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Effects of the holm-oak canopy on the distribution of terricolous bryophytes and lichens

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Abstract – The effects of holm-oak canopy (*Quercus ilex* ssp. *ballota*) on terricolous bryophytes and lichen were studied in the central part of the Spanish Mediterranean region. Three habitats were distinguised: understorey, crown border and open grassland. In all cases, the understorey is floristically poor compared with open grassland. In the N-exposed stands species richness is more homogenous between canopy border and open grassland, while in-S exposed ones differences among habitats are more pronounced. *Cladonia rangiformis*, *C. foliacea*, *C. cervicornis* and *Cetraria aculeata* have higher presence and cover values in all situations, and the bryophytes *Hypnum cupressiforme* and *Pleurochaete squarrosa* are the main species. Most of the acrocarpic mosses and fruticose lichens grow on the canopy border or open grassland, while pleurocarpic mosses and foliose lichen with cyanobacteria are most frequent under N-exposed canopies. The holm-oak crown causes variations in insolation, rain distribution, temperature and wind, and strongly influences the distribution of lichens and bryophytes.

bryophytes / lichens / terricolous / canonical ordination / Spain / species-environment relationships

Resumen – Se ha estudiado el efecto que el dosel arbóreo de las encinas (*Quercus ilex* ssp. *ballota*) ejerce sobre los briófitos y líquenes terrícolas en el centro de la región Mediterránea española. Se han diferenciado tres ambientes: bajo el dosel, borde del dosel y zona sin influencia. En todos los casos, el ambiente situado bajo el dosel es el más pobre desde un punto de vista florístico. En las exposiciones norte la riqueza de especies es más homogénea entre el borde del dosel y la zona sin influencia, mientras que en las exposiciones sur se aprecian diferencias más pronunciadas entre los tres ambientes. *Cladonia rangiformis, C. foliacea, C. cervicornis* y *Cetraria aculeata* tienen mayor presencia y cobertura en todas las situaciones, y los briófitos *Hypnum cupressiforme* y *Pleurochaete squarrosa* son las principales especies. La mayoría de los musgos acrocárpicos y de los líquenes fruticulosos crecen en el ambiente del borde del dosel y en la zona sin influencia, mientras que los musgos pleurocárpicos y los líquenes foliáceos con cianófitas son más abundantes en las exposiciones norte. El dosel arbóreo origina variaciones en la insolación, distribución de las lluvias, temperatura y viento, que afectan directamente a la distribución de los briófitos y líquenes terrícolas.

briófitos / líquenes / terrícolas / ordenación canónica / España / relaciones ambientales

INTRODUCTION

The distribution of terricolous bryophytes and lichens is affected by abiotic factors including soil characteristics and macroclimate (Eldridge & Tozer 1997). The presence of a canopy may vary the microclimatic conditions, especially in the Mediterranean region (Martínez Sánchez *et al.* 1994), may affect the floristic composition and structure of terricolous communities due to variations in moisture, illumination and soil nutrient resources.

There are few studies of terricolous cryptogams in relation to canopy influence. Some of them (Carleton 1990), describe the functional processes in Canadian boreal forests, in northern European beech and oak woods (Canters *et al.* 1991) or in semiarid areas of Australia (Eldridge & Tozer 1997), but no such study is available from the Mediterranean region. The "dehesas", an agro-sylvo-pastoral system that covers more than six millions of hectares in the plains of southern Iberian peninsula (Blondel & Aronson 1999), give an excellent opportunity to approach such effects under a Mediterranean climate. "Dehesas" are a man-induced park-like woodland of holm-oaks (*Quercus ilex* subsp. *ballota*) which results from selection of superior well-shaped trees or rarely intentional planting of acorns (Joffre *et al.* 1988). Several studies have shown conspicuous changes in herbaceous plant communities depending on whether they are under tree canopy or not (Gónzalez-Bernáldez *et al.* 1969; Marañón 1986; Joffre *et al.* 1988, Barbero *et al.* 1990). Causal factors are related to a greater moisture and higher organic stocks in the soil due to leaf shedding, animal excretion and lesser evapotranspiration rates under holm-oak canopy (Joffre *et al.* 1988; Joffre & Rambal 1993).

This research aims at exploring the influence of canopy of holm-oaks in terricolous communities of bryophytes and lichens. Including community composition, structural responses (life form shifts), the bryophyte-lichen balance, and the effects of some easily-controlled variables, such as exposure, or crown and trunk size.

MATERIAL AND METHODS

The study was carried out in 3 "dehesas" of *Quercus ilex* L. ssp. *ballota* (Desf.) Samp. (= *Q. rotundifolia* Lam.) located in the North of the Madrid province. The localities were situated between 900-1020 m (Fig. 1). Annual average temperature varies between 10.6-12.4 ºC and annual rainfall between 650-725 mm. The soils are distric cambisols with a pH varying between 5 and 6. Both areas are included in the Supramediterranean belt and the climax vegetation belongs to the association *Junipero oxycedri-Quercetum rotundifoliae* (Rivas-Martínez 1987).

It is based on 100 relevés and includes 41 taxa (14 bryophytes and 27 lichens). The influence area of three old isolated trees on three different "dehesas" was sampled along two straight transects oriented from trunk base-S and trunk base-N. Sampling was carried out in 25 cm side squares, separated 1 m among themselves. To avoid trunk influence, the area closest to the base of the trunk was avoided. Thus, the first relevé was situated at 10 cm from the tree trunk. The number of relevés from each tree is related to its crown diameter resulting a number of 5 to 6 relevés on each tree and orientation. Following the suggestions

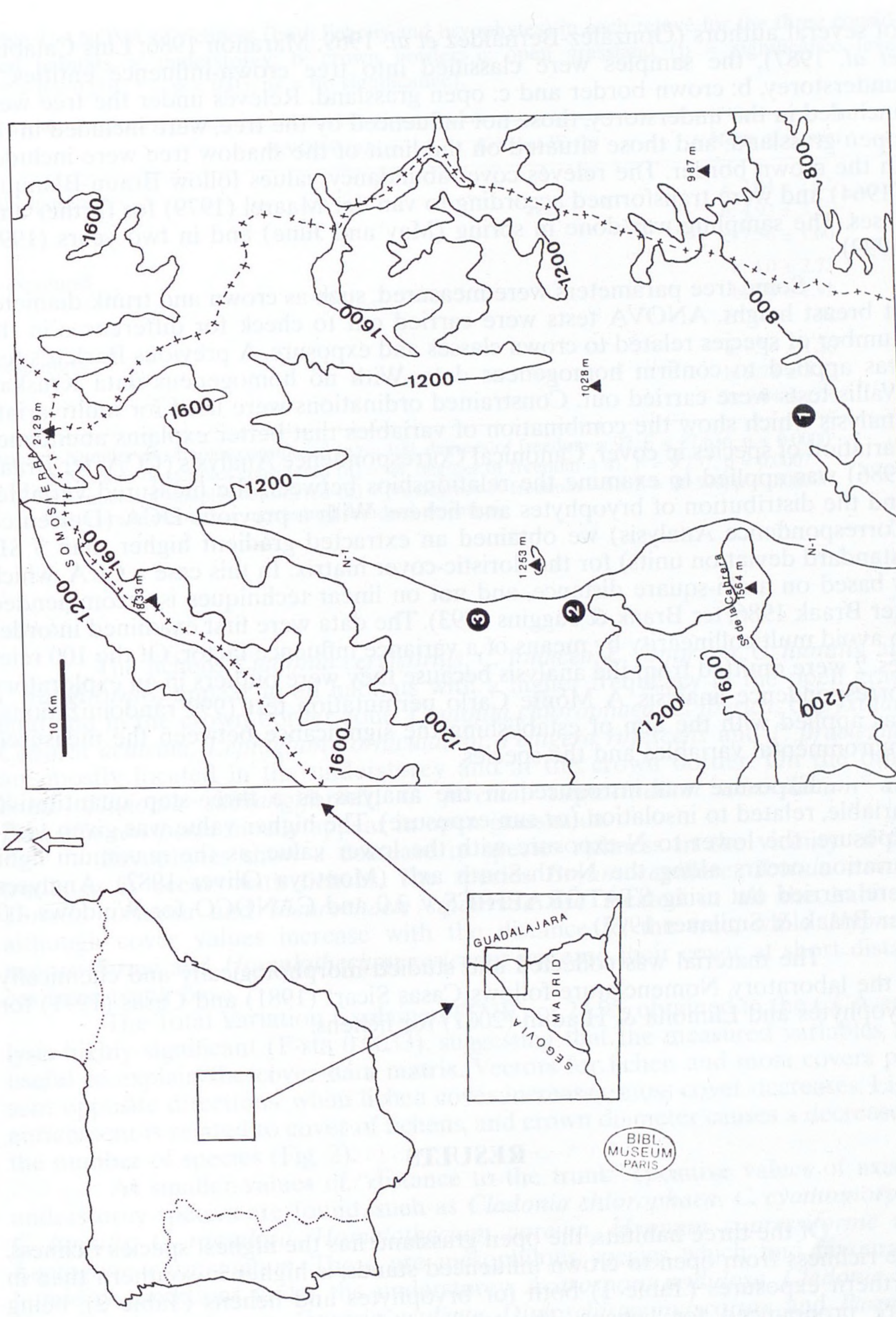

Fig. 1. Situation of the sampled areas in the Madrid Province. 1: Torrelaguna; 2: El Cuadrón; 3. Embalse de Riosequillo.

of several authors (González-Bernáldez *et al.* 1969; Marañón 1986; Luis Calabuig *et al.* 1987), the samples were classified into tree crown-influence entities, a: understorey, b: crown border and c: open grassland. Relevés under the tree were included in the understorey, those not influenced by the tree, were included in the open grassland, and those situated on the limit of the shadow tree were included in the crown border. The relevés cover-abundancy values follow Braun-Blanquet (1964) and were transformed according to van der Maarel (1979) for further analyses. The sampling was done in spring (May and June) and in two years (1997, 1999).

Some tree parameters were measured, such as crown and trunk diameter at breast height. ANOVA tests were carried out to check for differences in the number of species related to crown classes and exposure. A previous Barlett's test was applied to confirm homogeneus data. With no homogeneus data Kruskal-Wallis tests were carried out. Constrained ordinations were used for multivariate analysis which show the combination of variables that better explains abundance variation of species in cover. Canonical Correspondence Analysis (CCA, ter Braak 1986) was applied to examine the relationships between the measured variables and the distribution of bryophytes and lichens. With a previous DCA (Detrented Correspondence Analysis) we obtained an extracted gradient higher than 3 SD (standard deviation units) for the floristic-cover matrix. In this case a CCA, which is based on a chi-square distance, and not on linear techniques is recommended (ter Braak 1986; ter Braak & Juggins 1993). The data were first examined in order to avoid multicollinearity by means of a variance influence factor. Of the 100 relevés, 2 were omitted from the analysis because they were outliers in an exploratory correspondence analysis. A Monte Carlo permutation test (999 randomizations) was applied with the aim of establishing the significance between the measured environmental variables and the species.

Exposure was introduced in the analysis as a three-step quantitative variable, related to insolation (or sun exposure). The higher value was given to S-exposure, the lower to N-exposure with the lower value, as the maximum light variation occurs along the North-South axis (Montoya Oliver 1982). Analyses were carried out using STATGRAPHICS v. 3.0 and CANOCO for Windows 4.0 (ter Braak & Smilauer 1997).

The material was collected and studied morphologically and chemically in the laboratory. Nomenclature follows Casas Sicart (1981) and Casas (1991) for bryophytes and Llimona & Hladun (2001) for lichens.

RESULTS

Of the three habitats, the open grassland has the highest species richness. The richness from open to crown influenced stands, is higher in southern than in northern exposures (Table 1) both for bryophytes and lichens (Table 2), being more pronounced for lichens. The total number of taxa was 41, the genus *Cladonia*, with 14 species being the most frequent. The species *Cladonia rangiformis*, *C. furcata*, *C. foliacea* and *C. cervicornis* are the most frequent and relevant in relation to cover. *Pleurochaete squarrosa*, *Tortella tortuosa*, *Bryum capillare* and *Hypnum cupressiforme* are the most frequent species in bryophytes (Table 2).

Table 1. ANOVA of richness (both lichens and bryophytes) in each relevé for the three considered habitats. a: understorey; b: crown border; c: open grassland (p = significance level *** = $p < 0.001$; * = $p < 0.05$; ns = no significance).

	ANOVA (p)	*Kruskal-W. (p)*	*Mean of species*
All exposures*		***	a: 2.04 ± 2.62 b: 4.92 ± 3.35 c: 7.56 ± 1.60
N-exposure§	***		a: 4.0 ± 2.73 b: 7.0 ± 2.91 c: 7.88 ± 1.72
S-exposure‡		***	a: 0.36 ± 1.20 b: 3.72 ± 3.43 c: 7.54 ± 1.70

Note: * Number of samples considered (n) = 100, degrees of freedom = 97, F = 27.636, p = 0.0000
§ Number of samples considered (n) = 44, degrees of freedom = 41, F = 9.237, p = 0.0007
‡ Number of samples considered (n) = 56, degrees of freedom = 53, F = 26.590, p = 0.0000
Data are presented as means and standard deviation.

The lichens *Cladonia cervicornis*, *C. foliacea*, *C. fimbriata*, *C. humilis,* and *C. rangiformis,* appear in all habitats with a higher frequency in the open grassland and in the crown border zone. *Cladonia chlorophaea*, *C. iberica*, *C. pyxidata*, *Cetraria aculeata, Leptogium corniculatum*, *Peltigera rufescens* and *P. praetextata* are mostly located in the understorey and at the crown border. On the other hand, *Cladonia subrangiformis*, *C. furcata*, *Leptochidium albociliatum* and *Parmelia conspersa* mostly appear in open grasslands.

Bryophytes show a decrease in species richness in the vicinity of the trunk, as it occurs with lichens. The species *Bryum capillare*, *Tortula ruralis*, *Tortella tortuosa* and *Pleurochaete squarrosa* are located in all the habitats, although cover values increase with the distance to the tree, while *Hypnum cupressiforme* and *Homalothecium sericeum* increase their cover at short distances from trunk base.

The Total Variation Explained (TVE) of 23.95, obtained in the CCA analysis highly significant (F-sta 0.0033), suggesting that the measured variables are useful to explain the cover data matrix. Vectors for lichen and moss covers present opposite directions: when lichen cover increases, moss cover decreases. Light enrichment is related to cover of lichens, and crown diameter causes a decrease in the number of species (Fig. 2).

At smaller values of "distance to the trunk" (positive values of axis 1) understorey species are found, such as *Cladonia chlorophaea*, *C. cyathomorpha*, *C. humilis*, *C. ramulosa*, *Homalothecium aureum*, *Hypnum cupressiforme* and *Leptogium corniculatum*. These are mesophilous species which find favourable humidity conditions under the understorey. *Acarospora nodulosa*, *Cladonia iberica*, *C. subrangiformis*, *Cetraria aculeata*, *Diploschistes muscorum* and *Parmelia conspersa*, are related to higher distances to the trunk (negative values of axis 1). They mainly grow on the crown border and in the open grassland, as they are xerophilous and heliophilous species. Near the origin of the axis there are species such as *Cladonia cervicornis*, *C. coccifera*, *C. grayi*, *C. pyxidata*, *C. rangiformis*,

Table 2. List of species with the cover values. + : 1-9%; ░: 10-19%; ▒: 20-49%; ▓: 50-69%; █: 70-100%. a: understorey; b: canopy border; c: open grassland; N: North exposure; S: South exposure; T: all exposures.

		N			S			T		
	LICHENS	a	b	c	a	b	c	a	b	c
And	*Acarospora nodulosa* (Duf.) Hue			+			+			+
Cce	*Cladonia cervicornis* (Ach.) Flot.	+	+	░	▒	░	▒	▒	░	▒
Cch	*Cladonia chlorophaea* (Sommerf.) Sprengel	+	+		+	+		+	+	
Cco	*Cladonia coccifera* (L.) Willd.			+						+
Ccy	*Cladonia cyathomorpha* Stirton ex W. Watson				+	+	+	+	+	+
Cfi	*Cladonia fimbriata* (L.) Fr.	░	░	+		+	+	░	░	+
Cfo	*Cladonia foliacea* (Hudson) Willd.	+	▒	▒	░	▒	▒	░	▒	▒
Cfu	*Cladonia furcata* (Hudson) Schrader	▒	░	▓		+	▒	▒	░	▓
Cgr	*Cladonia grayi* G. Merr. ex Sandst.			+						+
Chu	*Cladonia humilis* (With.) Laundon	+	▒	+			+	+	▒	+
Cib	*Cladonia iberica* Burgaz & Ahti	+	+			+	+	+	+	+
Cpy	*Cladonia pyxidata* (L.) Hoffm.		+				+		+	+
Cra	*Cladonia ramulosa* (With.) Laundon			+					+	
Crg	*Cladonia rangiformis* Hoffm.	▒	▓	▒	░	█	█	▒	█	█
Csu	*Cladonia subrangiformis* Sandst.		+	░			+		+	░
Cac	*Coelocaulon aculeatum* (Schreber) Link	+	░	▒		▒	▒	+	▒	▒
Dmu	*Diploschistes muscorum* (Scop.) R. Sant.						+			+
Lal	*Leptochidium albocilliatum* (Desm.) M. Choisy			▒						▒
Lco	*Leptogium corniculatum* (Hoffm.) Minks	+	░				▒	+	░	▒
Lge	*Leptogium gelatinosum* (With.) Laundon						+			+
Pco	*Parmelia conspersa* (Ehrh. ex Ach.) Ach.		+	+		+	▒		+	▒
Ppo	*Parmelia pokornyi* (Körb.) Szat.					░	+		░	+
Pne	*Peltigera neckeri* Hepp ex Müll. Arg.	░						░		
Ppj	*Peltigera ponojensis* Gyeln.	░	▒	░			░	░	▒	░
Ppr	*Peltigera praetextata* (Flörke ex Sommerf.) Zopf				▒	░		▒	░	
Pru	*Peltigera rufescens* (Weiss) Humb.		▒			▓			▒	▓
Pmu	*Physconia muscigena* (Ach.) Poelt	+						+		
	BRYOPHYTES									
Bbi	*Bryum bicolor* Dicks.			+			░			░
Bca	*Bryum capillare* Hedw.	▒	+	▒	░	+	▒	▒	+	▒
Gpu	*Grimmia pulvinata* (Hedw.) Sm.	+		+		+	+	+	+	+
Hau	*Homalothecium aureum* (Spruce) Robins.	+	▒		+	+	+	+	▒	+
Hse	*Homalothecium sericeum* (Hedw.) Schimper	▒	+			░	+	▒	░	+
Hcu	*Hypnum cupressiforme* Hedw.	▓	▒	+	▓	░	▒	▓	▒	▒
Psq	*Pleurochaete squarrosa* (Brid.) Lindb.	+	▓	▓	+	▒	▒	+	▓	▓
Pju	*Polytrichum juniperinum* Hedw.	░	░	░		+	▒	░	░	▒
Ppi	*Polytrichum piliferum* Hedw.	▒	+	░			+	▒	+	░
Tfl	*Tortella flavovirens* (Bruch) Broth.		+				+		+	+
Tto	*Tortella tortuosa* (Hedw.) Limpr.	+	▓	▒		▒	▓	+	▓	▓
Tat	*Tortula atrovirens* (Sm.) Lindb.	+			▒	+	+	▒	+	+
Tin	*Tortula intermedia* (Brid.) De Not					░	+		░	+
Tru	*Tortula ruralis* (Hedw.) Gaertn. et al.	░	+	░	+	░	▒	░	░	▒

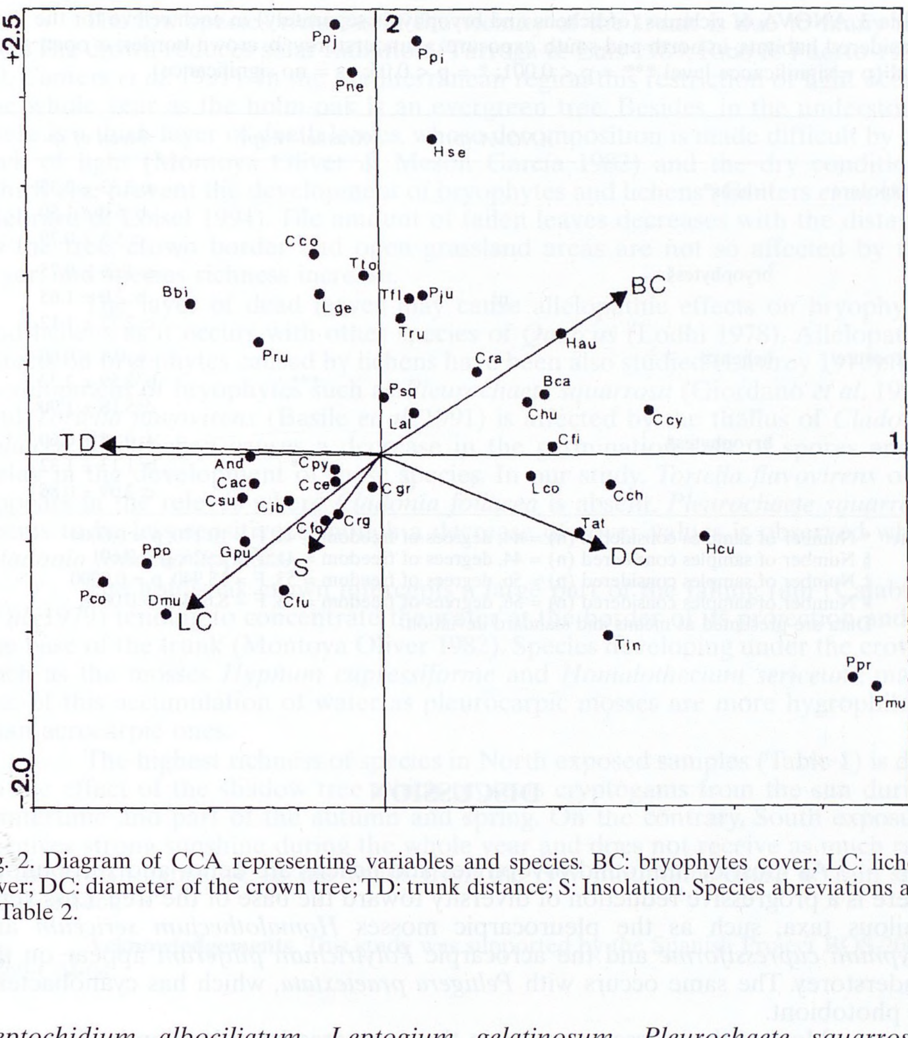

Fig. 2. Diagram of CCA representing variables and species. BC: bryophytes cover; LC: lichen cover; DC: diameter of the crown tree; TD: trunk distance; S: Insolation. Species abreviations are in Table 2.

Leptochidium albociliatum, *Leptogium gelatinosum*, *Pleurochaete squarrosa*, *Tortella tortuosa* and *Tortula ruralis*, which grow on the crown border, or in all habitats, as they have wide ecological requirements.

The exposure variable was introduced in the analysis as an indirect measure of insolation, the highest value being represented by the southern exposure; which is related to the variables "distance to the trunk" and "cover of lichens". In this situation we found species such as *Cladonia foliacea, C. furcata, C. rangiformis, Diploschistes muscorum, Parmelia conspersa and P. pokornyi*, most of them photophilous and xerophilous, with lichens being more abundant and with higher cover values. The opposite side of the axis represents the northern exposure, with the lowest value of insolation, which is related to the variable "cover of bryophytes", and is opposite to "distance to the trunk". *Cladonia ramulosa, Homalothecium aureum* and *Hypnum cupressiforme* have their optimum here, because they have higher moisture requirements. It is well known that in northern exposure bryophytes are more abundant and have higher cover values (Hébrard & Loisel 1994).

Table 3. ANOVA of richness (of lichens and bryophytes separately) in each relevé for the three considered habitats, in north and south exposure. a: understorey; b: crown border; c: open grassland (p = significance level *** = p < 0.001; * = p < 0.05; ns = no significance).

		ANOVA (p)	*Kruskal-W. (p)*	*Mean of sp*
N-exposure	lichens*		*	a: 2.33 ± 2.35 b: 5.0 ± 1.50 c: 5.5 ± 0.79
	bryophytes§	ns		a: 1.65 ± 0.75 b: 2.0 ± 1.65 c: 2.72 ± 1.12
S-exposure	lichens‡		***	a: 0.8 ± 0.60 b: 2.59 ± 2.32 c: 5.18 ± 1.90
	bryophytes#		***	a: 0.18 ± 0.60 b: 1.13 ± 1.32 c: 2.09 ± 0.86

Note: * Number of samples considered (n) = 44, degrees of freedom = 41, F = 10.170, p = 0.0004
§ Number of samples considered (n) = 44, degrees of freedom = 41, F = 2.926, p = 0.691
‡ Number of samples considered (n) = 56, degrees of freedom = 53, F = 18.940, p = 0.0000
# Number of samples considered (n) = 56, degrees of freedom = 53, F = 8.604, p = 0.0008
Data are presented as means and standard deviation.

DISCUSSION

As most of the found bryophytes and lichens are helio- and xerophilous, there is a progressive reduction of diversity toward the base of the tree. Less xerophilous taxa, such as the pleurocarpic mosses *Homalothecium sericeum* and *Hypnum cupressiforme* and the acrocarpic *Polytrichum piliferum* appear on the understorey. The same occurs with *Peltigera praetextata*, which has cyanobacteria as photobiont.

Most of the mosses growing in the open grassland develop hyaline hairs at the end of the leaves several of them having contorted leaves to avoid water loss. Bryophytes and lichens obtain liquid water in the early morning by dews (Canters *et al.* 1991). *Tortula ruralis* has a coordination of architectural and physiological characteristics to survive under xeric conditions (Hamerlynck *et al.* 2000). Some cyanobacterial lichens could be benefited with this water, too. Such as *Leptochidium albociliatum*, which also develops white hairs as protection against sun insolation.

The tree crown offers protection against frosts. There can be a mean difference of 5 ºC between the understorey and the open grassland (Montoya Oliver 1982). Freezing climatic conditions favour the dispersion of fruticose and foliose lichens, such as in species of *Cladonia* (Ahti 2000). Thallus fragmentation caused by frosts, and dispersion by wind and animals help species to colonize new open areas (Heinken 1999). Fragments of *Cladonia foliacea*, *C. furcata*, *C. rangiformis*, *Cetraria aculeata* and *Parmelia conspersa* are easily spread in the open grassland and show the highest cover values there.

The low species richness in the vicinity of the trunk is due to many factors. The crown reduces solar radiation (Tárrega & Luis 1989; Rico & Puerto 1988-89, Canters *et al.* 1991). In the Mediterranean region this restriction of light occurs the whole year as the holm-oak is an evergreen tree. Besides, in the understorey there is a thick layer of death leaves, whose decomposition is made difficult by the lack of light (Montoya Oliver & Mesón García 1982) and the dry conditions, which else prevent the development of bryophytes and lichens (Canters *et al.* 1991, Hébrard & Loisel 1994). The amount of fallen leaves decreases with the distance to the tree, crown border and open grassland areas are not so affected by this layer, and species richness increase.

The layer of dead leaves may cause allelopathic effects on bryophytes and lichens as it occurs with other species of *Quercus* (Lodhi 1978). Allelopathic effects on bryophytes caused by lichens have been also studied (Lawrey 1977). The development of bryophytes such as *Pleurochaete squarrosa* (Giordano *et al.* 1999) and *Tortella flavovirens* (Basile *et al.* 1991) is affected by the thallus of *Cladonia foliacea*. This lichen causes a decrease in the germination rate of spores and a delay in the development of these species. In our study, *Tortella flavovirens* only appears in the relevés where *Cladonia foliacea* is absent. *Pleurochaete squarrosa* seems to be less sensitive, although a decrease of cover values is observed when *Cladonia foliacea* appears.

The holm-oak crown intercepts a large part of the falling rain (Calabuig *et al.* 1979) tending to concentrate the water at the border of its projection and at the base of the trunk (Montoya Oliver 1982). Species developing under the crown, such as the mosses *Hypnum cupressiforme* and *Homalothecium sericeum*, make use of this accumulation of water as pleurocarpic mosses are more hygrophilous than acrocarpic ones.

The highest richness of species in North exposed samples (Table 1) is due to the effect of the shadow tree which protects cryptogams from the sun during wintertime and part of the autumn and spring. On the contrary, South exposure receives strong sunshine during the whole year and does not receive as much rain as the North exposure, as the winds from the NW mountains cause a "rain shadow" effect.

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