Effects of browsing in relation to vegetation cover on common yew (*Taxus baccata* L.) recruitment in Mediterranean environments

Emmanuele Farris · Rossella Filigheddu

Abstract Common yew (*Taxus baccata* L.) stands are recognized as prioritary habitats for biodiversity conservation within the European Union. The effects of browsing on the regeneration capacity and spatial dispersal of *T. baccata* recruits at the European southern limit of the species in the Mediterranean Basin have been herein studied. The efficacy of *T. baccata* recruitment has been evaluated at six localities in the Northern Sardinia mountains, which have similar altitude, climate, soil, and vegetation but have different types of uses (three were grazed by livestock and three were not). At each site, five habitats have been identified for *T. baccata* seed dispersal: reproductive female *T. baccata* canopy, reproductive female *Ilex aquifolium* canopy, non-fleshy-fruited tree canopy, fleshy-fruited shrubs, and open areas. The density of seedlings was found to be greater under fleshy-fruited trees (reproductive female *T. baccata* and *I. aquifolium*) than under shrubs, whereas the sapling density was higher in shrubby habitats, especially at grazed sites due to the mechanical protection afforded by the spiny shrubs against herbivores. Land use (LU) has been found to be the most important factor in determining the spatial distribution of seedlings and saplings in relation to forest habitats. Although browsers had an ephemeral but positive effect on seed germination through their trampling and the resultant scarification, this process eventually became ineffective as was shown by the occurrence of the lowest density of saplings in those habitats where the density of seedlings was the highest. The ultimate and most important effect of browsing was the sharp decrease in the density of saplings, and their almost complete extinction, in non-shrubby habitats. This study highlights the result that, in Mediterranean ecosystems, browsing constitutes the main negative factor on *T. baccata* seedling-sapling transition and furthermore confirms the necessity to preserve shrubby patches in the vicinity of reproductive female *T. baccata* and *I. aquifolium* to permit the regeneration of *T. baccata* in the presence of livestock. Moreover, at ungrazed sites, *T. baccata* is able to colonize non-shrubby shady habitats. The application of different management strategies to ungrazed and grazed sites should therefore be the main direction in the management and preservation of *T. baccata* stands in the Mediterranean region.

Keywords Biodiversity conservation · Forest management · Habitat Directive · Mediterranean Basin · Plant–animal interaction · Plant–plant interaction

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Introduction

Mediterranean stands of the common yew (*Taxus baccata* L.) are recognized as prioritary habitats for biodiversity conservation within the European Union, and they are designated as habitat code 9580* by the European Council Directive 43/92/EEC (European Commission 1992). This implies that they need adequate management within the Natura-2000 ecological network (Ostermann 1998).

Taxus baccata is a long-living tree species, the occurrence of which is progressively decreasing all over Europe (Tittensor 1980; Hulme 1996; Svenning and Magård 1999; García et al. 2000). Probably as a result of both regression after the previous Ice Age (Bennett et al. 1991) and human disturbance (O'Connell and Molloy 2001), the distribution *of T. baccata* is discontinuous throughout its range. In the Mediterranean Basin, the occurrence of *T. baccata* is limited only to mountain areas: its spread consists of a small number of isolated populations located mainly on shady northern slopes (García et al. 2000; Thomas and Polwart 2003). The Mediterranean Basin is the European low-latitude limit of *T. baccata* and thus can be considered its rear edge (Hampe and Petit 2005).

Although some populations of this species have been observed to increase in central-northern European areas under favorable conditions (Seidling 1999; Iszkuło and Boratyński 2005) or under active management (Svenning and Magård 1999), natural regeneration of *T. baccata* is probably limited due to overuse (Thomas and Polwart 2003), by pressure from seed-predators and herbivores, and due to scarcity of microsites for recruitment (Hulme 1996; García et al. 2000; García and Obeso 2003; Mysterud and Østbye 2004), in addition to the lack of adults. The populations occur at sites often characterized by heavily shaded conditions, so that, even if a small level of shade tolerance permits *T. baccata* to regenerate freely beneath a deciduous canopy, the light conditions within the yew-woods are probably not favorable for its extensive growth (Perrin et al. 2006). Previous reports have suggested that *T. baccata* regeneration depends on the facilitative effects of shrubs (Tittensor 1980; Hulme 1996; García and Obeso 2003), especially in systems wherein the browsing pressure is high (García et al. 2000).

Facilitation among plants occurs when the recruitment and survival of one species is enhanced by another species as a consequence of their spatial association (Callaway 1995; Callaway and Walker 1997; Bruno et al. 2003). Facilitation occurs through both direct and indirect interactions. In the former case, the nurse plant (Tewksbury and Lloyd 2001) facilitates the growth of the other plant by changing the physicochemical environment under its canopy so that it is better than the surrounding areas. In the latter case of indirect interaction, the positive interaction between the two species is mediated by a third organism as follows: (i) disperser-mediated facilitation: when frugivores are attracted by shrubs and disperse the seeds of the associated tree species (shrubs thus become the dispersal foci for trees; Verdú and García-Fayós 2003) and (ii) herbivore-mediated facilitation: when shrubs protect tree propagules from herbivores (García et al. 2000).

Disperser-mediated facilitation and herbivore-mediated facilitation can also occur together, for example, when a shrub acts as a dispersal focus for the seeds of a given tree and additionally protects its propagules against herbivores (Verdú and García-Fayós 2003): *T. baccata* has been already indicated as a species that benefits from both disperser-mediated and herbivore-mediated facilitation (García et al. 2000; García and Obeso 2003).

The importance of browsing pressure on *T. baccata* recruitment at northern latitudes (Mysterud and Østbye 2004; Perrin et al. 2006) prompts the belief that closer examination is necessary to quantify the effects of browsing on *T. baccata* regeneration in the Mediterranean environment, which have been poorly investigated until now. Considering the importance of browsing and grazing pressure on plant communities in the Mediterranean Basin (Le Houérou 1981), an understanding of the role of different vegetation types in conditioning both the regeneration capacity of yew and the spatial dispersal of its recruits under grazed versus ungrazed conditions at the European rear edge of *T. baccata* populations is proposed to be acquired in this study.

The results of two descriptive investigations on *T. baccata* regeneration carried out in the mountainous areas of Northern Sardinia (Italy) are presented in this study: the first investigation was designed to estimate the spatial variability in the abundance of *T. baccata* juveniles between the grazed and ungrazed sites and among different habitats, whereas the second one was designed to estimate the protective role of shrubs against herbivores with reference to *T. baccata* recruits.

Methods

Species and area under study

Taxus baccata is a dioecious, long-living (>1,000 years), slow-growing, nonresinous, evergreen gymnosperm that grows up to 28 m in size, reaching sexual maturity at about 70 years (Thomas and Polwart 2003). Female structures (Stützel and Röwekamp 1999) produce ovoid seeds (6–7 × 5 mm at maturity) with a tough seed coat, and which are partially surrounded by a fleshy red aril (9–7 mm) that falls with the seed at maturity. The aril ripens in the first year, but seedlings start to emerge in the second spring after seedfall (Melzak and Watts 1982). Seeds are dispersed by birds (García et al. 2000) and mammals (Tittensor 1980; Bermejo and Guitián 2000) and can be consumed by rodents after dispersal (Hulme 1996).

Populations of *T. baccata* in Sardinia are spatially scattered and are constituted by a few adult individuals growing within small areas in mountain ranges (Desole 1948; Desole 1966). This study was conducted during the year 2004 on autochthonous *T. baccata* populations at six localities in Northern Sardinia (Table 1), which had similar altitude, climate, soil, and vegetation but which differed in their types of uses (three were grazed by livestock and three were not). Livestock, only present at the sites 4, 5, and 6, was composed of 1.7 sheep ha^{-1} and 0.06 cattle ha^{-1} (average of the three sites for the period 1990–2007). Wild ungulates were absent, with the exception of *Sus scrofa* that was present at all the sites studied. At the sites 4, 5, and 6 of this study,

T. baccata was browsed by vertebrate herbivores in spite of its foliage being poisonous, similar to that reported from other regions of its occurrence range (Tittensor 1980; García et al. 2000; García and Obeso 2003; Thomas and Polwart 2003; Mysterud and Østbye 2004; Perrin et al. 2006). Farmers believe that yew is poisonous only to those animals that browse it for the first time during adulthood without having ingested it before and that it is harmless to those livestock that regularly browse yew foliage since their youth, thus developing tolerance to it.

The climate at the sites of study is of the Mediterranean mountain type: at site 3, the annual mean temperature is 10.3°C and the mean rainfall is 1270.8 mm year^{-1} (average of the period 1965–1987). Summer is usually hot and dry (in July, the average temperature is 19.2°C and the mean rainfall is only 14.8 mm), whereas the winter is mild and humid (in February, the average temperature is 3.3°C and the mean rainfall is 157.7 mm). *T. baccata* stands grow on all acidic soils that have developed on rhyolitic, schistic, and granitic substrata.

Adult yews at the examined sites ranged from 9 to 59 individuals (Table 1). The sex ratio was male-based and varied from 50.6% of males at site 6–61.1% at site 5. The average age of adult yews, as estimated from their diameter at breast height (DBH), assuming 1 mm = 1 year (Thomas and Polwart 2003), was the minimum at site 3 (107 years) and reached its maximum at site 4 (400 years).

All the yew populations studied were included within non-fleshy-fruited trees (NFFT) stands, composed mainly of *Quercus pubescens* Willd., *Q. ilex* L., *Acer monspessulanum* L., and *Fraxinus ornus* L.,

Table 1 Characteristics of the study sites

Site	Locality	Coordinates	Altitude m a.s.l.	Substratum	Surface (m^2)	No of adult yews	DBH (mm)	Livestock (heads ha^{-1})
1	Montiferru	40°09′N/8°37′E	880	Volcanic	5,330	20	216	Absent
2	Mt. Lerno	40°36′N/9°09′E	900	Granitic	4,866	9	165	Absent
3	Mt. Limbara	40°50′N/9°10′E	1,050	Granitic	5,960	27	107	Absent
4	Marghine	40°21′N/8°53′E	990	Volcanic	4,200	14	400	3.61 sheep; 0.03 cattle
5	Mt. Rasu	40°25′N/8°59′E	1,100	Schist	4,066	59	360	1.02 sheep; 0.08 cattle
6	Sa Fraigada	40°30′N/9°03′E	870	Schist	3,590	18	247	0.43 sheep; 0.07 cattle

DBH was measured with callipers. Livestock density is a mean for the period 1990–2007

which covered 54.4–68.5% of the studied plots (Table 2). *Ilex aquifolium* L. was also present at all the sites. In Sardinia, holly is a tree rather than a shrub (Camarda and Valsecchi 1983), reaching heights up to 12 m, and is the only other plant with a phenology similar to that of yew, as both species ripen simultaneously in November–December. Shrubby patches are found in the wood understory, dominated by *Rubus ulmifolius* Schott, with blackberries ripening in August–September. Other less frequent shrubs are *Crataegus monogyna* Jacq. and *Rosa canina* L. Nonfleshy-fruited shrubs do not occur at the study sites, except for some individuals of *Erica arborea* L. and *E. scoparia* L. at sites 1, 2, and 3. Glades are present at all sites as a consequence of wood clearing, burning, and/or grazing. The prevalent habitat at the sites is NFFT, followed by open areas, shrubs, *Ilex,* and *Taxus* (Table 2). Plant names have been provided following Conti et al. (2005).

The main yew-seed dispersers at these sites were frugivorous birds such as *Turdus merula*, *T. philomelos*, *T. viscivorus* and, to a minor extent, *Garrulus glandarius* and *Erithacus rubecula*; however, mammals such as *Vulpes vulpes* and *Martes martes* also have been observed to eat arils from the ground (personal observation of the authors). Occasionally, *Dendrocopos major* and *Parus major* were observed to eat the seeds.

Sampling design

To estimate the spatial distribution of juveniles, 3 ungrazed (1, 2, and 3) and 3 grazed (4, 5, and 6) sites were selected. At each site, five habitats were identified: *Taxus* (areas under the canopy of reproductive females of *T. baccata*), *Ilex* (areas under the canopy of reproductive females of *I. aquifolium*), NFFT (areas under the canopy of adult NFFT), shrubs (areas below the shrubs), and open (open areas, always forest gaps with herbaceous species cover). The areas under the canopy of reproductive females of *T. baccata* and *I. aquifolium* were sampled rather than those under the males, because, in dioecious species, the gender of the reproductive and nurse plants can significantly determine the spatial population structure (Montesinos et al. 2007).

Ten quadrats, 2×2 m in size, were randomly chosen for each combination of site × habitat, so that, overall, 300 quadrats were sampled for the complete experiment. Two response variables were considered: seedling abundance and sapling abundance. Sampling was carried out during the spring of 2004 by identifying individuals belonging to different life stages in each quadrat: the nonreproductive individuals with stem diameter <5 mm were considered as seedlings, whereas those with diameter >5 mm were considered as saplings.

Table 2 Vegetation structure as percent cover of the habitats at each site

Site	Taxus	Ilex	NFFT	Shrubs	Open	Main tree species	Main shrub species
1	2.8	5.4	68.5	12.8	10.5	*Quercus ilex, Q. pubescens, Ilex aquifolium, Acer monspessulanum*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina, Prunus avium, Erica arborea*
2	1.9	3.7	57.8	14.6	22.0	*Quercus ilex, Ilex aquifolium, Fraxinus ornus*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina, Prunus spinosa, Erica arborea, E. terminalis*
3	3.7	4.1	61.7	13.5	17.0	*Quercus ilex, Ilex aquifolium, Fraxinus ornus*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina, Erica arborea, E. scoparia*
4	8.2	12.6	56.3	11.4	11.5	*Quercus pubescens, Ilex aquifolium, Acer monspessulanum*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina, Sorbus torminalis*
5	10.1	7.2	54.4	9.1	19.2	*Quercus pubescens, Ilex aquifolium, Acer monspessulanum*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina*
6	6.3	9.1	63.6	11.1	9.9	*Quercus ilex, Q. pubescens, Ilex aquifolium*	*Rubus ulmifolius, Crataegus monogyna, Rosa canina*

The vegetation structure was described as the prevalence (%) of each habitat at each site and was determined by means of 5 transects 100 m long (Bullock 1996) randomly located at each site. At each meter along the transect, the habitat was qualitatively recorded so that at each site a total of 500 samples were gained

At each site, in the same 300 quadrats, the intensity of herbivory on the saplings was estimated as the proportion of shoots browsed per individual. These data permitted the determination of the average intensity of herbivory at each habitat and the risk of herbivory at each site, which was calculated as the percentage of browsed saplings.

To estimate the protective role of shrubs for *T. baccata* recruits against herbivores at each of the three grazed and three ungrazed sites, 24 saplings (144 saplings in total) that did not differ in any other characteristic related to the attraction to herbivores than the vicinity to shrubby patches were chosen at random. The following parameters were evaluated for each sapling: (1) the intensity of herbivory, as the proportion of shoots browsed per individual; (2) the overgrowth, as the difference (in cm) between the height of the *T. baccata* sapling and the maximum height of the shrub in direct contact with it (negative values were obtained when the shrub overgrows the *T. baccata* sapling; García et al. 2000); and (3) shrub cover as the percentage of soil surface covered by shrubs within a circle of 1-m radius from the base of the stem of the *T. baccata* sapling.

Statistical analysis

Mixed model ANOVAs were used to test the differences between the abundances of the seedlings and saplings with reference to LU (grazed versus ungrazed: Gr versus Ungr), Sites (3 levels), and Habitats (*Taxus, Ilex*, NFFT, shrubs, and open). LU was considered as a fixed factor, Site (S) as random and nested within LU, and Habitat (HA) as fixed and orthogonal.

ANOVAs were further used to test the differences in intensity of herbivory (I), overgrowth (OG), and shrub cover (SC) between the two types of LU (Gr versus Ungr) and among Sites (3 levels). LU was considered as a fixed factor and Site (S) as random and nested within LU.

Before proceeding with the analyses, the homogeneity of variances was tested by Cochran's *C*-test and, whenever necessary, data were appropriately transformed. Whenever transformations did not produce homogeneous variances, ANOVA was used after setting $\alpha = 0.01$ to compensate for the increased likelihood of Type I errors. Student–Newman–Keuls (SNK) tests were carried out to compare the mean

values of all significant factors (Underwood 1997). ANOVAs were conducted using the GMAV5 software package (University of Sydney).

Finally, to highlight the effects of the spatial arrangement of shrubs on the herbivory intensity for yew saplings, the intensity of herbivory for each sapling at the grazed sites (72 saplings in total) was correlated with individual overgrowth and shrub cover.

Results

Spatial distribution of seedlings and saplings

A higher total mean density of seedlings was observed (mean $\pm$ SE $= 0.53 \pm 0.05$ seedlings m^{-2}) at the grazed sites than at ungrazed sites (mean $\pm$ SE $= 0.17 \pm 0.02$ seedlings m^{-2}). Higher densities of seedlings were obtained under canopies of reproductive female *T. baccata* and *I. aquifolium*. No seedlings were found in open habitats at the ungrazed sites, and very few were observed at the grazed open habitats (Fig. 1a).

Conversely, the sapling density was greater at the ungrazed sites (mean $\pm$ SE $= 0.11 \pm 0.01$ saplings m^{-2}) than at the grazed sites (mean $\pm$ SE $= 0.04 \pm$
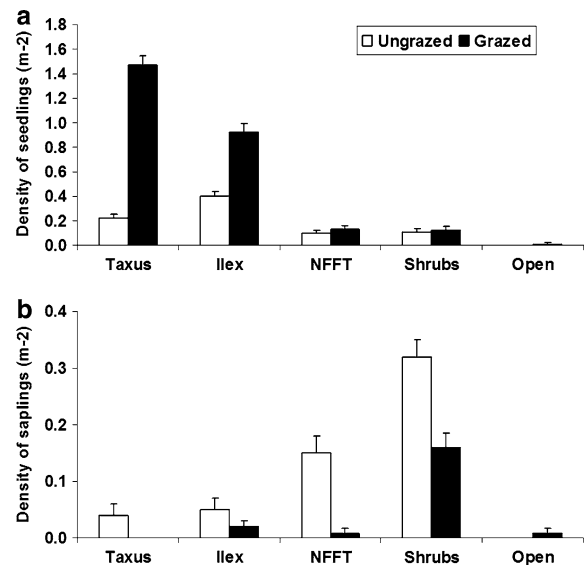

Fig. 1 Mean value (+1 S.E.) of the density (no. of individuals m^{-2}) of seedlings (**a**) and saplings (**b**) in different habitats and at different sites under two different types of land use (grazed versus ungrazed)

0.00 saplings m^{-2}). The habitats containing higher sapling density were shrubby ones. No saplings were found in the open habitat at ungrazed sites and very few were observed at the grazed sites (Fig. 1b).

Seedling density was significantly affected by the interaction between the types of both LU and habitat (Table 3). The SNK test (SE = 0.0095) showed the seedling density to be lower at the ungrazed sites in *Taxus* and *Ilex* habitats but no differences were observed for other habitats. Seedling density at the ungrazed sites was in the order *Ilex* > *Taxus* > shrubs = NFFT > open, whereas the same was in the order *Taxus* > *Ilex* > shrubs = NFFT > open at the grazed sites.

Further, the sapling density was significantly affected by the interaction between the types of LU and habitats (Table 3). The SNK test (SE = 0.0052) showed the sapling density to be lower at the grazed sites in all habitats but the open ones, in which no differences were observed between the grazed and ungrazed sites. Sapling density at the ungrazed sites was as follows: shrubs > NFFT > *Ilex* = *Taxus* > open, whereas the order of sapling density at the grazed sites was shrubs > *Ilex* = *Taxus* = NFFT = open.

The density of seedlings and saplings did not significantly vary at the scale of the site (Table 3).

Herbivory on saplings

The risk of herbivory on the saplings was 8.3% at the ungrazed sites, but it reached 95.8% at the grazed locations. The intensity of herbivory on *T. baccata* saplings was not determined in open habitats and under *Taxus* and NFFT canopy at the grazed sites due to the extremely low density of saplings (Fig. 1b). The intensity of herbivory at the ungrazed sites averaged 0.3% and ranged from 0.2% under *Taxus* canopy to 0.6% under *Ilex* (probably due to the mechanical damage caused by wild *Sus scrofa* or mechanical injuries other than browsing); conversely, at the grazed sites, saplings lost an average of 48.3% of their shoots when occurring under shrubs and 71.3% of the same when growing under *Ilex* (Table 4). Individually, the intensity of herbivory never exceeded 10% at the ungrazed sites but reached 100% for some individuals at the grazed locations.

Land use was a significant factor in determining the intensity of herbivory relative to *T. baccata* saplings in shrubby habitats. The SNK test for intensity (SE = 2.4) showed significantly lower values at the ungrazed sites. Overgrowth was 52.5 ± 9.3 cm at the ungrazed sites, but it decreased to −18.7 ± 7.1 cm at grazed sites. LU and site were significant factors in determining the overgrowth between the *T. baccata* saplings and shrubs. SNK test for overgrowth (SE = 10.6) showed lower values at the grazed sites. The shrub cover averaged 45.3% at ungrazed sites and 56.4% at grazed sites, but no significant effects were highlighted by ANOVA (Table 5).

Herbivory intensity on saplings at grazed sites (Fig. 2) was positively related to overgrowth

Table 4 Average intensity of herbivory on yew saplings (% of shoots browsed per individual) at five habitats between ungrazed and grazed sites

|	Taxus	Ilex	NFFT	Shrubs	Open
Ungrazed	0.2	0.6	0.3	0.3	nd
Grazed	nd	71.3	nd	48.3	nd

At open habitat and under *Taxus* and NFFT canopy at grazed sites, intensity of herbivory was not determined (nd) due to the extremely low density of saplings (see also Fig. 1b)

Table 3 ANOVA examining the density (individuals m^{-2}) of seedlings and saplings between type of land use (LU), sites (S), and habitats (HA)

Source of variation	df	Seedlings			Saplings		
		MS	F	P	MS	F	P
LU	1	3.2352	837.91	<0.0001	0.0883	47.50	0.0023
S (LU)	4	0.0039	0.20	0.9403	0.0019	0.81	0.5170
HA	4	3.6290	1362.76	<0.0001	0.1190	143.32	<0.0001
LU × HA	4	1.3596	510.56	<0.0001	0.0173	20.82	<0.0001
HA × S (LU)	16	0.0027	0.14	1.0000	0.0008	0.36	0.9891
Residual	270	0.0197			0.0023		
Transformation		ln (x + 1)			Sqrt(X + 1)		
Cochran's C-test		0.0958 n.s.			0.1721 (P < 0.01)		

Table 5 ANOVA examining intensity of herbivory expressed as percent (I), overgrowth in cm (OG) and shrub cover in percent (SC) between type of land use (LU) and sites (S)

Source of variation	df	I			OG			SC		
		MS	F	P	MS	F	P	MS	F	P
LU	1	83006.4117	194.14	0.0002	182706.3784	22.72	0.0089	4433.3403	3.69	0.1270
S (LU)	4	427.5487	1.01	0.4033	8043.1076	5.50	0.0004	1199.9444	1.30	0.2747
Residual	138	422.3184			1463.7048			926.0402		
Transformation		None			None			None		
Cochran's test		0.4531 ($P < 0.01$)			0.2685 n.s.			0.2001 n.s.		
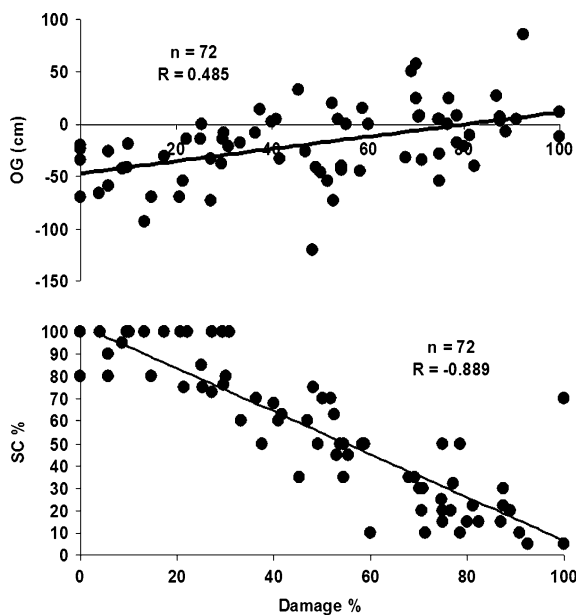
Fig. 2 Relation between intensity of herbivory (%) on saplings, shrub overgrowth (OG, cm) over them and shrub cover (SC, %) around them

($R = 0.485$, $n = 72$, $P < 0.0001$) and negatively related to shrub cover ($R = -0.889$, $n = 72$, $P < 0.0001$).

Discussion

Ecological factors affecting yew recruitment

This study shows that seedlings were concentrated mainly under the canopy of reproductive female yews and hollies at both grazed and ungrazed sites. Phenological observations in the field have highlighted that bramble (*Rubus ulmifolius*), the most important shrubby species in this study, fructifies earlier than the yew. At the time of aril ripening, holly, the unique fleshy-fruited plant, is able to attract frugivores. This can explain why the highest seedling densities have been observed under the canopy of yew and holly, similar to reports from the Cantabrian Range (García and Obeso 2003), and contrary to reports from Sierra Nevada, where holly is absent but many fleshy-fruited mountain shrubs are present (García et al. 2000). This result strongly emphasizes the most critical factor for the regeneration of plant species of boreoalpine origin in the Mediterranean area: the life history and biological and phenological traits of Mediterranean potential nurse species can be different from those of a boreoalpine facilitated tree. This can have important consequences on the regeneration of species, benefiting from positive interaction with other species (Callaway 1995): holly is the only species that is synchronous with the yew plants in the sites studied. This can explain the reduced importance of shrubby habitats and the increased importance of holly as a dispersal focus, which acts by attracting avian dispersers.

Many studies have concentrated on the microenvironmental conditions that nurse plants preserve under their foliage: these conditions are linked to shade and, consequently, to summer drought and nutrient availability (Valiente-Banuet and Ezcura 1991). The present study confirms that yew recruits in Mediterranean environments are shade-tolerant and are able to grow in any habitat except sunny ones (open), albeit at different densities, as presented by Perrin et al. (2006) in Ireland. Further studies will focus on the effects of factors such as solar radiation and correlate the different ecological factors regulating yew recruitment. Mechanisms that regulate this type of biotic and abiotic interactions provide valuable information because they are likely to affect the

patterns of recruitment on both local and the land-scape scales.

The density of *T. baccata* seedlings was higher at the grazed than the ungrazed sites in all shaded habitats. However, the density of saplings was higher at the ungrazed rather than the grazed sites in all habitats. The density of *T. baccata* recruits was particularly affected by the habitat with respect to LU; conversely, no significant effect was apparent due to the differences among the sites within the same type of LU.

The browsing of saplings caused a significant increase in the risk and intensity of herbivory and a decrease in the overgrowth, although the shrubby cover around *T. baccata* saplings did not change significantly between the grazed and ungrazed sites. The intensity of herbivory for the saplings at the grazed sites was correlated positively with overgrowth and negatively with shrub cover.

The current study highlights the contrasting effects of browsing on *T. baccata* regeneration. Browsers probably had positive effects on seed germination through their trampling and resulting scarification. However, this process gradually becomes ineffective because, at grazed sites, the lowest density of saplings was observed in habitats where the density of seedlings was the highest: in these terms, the positive effect of browsers on germination could be ephemeral. Moreover, the most important effects of browsing are the sharp decrease in the total density of saplings, their concentration in the shrubby habitats, and their nearly complete extinction in non-shrubby habitats.

Some previous studies reported that *T. baccata* regeneration was seed predator-limited and microsite-limited (Hulme 1996). Only recently, García et al. (2000) suggested facilitation to be herbivore-mediated in Sierra Nevada, whereas, in the Cantabrian Range, García and Obeso (2003) showed that the consequences of browsing on the recruitment of *T. baccata* were more evident in the late regeneration stages, such as for saplings, rather than for seedlings in their first year. This study confirms the opposite effects of browsing on *T. baccata* seedlings and saplings in Mediterranean environments, previously highlighted for *T. baccata* (García and Obeso 2003) and other tree species (Perrin et al. 2006) only in temperate-oceanic areas.

Moreover, these data confirm the essential role of shrubs in the regeneration of *T. baccata* as mechanical

protection in the presence of browsing, as already highlighted by applicative studies on the use of shrubs as nurse plants for forest species (Castro et al. 2002; Gómez-Aparicio et al. 2004). However, this study shows that, at the ungrazed sites, a significant share of *T. baccata* saplings was able to grow at all the shaded habitats. This suggests that grazed and ungrazed sites require different management strategies.

Consequences for yew conservation

For purposes of conservation, habitats need to be identified as being both potentially suitable for *T. baccata* recruitment and actually effective for seedling-sapling transition.

Therefore, from the conservation point of view, qualitative and quantitative patterns in the spatial distribution of *T. baccata* saplings should be considered to be very different in the grazed and ungrazed sites. The importance of shrubs and the need to preserve shrubby patches in the vicinity of reproductive female *T. baccata* and *I. aquifolium* for the regeneration of *T. baccata* in the presence of browsing has been herein confirmed, similar to the previous report that, in dioecious species, the act of attracting frugivorous birds by reproductive females and the improvement of environmental conditions beneath tree canopies were the factors mainly responsible for variation in juvenile density (Montesinos et al. 2007). Although the saplings are more abundant in shrubby habitats, they are shade-tolerant and can occupy any habitat in ungrazed oakwoods, except those having direct sunlight. At the ungrazed sites, 15.6% of saplings grew on an average under the NFFT canopy, whereas only 1.2% of saplings grew at the grazed sites under this habitat. This significant difference in the total density of *T. baccata* saplings under the NFFT canopy at grazed sites could be mainly due to the action of herbivores and could have long-term consequences for the spatial distribution of adult *T. baccata* stands, and therefore on the survival of populations.

Since *T. baccata* is able to colonize non-shrubby habitats at ungrazed sites, referring to Hulme (1996), browsing can be stated to constitute the main negative factor on *T. baccata* seedling-sapling transition in Mediterranean ecosystems. Considering the fact that, in many Mediterranean areas, browsing is directly driven by humans through domestic livestock

(as in the present sites of study), this article proposes the regulation of shepherding activities, in addition to the use of shrubs, in programmes that aim to protect *T. baccata* saplings.

The conservation of shrubby patches at the grazed sites, the regulation of domestic browsing with the enhancement of the potential for sustainable forest management, and the application of different management strategies for ungrazed and grazed sites are the main management directions that can preserve the relic of *T. baccata* stands in the Mediterranean area.

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