and (6)

and Meuleman 1996) states that site fertility for individual plants is governed by the availability of the limiting nutrient. The variability found (Brooker et al. 2008) could mean that growth response to the addition of a limiting nutrient might be extrapolated to any other limiting factor, not only nutritional, such as moisture or light availability (Ludwig et al. 2001).

Small-scale spatial heterogeneity in light, temperature and moisture conditions

The reduction of light by the canopy in spring was similar in both orientations for the two locations closest to and farthest from the tree, with all other southern locations receiving more radiation. The

maximum reduction of solar radiation was around 40%, which is similar to results from isolated savanna trees (Vetaas 1992). The reduction of light irradiance by the canopy reduces mean temperature values and temperature oscillation by increasing minimum temperatures in winter and decreasing maximum temperatures in summer with respect to locations beyond the canopy. Thus, it follows that the higher the amount of radiation intercepted, the greater the modification of the microclimate (Eviner and Chapin 2003). Modification of temperatures by trees may be playing an important role in grass ecology, for example as the limiting factor in winter (Vetaas 1992).

In Mediterranean ecosystems, the water content generally recovers in fall, bringing the soil close to field capacity until the end of spring, when it decreases until July as the soil dries out (Joffre and Rambal 1993; Cubera and Moreno 2007). The effect of the tree on soil moisture seems to be variable depending on the ecosystem (Vetaas 1992), so it should not be generalized that trees increase or decrease moisture availability below canopies. We found a moisture decrease below canopy for all months, and this decrease was smallest in winter, when the soil was likely to be at its field capacity. The decrease detected in moisture below canopy coincides with some studies conducted in the same ecosystem (Cubera and Moreno 2007) but not others (Joffre and Rambal 1993). Some of the differences might be a consequence of our soils being sandier (generally the first 20 cm are loamy sand) or of differences in precipitation (Cubera and Moreno 2007). Three main factors are likely to reduce water below canopies: (a) rainfall interception and redistribution by the canopy (Bellot and Escarre 1998), although this is likely to be of less importance than in closed forests and temperate climates (Joffre and Rambal 1993); (b) competition for water from tree roots; (c) greater water consumption from higher grass production. There are many examples of reduced moisture below canopy in other ecosystems (e.g., Belsky 1994; Ludwig et al. 2004). However, evaporation of soil moisture is likely to be lower below canopy, the balance of ETP is likely to be negative for the tree–grass component compared to only grass, as the tree–grass component is subject to a great evaporative demand (Joffre and Rambal 1993).

Effect of drought and light interception in grassland productivity

Variability in time and space can be considered the rule, both in terms of production and composition in these Mediterranean grasslands. Pasture yield was within the range found in other studies conducted in the same ecosystem (Olea and San Miguel 2006), and on average, herbage biomass increased below the canopy. Facilitation by nutrient enrichment counterbalanced competition for water and light interference in an average year. Abiotic stress associated with light and nutrients is subordinated to water availability in this ecosystem, as is commonly the case in arid and semiarid ecosystems. Microsite benefits are only apparent when enough water is available to profit from other factors such as nutrients (Maestre et al. 2005), and this might be generalized if any other limiting factor exists. This is similar to other nutrient poor ecosystems, like some African savannas (Belsky 1994; Rhoades 1997). Therefore, depending on the climate and ecosystem (soil, stand density), the balance between facilitation and competition can result in an increase in pasture yield (e.g., Belsky 1994; Rhoades 1997), have no effect (e.g., Ludwig et al. 2004; Thevathasan and Gordon 2004) or lead to yield reduction (e.g., Somarriba 1988).

The positive effect of light is likely to increase in soils with a higher nutrient content. Locations receiving more light (SW) produced significantly more, probably reflecting the fact that, in an average year there is no water limitation to annuals in spring, hence they are able to fully utilize nutrient availability and energy. However, Moreno (2008) found a positive effect of shade on herbage growth. In the aforementioned study, the positive effect of shade was recorded at 50% light reduction, equivalent to distance 0.75R, where the maximum growth was registered. Previous literature on the subject describes the reduction in understory production as a result of excessive shade, even in nutrient rich soils in the absence of drought (e.g., Somarriba 1988; Marañón and Bartolome 1994). In the ecosystem studied, it seems that the positive effect of trees (facilitation) is most evident in poor soils, which are colonized by annuals. According to other studies (Montalvo et al. 1980; Moreno 2008), in annual-perennial grassland communities in valley bottoms and fertilized crops or grasslands, the

balance tends to be negative (competition), reducing understory growth with respect to locations beyond the canopy.

In the very dry year, the relationship between the tree and the understory production changed. Likely the pasture community was unable to utilize the increased fertility below the canopy, and the production was homogeneous both below and beyond the canopy in the sunniest locations (SW). This seems to point towards not only the previously described spatial heterogeneity of pasture production but also a temporal variation depending on the interaction between precipitation, nutrients and light. Then, increasing water stress resulted in a neutral interaction and the balance between moisture–light–nutrients changed. These suggest that facilitation is likely to be mainly driven by an increase in soil fertility that will only be beneficial if there is enough water and light for photosynthesis, assuming that root competition from woody vegetation is counterbalanced (Maestre et al. 2005; Brooker et al. 2008).

Effect of drought and light interception on grassland composition dynamics

The preference of legumes for sunny conditions was evident. The legume content of plant systems is important because legumes fix atmospheric nitrogen which increases soil fertility, and their high protein content is readily accepted by grazing animals (Hauggaard-Nielsen and Jensen 2005). They are used as an index to estimate pasture quality within the system (Olea and San Miguel 2006). Shade reduced the abundance of legumes whereas in given years or locations it could increase the biomass of grasses. Forbs do not seem to have a clear response to shade, but rather, appear to be outcompeted by grasses in high nutrient soils. Grasses are dominant in more eutrophic conditions below the canopy and in soils with the highest nutrient content in the system like those found in foothills (Marañón 1986; Pérez Corona et al. 1995), which generally lead to an increase in biomass production.

There was an increase in the proportion of legume dry matter over the course of the season, with accumulation of ‘effective growing days’ (Henkin et al. 1998). Legumes constitute the fraction which shows the greatest variability (Luis Calabuig et al.

1980; Pérez Corona et al. 1995) and temporal variability is also evident throughout the life cycle of annuals: forbs were dominant at the beginning of the growing season, with grasses and legumes increasing their presence later, although this varies in other studies (Pérez Corona et al. 1998), probably as a result of different species composition. In some years, ‘poor quality’ pastures (from a pastoral point of view) such as those studied, can contain a high proportion of legumes, which is positive for livestock grazing and soil enrichment (Hauggaard-Nielsen and Jensen 2005). Regarding the variability in plant composition, the most important factor was the year, i.e., the climate in the current as well as in previous years, which influences the interannual variations in plant development and seed bank dynamics in this Mediterranean ecosystem.

There are still some unresolved issues regarding tree–grass interaction. Since the biomass of functional groups changes over the course of the vegetative period. Studies where samples are only taken at the end of the vegetative period may miss certain species and therefore the results regarding the abundance of functional groups might be biased. The role played by competition from tree roots is not assessed in this study, but is likely to be influential in the reduction of available soil moisture and hence, reduce pasture growth (Callaway et al. 1991; Ludwig et al. 2004; Moreno 2008). The effect of livestock grazing has not been analyzed in this study either, and overgrazing may shadow the influence of the tree.

In this study, we have centered on functional groups. However, if individual species management were required, it is possible that certain aspects of species specific behavior would differ from the behavior of the functional group. Shifts from positive or neutral effects to negative effects and viceversa have been found in aridity gradient studies in other plant–plant interactions (Brooker et al. 2008). The positive effect of nutrient enrichment will be ineffective if tree density is high. In this regard, Vetaas (1992) emphasized the fact that great care should be taken when extrapolating the results for interactions studied in isolated trees to higher tree densities since tree–grass interactions are unlikely to be lineal. All these aspects should be taken into account in future silvopastoral models including different climatic scenarios.

Conclusions

The interaction between trees and understory vegetation is a complex phenomenon, as facilitation, interference and competition relationships are involved. In the ecosystem studied, the balance of facilitation–competition for herbage growth tends to be positive only if there is no water limitation during growth (as is the case in Mediterranean annual grassland spring growth on average years) in nutrient-limited annual grasslands. Pasture production and the composition of functional groups are variable not only in space but also in time, both within and between years. Legume biomass responded negatively to shade and plant groups were displaced asymmetrically around trees, both within the canopy and around the tree. The contemplation of plant–plant interactions in a simple form in theoretical or management oriented models is not easy due to their complexity and variability. Factors such as light, nutrients, and moisture (ETP) interact within the ecosystem, and the one (or combination) which acts as a limiting factor may determine the understory growth and dynamics. Results from single periods or sites should not be extrapolated to all annual plant stages and sites, and might change if climate changes. Field experiments will be required to fully address some of the specific relationships studied.

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