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RESEARCH ARTICLE

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Forest structure of Mediterranean yew (*Taxus baccata* L.) populations and neighbor effects on juvenile yew performance in the NE Iberian Peninsula

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Abstract

Aim of study: In the Mediterranean region, yew (*Taxus baccata* L.) usually grows with other tree species in mixed forests. Yew recruitment and juvenile growth may depend on the structure of the forest and the net balance between competition for soil water and nutrients with neighbors and facilitation that these neighbors exert by protecting the plants from direct sun exposure. This study aims, at a regional scale, to analyze the structure of forests containing yew, and, on an individual level, to analyze the effect of the surrounding vegetation structure on the performance of yew juveniles.

Area of study: The structural typologies of yew populations were defined based on field inventories conducted in 55 plots distributed in 14 localities in the North-Eastern (NE) Iberian Peninsula, covering a wide range of yew distribution in the area. In a second step, an analysis of neighboring species' effects on juveniles was conducted based on the data from 103 plots centered in yew juveniles in five localities.

Main Results: A cluster analysis classified the inventoried stands into four forest structural types: two multi-stratified forests with scattered yew and two yew groves. Multiple regression modeling showed that the $\delta^{13}C$ measured in last year's leaves positively relates to the basal area of conifer neighbors, but negatively with the cover of the yew crown by other trees.

Research highlights: At a stand-level, the density of recruits and juveniles (625 ± 104 recruits ha^{-1}, 259 ± 55 juveniles ha^{-1}) in mixed forests was found to be higher than that on yew dominant stands (181 ± 88 recruits ha^{-1} and 57 ± 88 juveniles ha^{-1}). At an individual-level, the water stress (estimated from leaf $\delta^{13}C$) of yew juveniles seems alleviated by the crown cover by neighbors while it increases with the basal area of conifers. Yew conservation should focus on selective felling for the reduction of basal area of neighbors surrounding the target tree, but avoid affecting the canopy cover to contribute to enhanced yew juvenile growth.

Keywords: Biodiversity conservation; $\delta^{13}C$; forest management; plant-plant interaction; recruitment; *Taxus baccata*; water use efficiency.

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Introduction

Yew (*Taxus baccata* L.) is a European temperate species (Preston & Hill, 1997), widely distributed in regions with mild winters and high humidity. When climatic conditions become limiting factors, such as extreme temperatures, or severe drought, yew is restricted to favorable niches that are protected from these extreme conditions (Thomas & Polwart, 2003). Consequently, in the Mediterranean region, yew trees usually grow in isolated populations in shady mountain ravines and on cliffs, or as a sub-canopy tree in a variety of forest communities (Cortés *et al.*, 2000; Piovesan *et al.*, 2009). Mediterranean yew stands were probably isolated into small populations during the last glaciations (Bennet *et al.*, 1991) and are now endangered by current land-use changes and fire spread. Hence, the Mediterranean yew habitat is recognized as a priority habitat for biodiversity conservation within the European Union (Habitat 9580*, European Council Directive 43/92/EEC, European Commission, 1992).

Facilitation among plants occurs when the recruitment and survival of one species is enhanced by another species by making the physical environment under its canopy more suitable for the beneficiary (Bertness & Callaway, 1994; Verdú & García-Fayos, 1996; Garcia *et al*., 2000). However, the net result of plant interactions may depend on the stress induced by the direct environment, which could be positive in some conditions but become negative under others (Iskulo *et al.*, 2012). The need to identify appropriate management to maintain or enhance the resilience of forest ecosystems under the projected impacts of climate change has been highlighted by different authors (e.g. Lindner, 2000; Messier *et al.*, 2013; Coll, 2014). From a conservation point of view, the identification of facilitation mechanisms may be useful for the management of threatened plants, such as the yew, or for the enhancement of the resilience of ecosystems to the projected impacts of the climate change (e.g. Batllori *et al.*, 2009).

Although yew is an extremely shade-tolerant species (Niinemets & Valladares, 2006), the competition for light has been indicated as the main factor in explaining the decline of yew populations under a dense canopy (Ruprecht *et al*., 2009; Schwendtner, 2011). Recently, Devaney *et al*. (2015) reported a reduced number of juvenile yews in shade conditions in the southwest Ireland and suggested that light availability may be a limiting factor in the recruitment of yew to later demographic stages. However, some discrepancies may be found in the literature examining light responses in controlled environments. Hence, whereas Iszkulo & Boratyński (2006) showed that yew plants are able to establish under extremely dark conditions, with less than 2% photosynthetic photon flux density, but cannot grow to adult size, Perrin & Mitchell (2013) under experimental light conditions did not find mortality of yew saplings at heavy shade (<3% day-light). In Mediterranean conditions, while a shortage of light can compromise the survival of seedlings, juvenile yews may take advantage of growing in slight shade which provides a reduction of evaporative demand during drought periods.

Yew is a medium drought-tolerant species (Niinemets & Valladares, 2006). It usually grows in localities with a mean annual rainfall higher than 600 mm, though optimally being around 850 mm. The yew root system is mostly superficial, with an extensive horizontal root system; but roots penetrating deeply into the fissures of limestone and chalk pavements have been described in Irish yew woods (Kelly, 1981). In dense Mediterranean evergreen woodlands, the competition for soil water may be severe between yew plants and other species, such as pines or oaks, that present a higher ability to extract water at lower potentials (e.g. Martínez-Vilalta *et al*., 2014). In summary, water stress in yew trees may mostly depend on the net balance between the competition for soil water with neighbors and the facilitation by the same neighbors' cover, which may reduce the overall evaporative demand. These effects may be especially relevant in the juvenile stage, whether or not they allow for the plants' transition to adult status.

The aim of this study is twofold, first, to analyze the structure of forest with yew in the North-Eastern region of the Iberian Peninsula at a regional scale. Then, at an individual scale, it attempts to analyze the role of the surrounding woody neighbors in the performance of the yew juveniles. Specifically, it was hypothesized that in mixed Mediterranean forest, (1) high-density neighbors may negatively affect the growth of juvenile yews, but (2) the effect of moderately dense neighbors covering yew crowns may attenuate the negative effects of water deficit on yew performance.

Material and Methods

Study area and study sites

The work involves yew populations of the NE Iberian Peninsula (40°34' to 42°26'N and 0°10' to 3°10'E; Figure 1). In this region, three main physiographic units can be distinguished: the Pyrenean ranges in the North, the Coastal ranges bordering the Mediterranean Sea and the interior Catalan depression belonging to the Ebro geomorphologic formation. Altitude distribution ranges from sea level up to 3,000 m a.s.l., with an average altitude of 700 m. The dominant climate is Mediterranean with a wide array of local microclimates, varying with altitude and topography. In the foothills of the Pyrenees and on the northern aspect of the Mediterranean Coastal ranges, Submediterranean conditions were also common, according to the definition assigned by Ozenda (1994) as the area with climatic characteristics between those of typically Mediterranean and temperate European climate area (see Sánchez de Dios *et al.*, 2009 for further details). In the NE Iberian Peninsula, and similarly in other Mediterranean regions in Europe, traditional forest activities were abandoned during the second half of the last century, leading to increased forest density (Lasanta-Martinez *et al.*, 2005, Ameztegui *et al.*, 2010) especially in the Coastal range, with multi-stemmed stump structures.

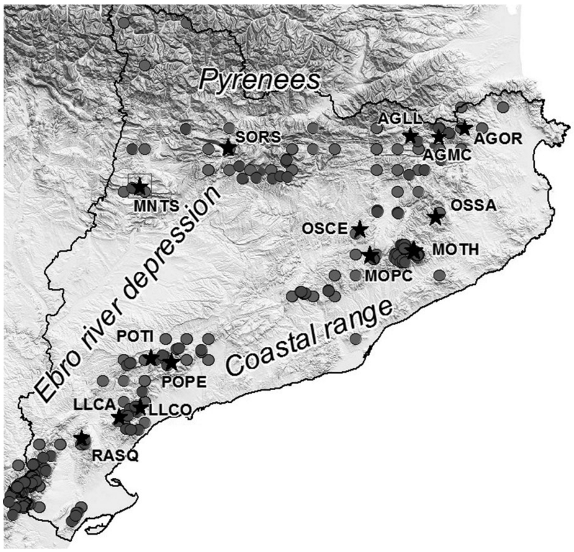

Figure 1. Location of the studied yew populations (stars) and the known forests with yew localities (dots) in Catalonia, NE Iberian Peninsula. The characteristics of studied sites are described in Table 1.

In the study region, yew is largely distributed in the mountain ranges along the coast and the meridian foothills of the Pyrenees. In these ranges, yew has naturally established and grows in small isolated groups in ravines and on cliffs or as a sub-canopy tree in mixed forests dominated by pines (*Pinus nigra* ssp *salzmanii* (Dunal) Franco, *P. sylvestris* L.) or oaks (*Quercus pyrenaica* Willd., *Q. pubescens* Willd.) with other deciduous trees (*Sorbus aria* (L.) Crantz, *Acer* sp.pl.). Although yew grows mostly on calcareous lithologies it can be also found growing on acidic rocks in the northern coastal range. The habitat of yew (9580*) has been mapped in 46 localities, widely distributed in both Pyrenean and Costal ranges, between 300 and 1600 m a.s.l. (Figure 1).

Stand structural attributes

To ensure that the study cover the entire habitat area, the structure of yew stands was inventoried in a total of 55 plots distributed over 14 sites in the NE Iberian Peninsula (Figure 1, Table 1). Sites were systematically selected to include the main distribution areas of the yew habitat: five were located in the Southern foothills of the Pyrenees; another four and five in the northern and southern coastal ranges, respectively (Figure 1). In each site, and according to the area of the yew population, between 1 and 17 plots were randomly placed for analyzing the structure of forest with yew (Table S1 [online supplement]). In each site, plots were selected based on the density of yew trees. Circular inventory plots had an 8 m radius, except in the Mediterranean sites of Capçanes and Colldejou (LLCA and LLCO), where the radius was 5 m due to high stem density. In each plot, we recorded the species name and the diameter of all trees at breast height (1.3 m), greater than 7.5 cm. These measures were used to estimate stand over story variables: stocking density (stems ha^{-1} with dbh>7.5 cm), basal area (m^2 ha^{-1}), mean diameter (dbh_mean, cm), the distribution of basal area into three diameter classes: fine wood (FW, 7.5 cm <dbh< 17.5 cm), medium wood (MW, 17.6 cm <dbh <27.5 cm) and thick wood (TW, dbh> 27.5 cm) and the contribution to the stand basal area of five species groups: yew, pines, oaks, beech, and other broadleaved trees. In each plot we also recorded the number of yew recruits (dbh<2.5 cm) and juveniles (7.5 cm >dbh> 2.5 cm).

Table 1. Geographic characteristics of localities with yew populations in the NE Iberian Peninsula

Ref	Locality	Region	Long.	Lat.	Altitude m a.s.l.	Annual rainfall[1] mm	Mean temp[1] °C	Climate Region[2]
AGLL	Llongarriu	Pyrenees	2°26'	42°15'	695-705	1100-1150	11-12	Submed
AGMC	Miseclòs	Pyrenees	2°31'	42°14'	360-365	950-1000	13-14	Submed
AGOR	Orri	Pyrenees	2°38'	42°16'	915-920	1050-1100	11-12	Submed
MNTS	Montsec	Pyrenees	0°51'	42°02'	1380-1385	750-800	12-13	Submed
SORS	Ribera Salada	Pyrenees	1°26'	42°05'	870-880	750-800	11-12	Submed
LLCA	Capçanes	South. costal r.	0°48'	41°04'	557-586	550-600	14-15	Med
LLCO	Colldejou	South. costal r.	0°51'	41°05'	644-774	600-650	14-15	Med
MOPC	Pla Calma	North. costal r.	2°20'	41°46'	1093-1275	950-1000	8-9	Mid-Temp
MOTH	Turó Home	North. costal r.	2°26'	41°46'	1504-1529	1000-1050	6-7	Mid-Temp
OSCE	Centelles	North. costal r.	2°12'	41°45'	805-838	700-750	12-13	Submed
OSSA	Savassona	North. costal r.	2° 20'	41°57'	650-680	950-1000	12-13	Submed
POPE	La Pena	South. costal r.	1°04'	41°21'	950-1000	650-700	12-13	Submed
POTI	Titllar	South. costal r.	1°00'	41°19'	990-1000	650-700	10-11	Submed
RASQ	Rasquera	South. costal r.	0°35'	40°57'	700-750	650-700	14-15	Med

[1] Climatic variables were estimated using a georeferenced model (Ninyerola *et al*. 2000); http://territori.gencat.cat/ca/atles_climatic/02/.
[2] Climate regions defined following the temperature and rainfall criteria of Sánchez de Dios *et al*. (2009).

Juvenile yew characteristics and structure of the neighbors

The effect of surrounding woody neighbors on juvenile yews was studied in 103 circular plots distributed in 5 of the 14 previously inventoried sites. These 5 sites corresponded to the mixed forest typologies defined by a cluster analysis based on the stand structure characteristics (see results section). A total of 67 plots were placed in the two Mediterranean sites (LLCA, LLCO) and the rest of the plots (35) in the three Submediterranean sites (AGOR, POPE, POTI).

The plots were randomly located within each site but spaced at least 25 m apart. Each circular plot (3 m radius) was centered with one juvenile (7.5 cm >dbh> 2.5 cm), which was characterized by its dbh, height and maximum and normal crown diameters. In each yew, three branches located in the upper, southernmost part of the crown were measured to determine the length of the last two years' twig growth. At least three twigs were also cut from the upper-part of the crown of each yew to later separate, in the lab, at least 30 one year-old leaves which would be used to analyze the ^{13}C:^{12}C abundance isotope ratio ($\delta^{13}C$). This ratio has been used to investigate the relative water use efficiency (WUE) over extended periods (e.g. Donovan & Ehleringer, 1994, Lloret *et al*., 2004). We assumed that the growth status of juvenile yews may be estimated by the WUE efficiency measured from the $\delta^{13}C$ of the last year's leaves and the growth of the last two years determined from twigs measured in three canopy branches. The structure of neighbors was characterized by recording the species name and the dbh of all woody plants (dbh>1 cm) growing in the 3 m radius plot surrounding each yew. These measures were used to estimate the basal area of neighbors (cm^2 m^{-2}), which was subsequently classified into conifer, deciduous or evergreen functional groups. In each plot, we visually estimated the percentage of the yew crown covered by trees. To estimate total canopy cover, the percentage of all species was added together.

Statistical analysis

The 55 inventoried yew populations were classified into different structural typologies using a Ward's hierarchical cluster with the squared Euclidean distance method on the variables indicated in Table 2 (except total and yew densities and other broadleaf or thick wood basal area proportions). Differences in the density of yew recruits or juveniles, characteristics of yew

Table 2. Structural stand variables[1] for each forest typology obtained by the cluster analysis[2], interpretation and locality references[3] belonging to each group. Mean and standard error indicated between parentheses. The number of stands in each typology is indicated (n)

		T1 n=24		T2 n=15		T3 n=8		T4 n=8	
Tree density	stems ha^{-1}	1564	(165)	2047	(304)	1386	(156)	596	(96)
Yew density	stems ha^{-1}	291	(59)	75	(21)	839	(103)	307	(76)
Basal area (G)	m^2 ha^{-1}	40.3	(2.6)	24.9	(3.6)	31.0	(4.3)	45.4	(5.3)
dbh mean	cm	19.0	(0.9)	12.4	(0.5)	16.7	(0.4)	33.1	(2.9)
dbh CV	%	56.0	(2.7)	30.0	(2.8)	41.0	(2.2)	69.1	(6.9)
Taxus b.	%G	15.4	(3.0)	6.3	(4.7)	63.1	(2.9)	83.6	(5.6)
Pinus sp.	%G	42.7	(5.7)	9.1	(3.6)	8.7	(5.0)	8.0	(5.5)
Quercus	%G	26.5	(4.3)	62.8	(6.6)	22.0	(5.1)	4.9	(1.9)
Fagus	%G	6.8	(4.7)	0.0	(0.0)	0.0	(0.0)	2.5	(1.7)
Other broadleaf	%G	8.7	(2.7)	21.8	(4.6)	6.2	(4.5)	0.9	(0.7)
Fine wood	%G	28.4	(3.2)	79.9	(4.6)	35.3	(1.6)	7.5	(1.4)
Medium wood	%G	19.1	(2.2)	18.8	(4.8)	44.2	(5.2)	9.7	(3.9)
Thick wood	%G	52.5	(3.0)	1.2	(1.2)	20.5	(5.5)	82.8	(5.0)
Forest structure interpretation		**Mixed pine, oak forests with yew**		**Mixed dense broadleaf forest with yew**		**Yew groves with oak trees**		**Mature yew groves**	
Locality reference[3]		AGLL	LLCA	LLCA		AGMC		AGOR	
		AGMC	LLCO	LLCO		OSCE		MOTH	
		AGOR	OSSA	MOTH		SORS		RSQA	
		MOPC	POPE	POPE				MNTS	
		MOTH	POTI	POTI					

[1] Structural variables of woody plants with dbh>7.5 cm.

[2] All the variables were used in the cluster analysis except total or yew densities, other broadleaf or thick wood basal area proportions.

[3] The characteristics for each locality reference are described in Table 1.

juveniles or neighbor structure variables between the obtained structural types were analyzed by One-way ANOVA. Multiple linear regressions were used to relate the juvenile yew twig growth or WUE with the neighbors' structural and compositional variables. Step-wise method was used to select the significant variables in the regression model. Model residuals distribution and spatial autocorrelation were tested by graphs and the Durbin-Watson test. Data used in the ANOVA and linear regressions was tested for normality and homoscedasticity and log-transformed if necessary. Statistical analyses were performed using SPSS v.20.

Results

Structural characterization of forest stands with yew

The inventoried 55 forest stands with yew trees were mostly located on north facing aspects (74% of stands in N, NE or NW), with slopes ranging from 10° to 45° and altitudes extending from 360 m to 1,529 m a.s.l. (Table S1 [online supplement]). Annual rainfall in the forest localities with yew ranges from 600 mm to 1,100 mm and mean annual temperature from 6°C to 15°C (Table 1). Total stocking density expanded from 149 stems ha^{-1} to 4,584 stems ha^{-1} and the total basal area, from 0.85 m^2 ha^{-1} to 75.6 m^2 ha^{-1} (Table S1 [online supplement]). The proportion of yew basal area to total stand basal area extends from less than 1% to 99.6% (Table S1 [online supplement]). A cluster analysis classified the 55 stands into four structural typologies (Table 2). The cut-off point of the cluster corresponded to a sharp increase in the linkage distances in clustering steps (Fig. S1 [online supplement]). Two forest types (T1 and T2) corresponded to multi-stratified forests, dominated either by pine and oak trees (T1) or other broadleaved tree species (T2) with scattered presence of yew. In these types, yew represented only a minor contribution to the total basal area of the stand, less than 20% (Table 2). In contrast, in the other two groups (T3 and T4) more than half of the total basal area corresponded to yew trees. The stands belonging to the T3 group corresponded to a dense forest, with the lowest basal area and a dominance of fine wood, while the T4 stands had the lowest stocking density but the highest basal area and a dominance of thick wood (Table 2). About three quarters of the inventoried stands (71%) were classified into the first two groups, which included stands from both Costal range and Pyrenean localities (Table 2).

Yew recruitment reached from nil to 4,129 recruits ha^{-1} and 1,019 juveniles ha^{-1} (mean ± SE: 625 ± 104 recruits ha^{-1}, 259 ± 55 juveniles ha^{-1}; Suppl. Table S1 [online supplement]). The number of recruits and juveniles in the stands belonging to the T4 group was clearly lower than in the rest of typologies (Table 3). Moreover, only three stands of the total eight in this group had recruits (Table 3). Since the percentage of juveniles respect to the number of recruits stand by stand was calculated only for those plots with regeneration (n=3 in the T4 group), we did not find significant differences in the ratio between typologies (Table 3).

Juveniles' yew growth and structure of neighbors

The individual basal area of the 103 studied juvenile yews spanned from 5.0 cm^2 to 43.0 cm^2 and the height from 0.3 m to 6.0 m (Table 4). Both basal area and height of juveniles were higher in Submediterranean localities than in Mediterranean ones. The yearly growth length of twigs during the last two years extended from less than 1 cm y^{-1} to 9.8 cm y^{-1}, and the $\delta^{13}C$ from -33.37 ‰ to -28.05 ‰. No differences were detected in any of these two variables between regions (Table 4).

Table 3. Number of yew adults (dbh > 7.5 cm), juveniles (7.5 cm > dbh > 2.5 cm) and recruits (dbh < 2.5 cm) and the proportion of juveniles vs recruits for each forest typology obtained by the cluster analysis. The number of stands in each typology is indicated (n). Mean and standard error between parentheses. The significance of One-way ANOVA was shown. For each variable, different letters indicate differences between forest typologies

		T1 n=24			T2 n=15			T3 n=8			T4 n=8			Significance p-valor
Adults	nº ha^{-1}	291	(59)	a	75	(21)	b	839	(103)	c	307	(76)	a	*0.001*
Juveniles	nº ha^{-1}	340	(114)	a	253	(48)	a	292	(119)	a	57	(17)	b	*0.016*
Recruits	nº ha^{-1}	849	(213)	a	622	(130)	a	373	(117)	ab	181	(88)	b	*0.029*
Juv : Recr	%	80	(17)		63	(19)		77	(29)		28	(15)		*0.810*

T1. Mixed pine, oak forests with scattered yews; T2. Mixed dense broadleaf forest with yew; T3. Yew groves with oak trees; T4. Mature yew groves.

Table 4. Characteristics of yew juveniles and of the forest structure of neighbors growing in a 3m radius plot centered in the yew in Mediterranean and Submediterranean regions. Mean, standard error between parentheses, maximum and minimum. The significance of the difference between localities is indicated for each variable

		Mediterranean (n=68)				SubMediterranean (n=35)				Signif.
		Mean	SE	Max	Min	Mean	SE	Max	Min	p-valor
Yew Juvenile [1]										
Basal area	cm	15.6	(1.5)	43.0	5.0	28.4	(1.4)	44.2	10.5	*0.001*
Height	cm	290	(18)	550	34	409	(16)	600	197	*0.001*
Crown diam.	cm	105	(17)	437	15	337	(19)	648	20	*0.001*
Leaf δ^{13}C	‰	–30.7	(0.1)	–28.0	–33.4	–30.9	(0.2)	–29.4	–33.1	*0.415*
twig length	cm	4.0	(0.2)	7.3	0.1	3.8	(0.3)	9.8	0.0	*0.436*
Neighbors structure [2]										
Yew crown cover [3]	%	119	(6)	260	5	92	(6)	180	0	*0.010*
Total basal area	cm m^{-2}	52.7	(4.6)	190.0	0.0	36.6	(5.2)	114.8	0.1	*0.033*
Conifer basal area [4]	cm m^{-2}	18.7	(3.9)	182.0	0.0	20.3	(4.8)	83.0	0.0	*0.760*
Deciduous b.a. [4]	cm m^{-2}	8.0	(1.5)	71.0	0.0	5.5	(3.3)	113.0	0.0	*0.007*
Evergreen b.a. [4]	cm m^{-2}	26.1	(2.8)	132.0	0.0	10.8	(2.0)	52.0	0.0	*0.001*

[1] *Crown diam.* Mean between maximum and normal crown diameters; *Twig length*. Median of the annual growth of the two last years of three crown branches; δ^{13}C. Isotope C abundance ratio of one-year old yew leaf collected from at least three crown branches.

[2] The structural variables of neighbors were recorded in all the woody species with dbh >1 cm.

[3] Proportion of yew crown covered by neighbor crowns. The values are higher than 100 as they are calculated as the sum of different neighbors crowns.

[4] Total, conifer, deciduous and evergreen basal area of woody species of each group growing in the 3 m radius plot.

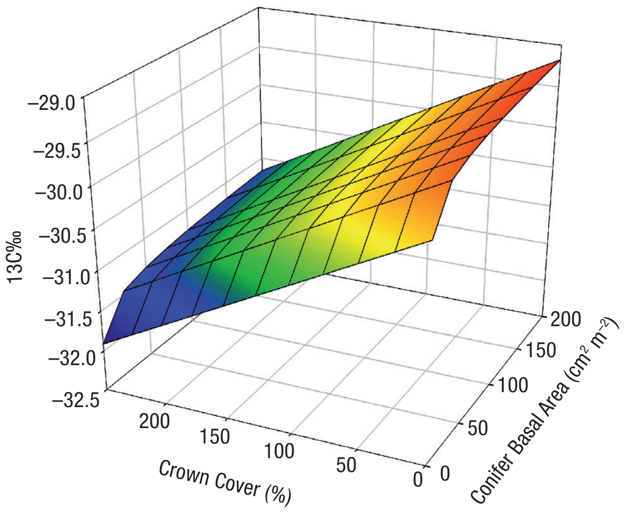

Figure 2. Predicted δ^{13}C (‰) of juvenile yew along the proportion of yew crown covered by neighbours (%) and the basal area of conifer neighbors (Log-transformed, cm m^{-2}) according to regression model in Table 5 (Region dummy variable was set as 0). To reflect the layering of the cover of the yew crown cover by neighbors, the canopy percentage cover of each species was summed up.

The forest structure surrounding the yew juveniles was different between regions (Table 4). Both the proportion of the juvenile yew crown covered by other woody species and the total basal area of woody neighbors were higher in the Mediterranean plots than in Submediterranean ones. Among functional groups, the basal area of deciduous and evergreen neighbors was also higher in the Mediterranean plots, while no differences were found in the basal area of conifers (Table 4).

Yearly twig length growth and δ^{13}C did not correlate (r=0.04, p=0.718, n=103). Twig length growth did not show any relationships with any neighbors' measured variable. The multiple regression model showed that leaf δ^{13}C of yew juveniles decreased with the percentage of yew crown covered by neighbors and increased with the basal area of conifers (log-transformed) (Figure 2, Table 5). Basal areas of the evergreen or deciduous functional groups were excluded from the model. Adding the region into the model (as a dummy variable) increased the explained part of the δ^{13}C variability from 14.5% to 17.0%; a change which was significant (p=0.048). This dummy variable shifted the equation upwards or downwards by modifying the constant (k, Table 5) and indicated higher δ^{13}C in the Mediterranean than in the Submediterranean region.

Discussion

In the NE Iberian Peninsula, the habitat of yew has been mapped mostly in northward facing forest stands, widely distributed through the coastal range and the

Table 5. Multiple linear regression stepwise model ($y=k+ax_1+bx_2+cx_3$) between the $\delta^{13}C$ of juvenile yew and the region, the proportion of yew crown covered by neighbors (%) and the basal area of conifer neighbors (log-transformed conifer G). For each independent variable the standard error of each parameter is shown in parenthesis and the statistical significance by (*) p<0.05, (**) p<0.01, (***) p<0.001. The adjusted coefficient of determination (adjusted r^2) and the signification (p-value) of the model is indicated

	Parameters												Signification	
	k			Region[1]			Cover			conifer G (log)			$_{adj}$ r^2	p-valor
Leaf $\delta^{13}C$ (‰)	–29.91	(0.28)	***	–0.43	(0.21)	*	–0.01	(0.01)	***	0.32	(0.12)	**	0.17	*0.001*

[1] Region dummy variable: 0. Mediterranean; 1. Submediterranean.

southern foothills of the Pyrenees, in a wide range of altitudes (between 300 – 1,600 m a.s.l.) and in Mediterranean or Submediterranean bioclimatic regions (Font, 2014 and unpublished data). In these conditions, yew is found in a wide spectrum of forest structures, from clear stands to dense forests as indicated by the total stocking density (ranging from 149 stems ha^{-1} to 4,584 stems ha^{-1}) and the total basal area (ranging from 0.85 m^2 ha^{-1} to 75.6 m^2 ha^{-1}).

In general, the density of recruits and juveniles (625 ± 104 recruits ha^{-1}, 259 ± 55 juveniles ha^{-1}) found in the monitored stands was higher than the ones reported in other Mediterranean forests in which yew appears (e.g. García *et al.*, 2000; but see Farris & Filigheddu, 2008) and similar to those from more temperate European areas (Hulme, 1996; García & Obeso, 2003; Dhar *et al.*, 2006; Piovesan *et al.*, 2009). However, and similar to other regions, the recruitment of yew is low or nonexistent in yew dominated stands (181±88 individuals ha^{-1}). In Mediterranean localities and under these conditions, low yew recruitment may be explained, at least partially, by (i) severe droughts (ii) high seed-predation rates (Sanz & Pulido, 2014), (iii) high browsing pressure caused by herbivores due to the absence of the protection of nursery plants (*sensu* Garcia & Obeso 2003; Mendoza *et al.*, 2009) and (iv) the extremely dark conditions under the canopy of the mature yews (Iszkulo & Boratyński, 2006; Perrin *et al.*, 2006).

Light is one of the main factors structuring forests and affecting the composition of species. In Mediterranean climate areas, where water supplies vary intra- and inter-annually, the plant water stress has also an important role in structuring the forests. When water is limited, adjacent plants may compete for soil water. In such cases, the competitive advantage of one species over another is triggered by the capacity to extract water from the soil at lower potential or the capacity to reduce the water losses by evapotranspiration. Drier conditions increase the WUE of plants, which culminates in higher $\delta^{13}C$ values of plant tissues (e.g. Donovan & Ehleringer, 1994, Lloret *et al.*, 2004). Hence, higher $\delta^{13}C$ values in leaves of adult yews (data not shown) compared with those in juveniles growing in the same Mediterranean sites suggest that adults are more water-stressed than young ones. Although no differences in $\delta^{13}C$ were detected among juvenile yews growing in Mediterranean or Submediterranean localities, the regression model predicts that Mediterranean juveniles were more water stressed than Submediterranean ones. Even though other factors related with micro-site characteristics (e.g. soil depth) can also modulate the observed patterns, our results indicated that the yew juveniles benefit from the canopy of neighbors covering yew crowns. The cover of yew by the neighbors' crowns probably reduces the evapotranspiration of juvenile yew during periods with high atmospheric evaporation demand. However, a negative effect was found when the density and size of neighbors growing close to the yew juveniles is too high, likely due to an increase in the competition for soil water between the yews and the other woody species.

Management practices such as traditional selective thinning of Mediterranean oak coppices have been demonstrated to reduce the consequences of long drought periods compared with unthinned plots (Cotillas *et al.*, 2009). However, it is worth highlighting that these authors also stated that the intensity and frequency of this management should be considered to ensure the efficacy of the treatments and to avoid non-desired effects. In Slovakia, for example, Saniga (2000) found that a reduction of around 18-20% of volume in the surrounding density in a stand dominated by *Fagus* and *Picea abies* improved the height growth of yew, whereas a reduction by 7-8% resulted in no growth above the control plots (cited in Thomas & Polwart, 2003).

In conclusion, the lack of yew recruitment in dense mature forest and the juvenile performance in less dense structures may constrain yew conservation in the midterm. As water availability in the Mediterranean region is likely to decrease in the near future (IPCC, 2013) and forest densification is expected to continue to rise, selective cuttings addressing the reduction of basal area of neighbors surrounding the target yew should be promoted since they may increase soil moisture and encourage juvenile growth. However, it would be suggested that removing neighboring woody plants be done with care in order to prevent excessive exposure of the juvenile yew crown to light. As other factors at the tree scale may be relevant, further studies should focus on the thresholds of thinning management.

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