Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate

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Abstract Tree architecture has important consequences for tree performance as it determines resource capture, mechanical stability and dominance over competitors. We analyzed architectural relationships between stem and crown dimensions for 13 dominant Iberian canopy tree species belonging to the Pinaceae (six *Pinus* species) and Fagaceae (six *Quercus* species and *Fagus sylvatica*) and related these architectural traits to wood density, shade tolerance and climatic factors. Fagaceae had, compared with Pinaceae, denser wood, saplings with wider crowns and adults with larger maximal crown size but smaller maximal height. In combination, these traits enhance light acquisition and persistence in shaded environments; thus, contributing to their shade tolerance. Pinaceae species, in contrast, had low-density wood, allocate more resources to the formation of the central trunk rather than to branches and attained taller maximal heights, allowing them to grow rapidly in height and compete for light following disturbances; thus, contributing to their high light requirements. Wood density had a strong relationship with tree architecture, with dense-wooded species having smaller maximum height and wider crowns, probably because of cheaper expansion costs for producing biomechanically stable branches. Species from arid environments had shorter stems and shallower crowns for a given stem diameter, probably to reduce hydraulic path length and assure water transport. Wood density is an important correlate of variation in tree architecture between species and the two dominant families, with potentially large implications for their resource foraging strategies and successional dynamics.

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Introduction

Tree architecture refers to the overall shape of the tree, and has important consequences for the performance of species and individuals, as it determines resource capture, mechanical stability and dominance over competitors (Kohyama 1987; King et al. 2006). Tree height relative to its neighbours and crown size and shape determines total leaf area and foliage distribution, and hence, light capture and carbon gain. Resource allocation tradeoffs are likely to influence tree architecture throughout ontogeny and these tradeoffs are of paramount importance to explain mechanisms of tree species coexistence (Tilman 1988; Kitajima and Poorter 2008).

A number of studies have emphasized the relationship between tree architecture and wood material properties such as wood density. This variable is closely related to the resistance to wood to rupture and self-loading (van Gelder et al. 2006; Chave et al. 2009), and hence, to the production of stable horizontal branches, resistance to external forces, and mechanical stability. Wood density also plays a central role in the life history variation of tree species as low-density wood is cheap to construct, allowing for rapid growth in stem dimensions, whereas high-density wood allows for a high survival rate and long lifespan (Loehle 1988; Poorter 2008; King et al. 2006). Wood density may therefore be closely related to the shade tolerance of the species. In evergreen broad-leaved tropical forests, for example, do shade-tolerant species have denser wood (van Gelder et al. 2006), although for temperate forest the relationship is sometimes less clear, for example, many coniferous species are very shade tolerant, but they tend to have a low wood density because of the lack of fibre in their wood.

In addition, tree architecture is hypothesized to be related to important axes of life history variation, such as the regeneration light requirements and adult stature of the species (Givnish 1988; Kohyama and Hotta 1990). Light-demanding species must rapidly grow to maintain a leading position in forest gaps and should thus have slender stems and narrow crowns compared with shade-tolerant species, which place preference on light capture (Givnish 1988). Light-demanding species are also expected to have long crowns with several leaf layers to maximize light interception under high radiation (Horn 1971), although empirical data show

that often the reverse is the case. Taller species are expected to have slender stems and narrow crowns that minimize extension costs; in contrast, shorter species should have thick stems that are mechanically strong and wide, shallow crowns that enhance their ability to intercept light and reduce the risk of mechanical damage by falling debris (Aiba and Nakashizuka 2009).

Tree architecture can also be influenced by ecological factors, such as climate. Climate modulates, for example, the intraspecific relationships between tree height and stem diameter (Aiba and Kitayama 1999; Wang et al. 2006). Tree height is reduced in areas with lower water availability, because of hydraulic limitations and because relatively more biomass is invested belowground for water uptake (Martinez and López-Portillo 2003). Nevertheless, there is no conclusive answer on how climate affects architectural relationships across species (López-Serrano et al. 2005).

This study focuses on continental Iberia, which shows a large range of different climates (from semiarid to humid Atlantic climates, Montoya et al. 2009) and provides therefore an ideal setting to test whether Iberian tree species are adapted to the climate in which they occur, and whether they show different allometries. The dominant canopy tree species in Spain belong to two families: the Pinaceae (mainly *Pinus* species) and Fagaceae. Iberian forest structure and dynamics is largely defined by the alternation and co-dominance of these two families (Carrión 2001). *Pinus* species have a strong apical control (Harold and Hocker 1979; Spurr and Barnes 1983), low wood density (Guindeo et al. 1997) and are light-demanding in the juvenile stage (Niinements and Valladares 2006). As a consequence, *Pinus* species grow rapidly, and are expected to have slender stems and narrow and deep crowns, whereas Fagaceae are expected to possess the opposite suite of traits (thick stems and wide and shallow crowns), although quantitative tests of these architectural hypotheses are lacking so far. Pinaceae and Fagaceae also strongly differ in their wood structure; the Pinaceae have no vessels and no fibres and rely on water-conducting tracheids for mechanical strength.

In this study, we compare architectural relationships between stem and crown dimensions for 13 dominant canopy tree species in Iberia. We address the questions: (1) How do height, crown diameter and crown length vary with stem diameter? (2) How are tree architectural

parameters associated and what architectural strategies can be distinguished? (3) How do Pinaceae and Fagaceae differ in their architectural traits? and (4) How do interspecific differences in architecture relate to stem material properties, ecological strategies, and climate? We show that wood density is an important correlate of variation in tree architecture between species and the two dominant families, with potentially large implications for their light foraging strategies and shade tolerance. In addition, belowground resource acquisition and drought tolerance are important factors in these forests, strongly shaping tree architecture.

Materials and methods

Site and species

The study is carried out in the forests of Continental Spain, ranging from 35°82′N–43°80′N to 9°29′W–4°33′E, covering an area of 139,047 km². Altitude varies from sea level to 2,500 m and the area is characterized by a large range of different climates (from semiarid to humid Atlantic climates, Montoya et al. 2009).

Thirteen native species (six Pinaceae and seven Fagaceae) were selected that dominate the canopy throughout Spain (Table 1). We refer for sake of simplicity to these groups as Pinaceae and Fagaceae, although we acknowledge that all Pinaceae are from the genus *Pinus* and, with the exception of *Fagus*, all Fagaceae consist of *Quercus* species. *Pinus* forms a lineage distinguished from other ecologically important genera of Pinaceae. The genus *Pinus* has been adapted to arid environments compared with other genera (although in our study several "relatively wet" pine species were included) and is relatively light demanding, compared with other genera (e.g., *Picea* and *Abies*). For each species, a different study area (see Online Resource 1) was selected based on the Spanish Regions of Provenance (Alía et al. 2009). The rationale for this is to compare species under environmental conditions that are close to their optimum, and to decrease potential intraspecific sources of variation, such as genetic variability, soil variation and management history. We chose the regions of provenance where the species attained its highest presence in Spain (in terms of percentage of the total surface in which a particular species is present as a mixed or monospecific stand).

Data collection

Tree architectural data were obtained from the second Spanish Forest Inventory (SFI) (Inventario Forestal Nacional 1995). The SFI consists of a systematic sampling of forest areas with a 1-km square grid of which each intersection is sampled. Plots are circular with a radius of 25 m, in which trees more than 7.5-cm diameter at breast height (dbh) were sampled in a nested design. Crown measurements were made for a subsample of 4–6 trees per plot that did not experience intensive management (i.e., thinning, pruning or pollarding). Two perpendicular values of diameter at breast height, crown diameter (CD) and height of the tree (H) and first living branch were measured. Crown length (CL) was calculated as the difference between the height of the tree and the first living branch. In this study, 3,832 trees were included per species (range 899–16,175). Crown length was measured for a subset of 262 trees per species (range 3–941, Table 1).

Stand characteristics (such as tree density and basal area) reflecting past human disturbances and canopy openness do affect tree architecture, but are less important than interspecific differences and environmental variables (Lines et al. 2012). Variation in stand characteristics was therefore not included in this analysis.

Wood density (kg m⁻³) at a moisture content of 12% (i.e., air-dry density) was obtained from Guindeo et al. (1997). A shade tolerance index (Niinements and Valladares 2006) was used to describe species ability to grow in the shade: 1 = very intolerant, 2 = intolerant, 3 = moderately tolerant, 4 = tolerant, 5 = very tolerant, corresponding to >50, 50–25, 25–10, 10–5 and 5–2% full light. For five species, shade tolerance was classified based on Serrada et al. (2008). The environmental requirements of the species were characterized by the climatic conditions in the region of provenance (Alía et al. 2009). Climatic data were obtained from an interpolation map (spatial resolution of 1 km) of meteorological station data covering 1951–1999 (Gonzalo 2008). Selected climatic variables were mean annual precipitation (mm), frost period (months when minimum average temperature ≤0°C) and drought period (number of months in which monthly precipitation [in

Table 1 Tree architectural parameters of 13 dominant copy tree species of continental Spain relating height, crown diameter and crown length to stem diameter at breast height

Species	Abbreviation	Trees		Diameter (cm)	Height (m) = $H_{asy}[1 - \exp(-H_a[dbh]^{Hb})]$					Crown diameter (m) = $CD_{int}dbh^{CDslo}$				Crown length (m) = $CL_{int}dbh^{CLslo}$		
		N[a]	n[b]	D_{max}[c]	H_{asy}[d]	H_a[e]	H_b[f]	r^2[g]	H_{max}[h]	CD_{int}[i]	CD_{slo}[j]	r^2	CD_{max}[k]	CL_{int}[l]	CL_{slo}[m]	r^2
Pinus halepensis	P.h	5458	941	99	139	0.01	0.61	0.48	21	0.52	0.69	0.68	12	1.80	0.34	0.08
Pinus nigra	P.n	5331	624	96	22	0.03	0.95	0.52	20	0.34	0.80	0.73	13	1.62	0.36	0.09
Pinus pinaster	P.pt	5146	473	115	15	0.02	1.25	0.60	15	0.21	0.92	0.73	16	4.52	−0.21	0.01
Pinus pinea	P.pn	1837	169	100	17	0.02	1.02	0.67	16	0.24	0.92	0.84	17	1.69	0.25	0.03
Pinus sylvestris	P.s	4677	456	71	17	0.03	1.13	0.39	16	0.53	0.67	0.51	9	1.79	0.35	0.04
Pinus uncinata	P.u	1749	200	126	13	0.01	1.46	0.39	13	0.43	0.66	0.58	10	1.96	0.35	0.05
Fagus sylvatica	F.s	1204	43	172	17	0.03	1.29	0.28	17	0.77	0.64	0.67	21	2.60	0.41	0.22
Quercus faginea	Q.f	1248	203	130	11	0.04	1.12	0.45	11	0.75	0.60	0.68	14	0.71	0.73	0.23
Quercus ilex	Q.i	16175	51	129	10	0.13	0.61	0.40	9	0.94	0.57	0.57	15	2.26	0.17	0.03
Quercus petraea	Q.pe	961	60	204	17	0.04	1.09	0.41	17	0.48	0.76	0.69	27	0.65	0.80	0.19
Quercus pyrenaica	Q.py	899	145	172	13	0.08	0.90	0.47	13	0.82	0.54	0.60	13	1.76	0.41	0.12
Quercus robur	Q.r	4029	40	172	16	0.06	0.99	0.36	16	0.81	0.62	0.51	19	1.55	0.52	0.20
Quercus suber	Q.s	1104	3	143	10	0.04	1.06	0.36	10	0.91	0.50	0.50	11	5.24	−0.28	0.86

[a] Number of trees measured for estimating the architectural equation of height and crown diameter as a function of dbh

[b] Number of trees measured for estimating the architectural equation of crown length as a function of dbh. They are a subset of N

[c] Maximum measured diameter at breast height

[d] Asymptotic height

[e] Coefficient of height equation

[f] Slope of height equation

[g] Coefficient of determination

[h] Maximum estimated height (in m) calculated for the thickest tree (D_{max}) using the height equation

[i] Crown diameter intercept for trees of 1-cm dbh

[j] Crown diameter slope (power function exponent)

[k] Maximum estimated crown diameter (in m) calculated for the thickest tree (D_{max}) using the crown diameter equation

[l] Crown length intercept for trees of 1-cm dbh

[m] Crown length slope (power function exponent)

mm] is less than twice the average monthly temperature [in °C]).

Data analysis

Tree architecture is analyzed in terms of tree height, crown diameter and crown length. Tree height is regressed against diameter with a non-linear regression analysis (Thomas 1996): $H = H_{asy}[1 - \exp(-H_a[dbh]^{Hb})]$, where H is tree height (m), dbh is tree diameter at breast height (cm), H_{asy} is the asymptotic maximal tree height (m) and H_a and H_b are coefficients that, in combination with H_{asy}, determine the initial height at 1-cm dbh and height slope, respectively. Crown diameter was regressed against stem diameter using an allometric power relation (Huxley and Teissier 1936): $CD = CD_{int}dbh^{CDslo}$, where CD is crown diameter (m), CD_{int} is the crown diameter intercept (for trees of 1-cm dbh) and CD_{slo} represents the crown diameter "slope" (i.e., the diameter exponent or scaling component). The power relation for crown length is $CL = CL_{int}dbh^{CLslo}$, where CL_{int} represents the crown length intercept (for trees of 1-cm dbh) and CL_{slo} is the crown length "slope" (i.e., the diameter exponent or scaling component). Type 1 regression rather than standard major axis (type 2) regression was used, because we wanted to predict tree dimensions from stem diameter, as such equations can be used for forestry and modelling purposes.

Multivariate associations of tree architectural traits were analyzed with a principal component analysis (PCA) using species as data points because our architectural questions are at the species level. Ten architectural traits were included: maximum dbh (D_{max}), $\log_{10}(H_{asy})$, $H_{7.5}$, H_b, $CD_{7.5}$, CD_{slo}, $CL_{7.5}$ and CL_{slo}. Maximum estimated height (H_{max}) and maximum crown diameter (CD_{max}) were calculated using the species-specific height and crown diameter regression equation for the tree which has D_{max}. Trees used in this study had a minimum dbh of 7.5 cm. To avoid extrapolation, we did not use the allometric intercepts at 1-cm dbh, but calculated the stem length ($H_{7.5}$), crown diameter ($CD_{7.5}$) and crown length ($CL_{7.5}$) at 7.5-cm dbh. Differences between Pinaceae and Fagaceae species in architectural traits were analyzed with a t test. Pearson's correlation was used to relate species architectural traits to wood density, shade tolerance and climatic conditions. The correlation analysis was repeated three times; for all species, for the Fagaceae

and for the Pinaceae. Families differed in many architectural traits. To evaluate whether, apart from family, wood density, shade tolerance and climate had independent effects on tree architecture, or whether their effects varied with family, a series of ANCOVAs was carried out, with family as factor and each time one of the other continuous factors as a covariate. First, it was tested whether there was a significant interaction between family and the covariate, which would indicate whether architectural relationships with covariates differed between the two families. If the interaction effect was not significant, then a simple ANCOVA was carried out without an interaction effect. The sign of the slope (β) of the covariate indicates whether it had a positive or negative effect on tree architecture. Statistical analyses were carried out using STATISTICA (2004) and SPSS (2006).

Results

Tree architectural relations with stem diameter

Maximum diameter of the species ranged from 71 cm for *Pinus sylvestris* to 204 cm for *Quercus petraea*. Tree height approached an asymptote for each Fagaceae species but not for some of the Pinaceae species (Fig. 1a). The asymptotic formula fitted the height–stem diameter curve with an average r^2 of 0.44 (range 0.28–0.67; Table 1). The height of 7.5-cm diameter trees ranged from 2.2 to 5.7 m and the coefficient H_b ranged from 0.6 to 1.5. The calculated H_{max} at the largest observed diameter varied 2.3-fold across species, from 9 m for *Quercus ilex* to 21 m for *Pinus halepensis* (Table 1).

Crown diameter increased in a curvilinear way with stem diameter with little variation amongst species (Fig. 1b). The power relation fitted the crown diameter–stem diameter curve well with an average r^2 of 0.64 (range 0.50–0.84). The crown diameter of 7.5-cm diameter trees ranged from 1.3 to 3.0 m and the power function exponent (CD_{slo}) ranged from 0.5 to 0.9. The calculated CD_{max} at the largest observed diameter varied 3-fold across species from 9 m for *Pinus sylvestris* to 27 m for *Quercus petraea* (Table 1).

The increase in crown length with stem diameter varied considerably amongst species with some Fagaceae species showing a steep linear increase, other species showing a less steep curvilinear increase and
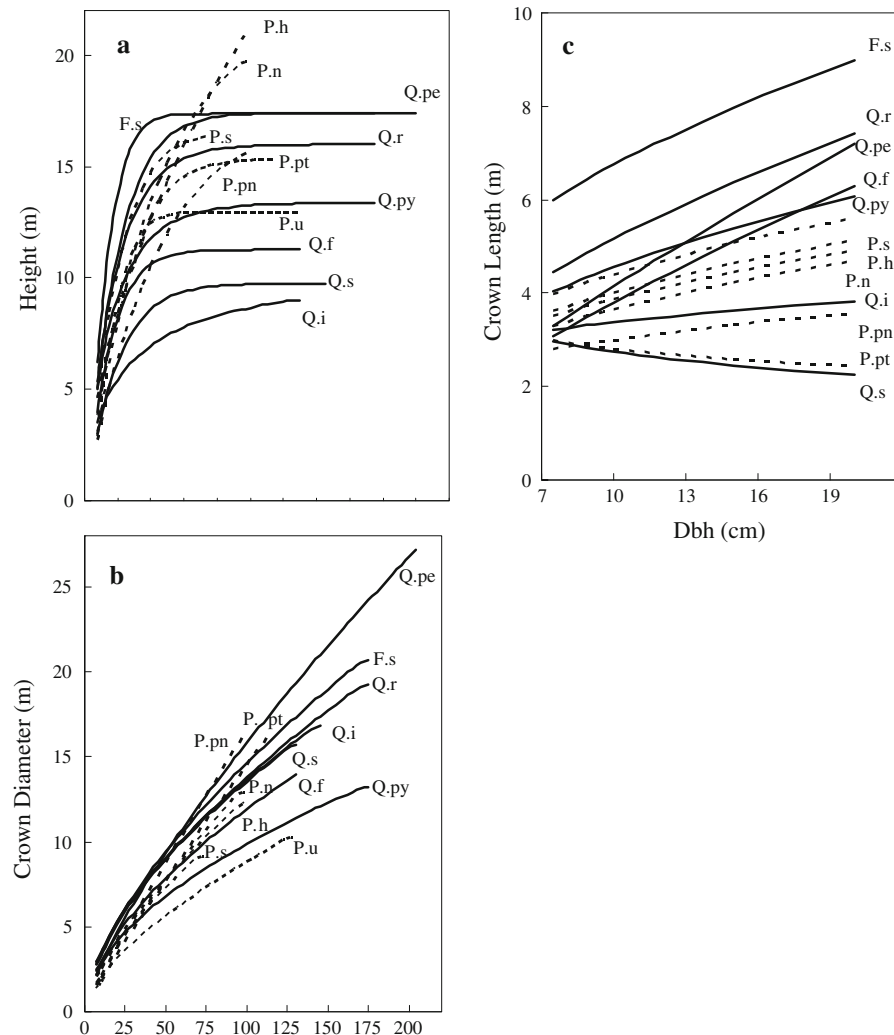
Fig. 1 Interspecific architectural trends of Iberian canopy tree species. **a** Height, **b** crown diameter and **c** crown length versus stem diameter at breast height (dbh). *Dotted lines* indicate Pinaceae species ($n = 6$) and *continuous lines* indicate Fagaceae species ($n = 7$). *Curves* start from the minimum dbh of 7.5 cm. Height and crown diameter curves end at the largest stem diameter measured for each species. Crown length was measured for a subset of the trees and its curve ends at the common maximum stem diameter measured for the subset (20 cm). See Table 1 for an explanation of species abbreviation

four species showing a nearly constant or even declining crown length (Fig. 1c). The power relation fitted the crown length–stem diameter curve poorly with an average r^2 of 0.16 (range 0.01–0.86). The crown length of 7.5-cm diameter trees ranged from 2.8 to 6.0 m and the power function exponent (CL_{slo}) ranged from (non-significant) −0.3 to 0.8 (Table 1).

Tree architectural trait associations

Tree architectural trait association was explored with a PCA (Fig. 2a). The first PCA axis explained 34% of the variation in architectural traits and was highly positively correlated with the maximum stem and crown diameter, and with the height, crown diameter and crown length of 7.5-cm thick trees. The second axis explained 26% of the variation in architectural traits and was highly positively correlated with H_{max}, H_{asy} and CD_{slo}. Five pairs of architectural parameters showed also significant bivariate correlations: H_{max}–H_{asy}, D_{max}–CD_{max} and $H_{7.5}$–$CD_{7.5}$ were highly positively correlated, whereas $CD_{7.5}$–CD_{slo} were negatively correlated (data not shown). Pinaceae and Fagaceae occupied different positions along the first
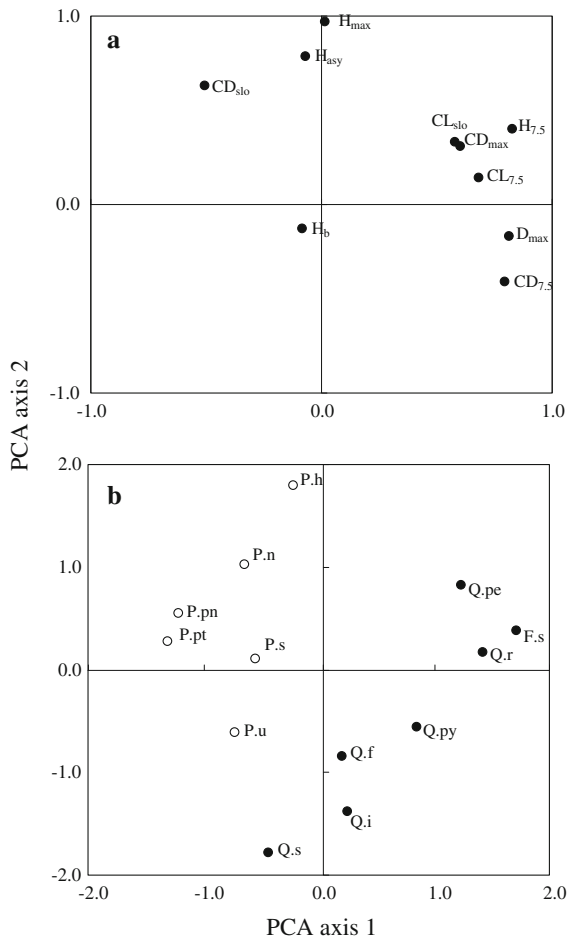
Fig. 2 Associations of ten architectural parameters of 13 dominant Iberian canopy tree species as analyzed with a principal component analysis (PCA). **a** Loading plot and **b** species' regression scores. PCA axis 1 explains 34% of the variation and PCA axis 2 explains 26% of the variation. Fagaceae species are indicated with *closed symbols* and Pinaceae species with *open symbols*. See Table 1 for an explanation of architectural parameters and species abbreviations

PCA axis (t test, $t = -4.32$, $P < 0.001$, df = 11); Fagaceae species were grouped at the right side of the first axis and they were characterized by large maximal stem and crown diameter and long and wide crowns when being young (Fig. 2b). Pinaceae species were grouped at the left side and were characterized by the opposite suite of traits.

Pinaceae versus Fagaceae

Fagaceae and Pinaceae species significantly differed for two out of six analyzed architectural parameters

(Fig. 3). Fagaceae and Pinaceae had statistically similar intercepts (at 7.5-cm dbh) and slopes for height and crown length. Fagaceae had a significantly wider crown for 7.5-cm thick trees (Fig. 3c) and a lower crown diameter slope (Fig. 3d) than Pinaceae. This means that when young, Fagaceae have a wider crown diameter, but a smaller increase in crown diameter with stem diameter than Pinaceae. In addition, Fagaceae had, compared with Pinaceae, a significantly higher wood density (790 ± 52 vs. 507 ± 18 kg/m^3, t test, $t = 5.2$, $P < 0.001$) and shade tolerance index (2.8 ± 0.3 vs 1.6 ± 0.1, t test, $t = -3.4$, $P = 0.006$), but they are found under similar climatic conditions (t test, $P > 0.23$ in all cases).

Tree architecture versus wood density, shade tolerance and climate

Several architectural traits were strongly correlated with wood density when all 13 species were compared (Table 2). Species with high wood density had a low H_{max} (Fig. 4a), high $CD_{7.5}$ (Fig. 4c) and low score on the second PCA axis (Fig. 4c). In contrast, other architectural traits tended to be related with shade tolerance. Shade-tolerant species also had a high $CD_{7.5}$ (Fig. 4d), but apart from that, they were characterized by a high D_{max} (Fig. 4b), $CL_{7.5}$ and high scores on the first PCA axis (Fig. 4f). It should be noted that for these relations, Pinaceae and Fagaceae occupy different positions in the scatter plots. Wood density and shade tolerance may, therefore, partly contribute to architectural differences between families, but the question is whether they also contribute to architectural differentiation within families. With the ANCOVA, wood density was still negatively related with H_{max} and the second PCA axes, whereas a relation with the first PCA axis appears, and the relationship with $CD_{7.5}$ disappears (Table 3). For shade tolerance, most architectural relationships disappear, with the exception of the relationship with $CL_{7.5}$. When correlations are made within each family, broadly the same patterns emerge for the seven Fagaceae species as for all species combined (Table 2). For the six Pinaceae species, none of the correlations were significant.

Architectural parameters were weakly correlated with climatic variables when all 13 species were compared, and only significant for 3 out of 33 cases evaluated (Table 2); the allometric slope of tree height against stem diameter, H_b, was negatively correlated
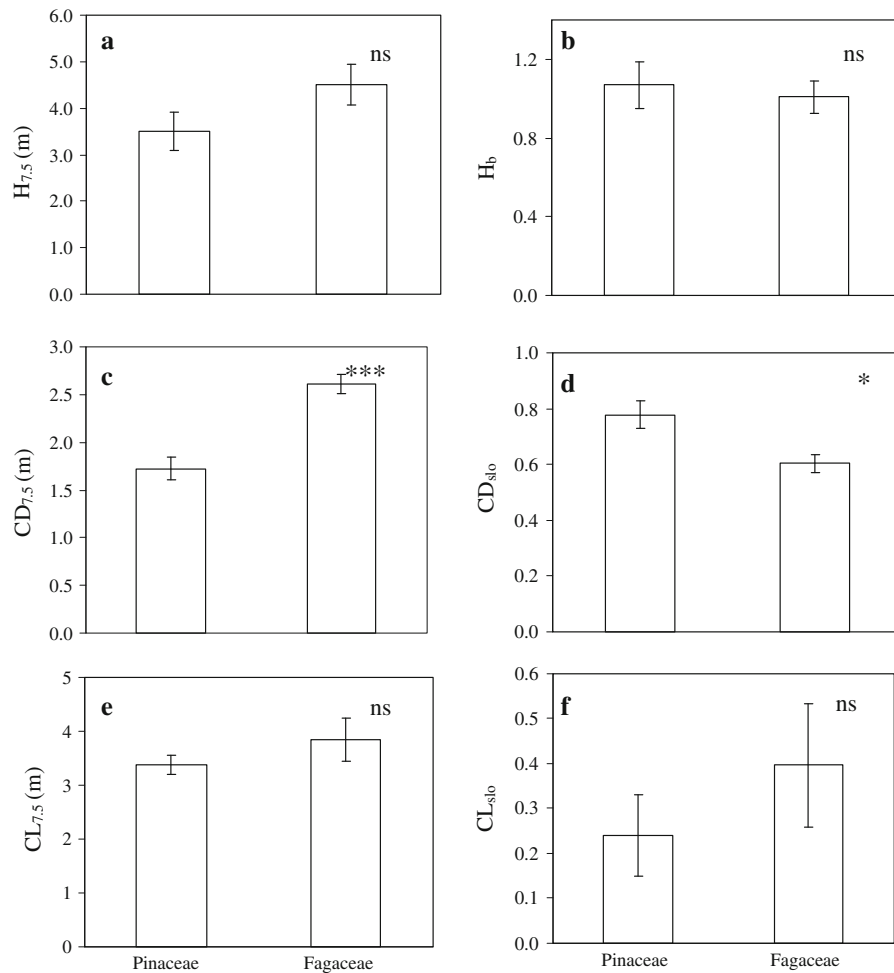
Fig. 3 Mean (± standard error mean) of architectural parameters (size at 7.5-cm dbh and slopes) of Pinaceae species ($n = 6$) and Fagaceae species ($\mathbf{n} = 7$). **a**, **b** Height, **c**, **d** crown diameter and **e**, **f** crown length. Results of a *t* test are shown: *ns* $P > 0.05$; *$P < 0.05$; ***$P < 0.001$. See Table 1 for an explanation of architectural parameters

with drought period ($r = -0.63$, $P < 0.05$, Fig. 5a) and positively correlated with frost period ($r = 0.71$, $P < 0.01$). The power function exponent of crown length against stem diameter, CL_{slo}, was negatively correlated with drought period ($r = -0.67$, $P < 0.05$; Fig. 5b). In the ANCOVA analyses, the climatic variables became more important: Drought period was significant in six cases, followed by rainfall (3) and frost (2) (Table 3). The relationship between drought period, H_b and C_{slo} was qualitatively still the same, whereas drought had now a negative effect on H_{max} and CD_{slo}. Drought had now also a negative effect on PCA axis 2 score of the Fagaceae (as indicated by the strong interaction effect between family and drought). When correlations were made within each family,

broadly the same patterns emerge for the seven Fagaceae species as for all species combined in the ANCOVA analysis, with strong responses to drought (Table 2). In contrast, for the Pinaceae, only two architectural parameters were affected by climate (i.e., frost).

Discussion

Iberian canopy species showed important interspecific variation in the architectural relationships between stem and crown dimensions, and Fagaceae and Pinaceae species differed in these architectural relationships. Our results show that tree architecture is

Table 2 Pearson's correlations between the architectural parameters of all species ($n = 13$), Fagaceae ($n = 7$) and Pinaceae ($n = 6$) with wood density (WD), shade tolerance (ST) and climate variables (rainfall, drought period, and frost). Climate variables were determined for each species in its area of optimal occurrence and the trees were measured. Each species is a data point

Trait	All					Fagaceae					Pinaceae				
	WD	ST	Rain	Drought	Frost	WD	ST	Rain	Drought	Frost	WD	ST	Rain	Drought	Frost
D_{max}	0.45	**0.62**	0.50	−0.34	0.44	**−0.76**	0.16	0.61	**−0.77**	−0.03	−0.11	0.00	0.16	0.12	0.37
$H_{7.5}$	−0.03	0.50	0.33	−0.38	0.46	***−0.90***	0.40	**0.76**	**−0.76**	−0.17	−0.55	−0.01	−0.33	0.20	−0.62
H_b	−0.27	0.12	0.45	**−0.63**	0.50	−0.50	0.38	0.28	−0.65	**0.71**	0.06	0.30	0.70	−0.69	**0.88**
H_{max}	***−0.77***	−0.15	−0.13	−0.15	0.47	***−0.91***	0.42	0.73	**−0.84**	0.11	−0.19	0.01	−0.57	0.55	−0.73
$CD_{7.5}$	***0.74***	0.72	0.33	−0.08	−0.44	0.21	0.43	−0.03	0.33	−0.46	−0.30	0.08	0.10	−0.12	−0.33
CD_{slo}	***−0.69***	−0.45	−0.43	0.10	0.32	−0.72	0.30	0.42	−0.70	0.20	0.46	−0.40	−0.65	0.56	−0.27
CD_{max}	0.09	0.49	0.14	−0.24	0.28	−0.72	0.42	0.46	−0.66	−0.11	0.47	−0.51	−0.75	0.73	−0.39
$CL_{7.5}$	−0.07	***0.70***	0.50	−0.52	0.44	−0.58	**0.77**	0.39	−0.51	0.28	−0.51	0.53	0.78	−0.64	0.46
CL_{slo}	−0.14	0.26	0.48	***−0.67***	0.54	**−0.82**	0.03	0.50	**−0.85**	0.26	0.21	0.51	0.41	−0.36	0.16
PCA_1	0.37	***0.78***	0.54	−0.46	0.48	***−0.90***	0.54	0.68	**−0.79**	−0.12	−0.47	0.30	0.22	−0.14	−0.19
PCA_2	***−0.78***	0.22	−0.22	−0.08	0.51	***−0.94***	0.38	0.68	**−0.88**	0.07	−0.14	−0.28	−0.76	0.76	**−0.88**

See Table 1 for an explanation of the architectural parameters. PCA_1 and PCA_2 refer to the axes scores of the first and second principal component analysis axis. Correlations with $P < 0.05$ are given in bold, and correlations with $P < 0.01$ are bold and italicized

mainly correlated with wood material properties and length of the drought period and to a minor extent with shade tolerance and other climatic variables.

Architectural relations with stem diameter

Tree height

Tree height increased asymptotically for most species. Height growth ceases once mature trees reach the canopy; they do not need to invest in height to attain higher light conditions but instead, they invest in stem diameter for stability and for replacing old dysfunctional vessels. Interestingly, four *Pinus* species (*P. halepensis*, *P. nigra*, *P. sylvestris* and *P. pinea*) did not show an asymptote. For *P. nigra* and *P. sylvestris*, this is probably because they occur in more closed and taller vegetation types where it pays off to continue investing in height growth. Alternatively, no clear asymptote is found because mature undisturbed pine forests are rare in the Mediterranean. Although it is generally assumed that height–diameter relationships should be asymptotic, studies from different forests show that a quarter of the species evaluated do not show such an asymptotic relationship (Thomas 1996; Chave et al. 2003; Poorter et al. 2006; but also see Aiba and Nakashizuka 2009). Species that do show an asymptote are canopy species from closed forest types, or species from more open woodland. In contrast, species that show a linear height–diameter relationship tend to be the smallest understory species growing in deep shade, for which the opportunity cost of diameter growth may be high, and some of the strongest light-demanding species that favour height growth over diameter growth to overtop competing neighbours (Poorter et al. 2006).

Crown diameter

The strongest architectural relationships were found between crown diameter and stem diameter, which indicates that they are closely coordinated. Larger trees have wider crowns to maximize light interception, whereas at the same time, they have thicker stems to provide biomechanical (King 1991) and hydraulic support. According to the pipe model theory (Shinozaki et al. 1964), each leaf is connected to its own vessel, and hence, large and leafy crowns need a large xylem cross-sectional area.
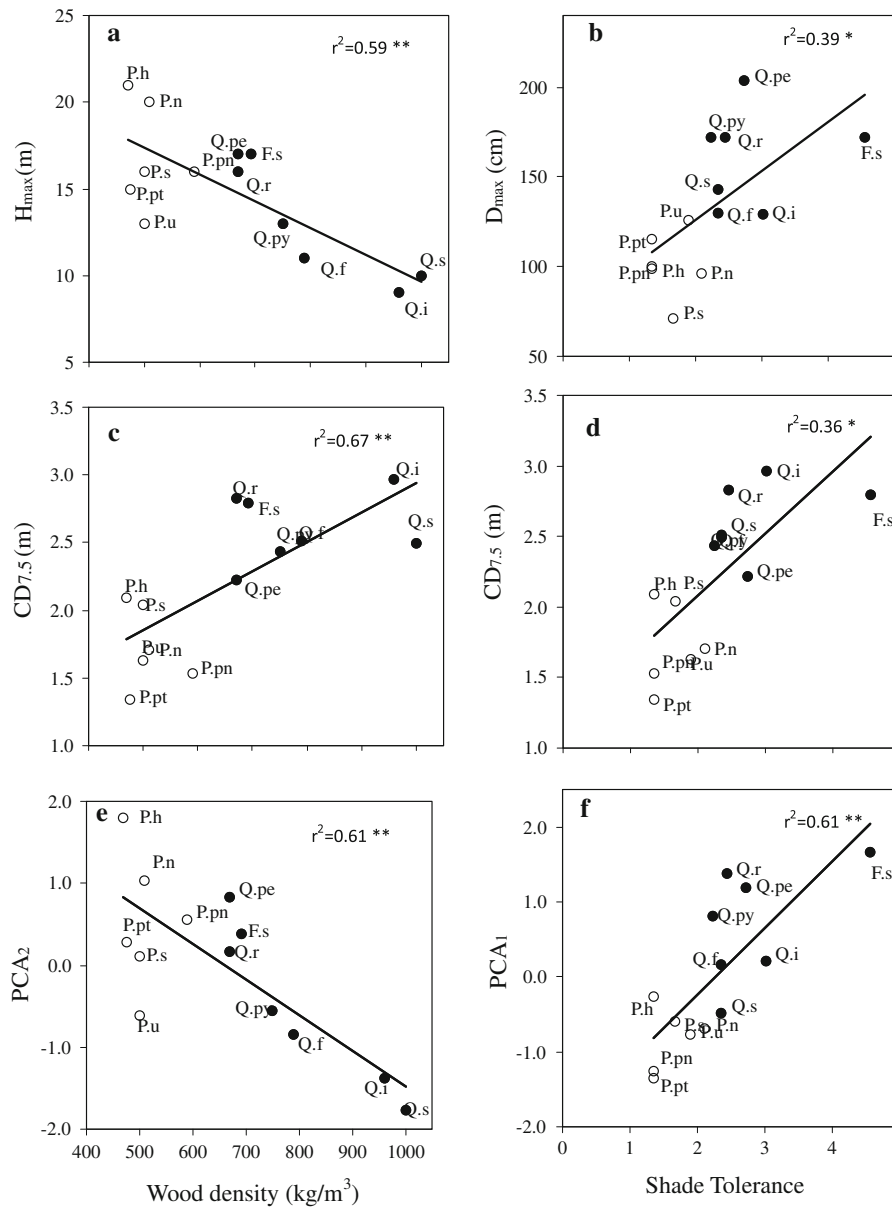
Fig. 4 Relationships between tree architectural parameters, air-dry wood density and shade tolerance of 13 Iberian canopy tree species. **a** Maximum height (H_{max}), **b** crown diameter for 7.5-cm thick trees ($CD_{7.5}$), **c** first axis of the principal component analysis (PCA_1) versus air-dry wood density. **d** Maximum measured diameter at breast height (D_{max}), **e** crown diameter for 7.5-cm thick trees ($CD_{7.5}$), **f** first axis of

the principal component analysis (PCA_1) versus shade tolerance. Regression lines, coefficients of determination (r^2) and significance levels are shown. *Open symbols* indicate Pinaceae species ($n = 6$) and *closed symbols* indicate Fagaceae species ($n = 7$). See Table 1 for an explanation of species abbreviations. *$P < 0.05$; **$P < 0.01$

Crown length

The relationship between crown length and stem diameter was very variable, ranging from an increase

of crown length with stem diameter to a decrease. This large variation can partly be attributed to the small stem diameter range considered (from 7.5 to 20 cm) leading to poor slope estimates and regression fits.

Table 3 Results of a series of ANCOVA analyses, with family (Pinaceae/Fagaceae) as factor and wood density, shade tolerance and climatic variables as continuous covariates (C) and species (N = 13) as data points

	Wood density			Shade tolerance			Rainfall			Drought			Frost		
	β	C	I	β	C	I	β	C	I	β	C	I	β	C	I
D_{max}	−	*	ns		ns	ns		ns	ns		ns	ns		ns	ns
$H_{7.5}$	−	**	ns		ns	ns	+	ns	*		ns	ns		ns	ns
H_b		ns	ns		ns	ns		ns	ns	−	*	ns	+	**	ns
H_{max}	−	**	ns		ns	ns	+	ns	*	−	ns	*		ns	ns
$CD_{7.5}$		ns	ns		ns	ns		ns	ns		ns	ns		ns	ns
CD_{slo}		ns	ns		ns	ns		ns	ns	−	ns	*		ns	ns
CD_{max}		ns	ns		ns	ns		ns	ns	−	**	*		ns	ns
$CL_{7.5}$		ns	ns	+	**	ns		ns	ns		ns	ns		ns	ns
CL_{slo}	−	*	ns		ns	ns		ns	ns	−	*	ns		ns	ns
PCA_1	−	***	ns		ns	ns		ns	ns		ns	ns		ns	ns
PCA_2	−	**	ns		ns	ns	+	*	ns	−	ns	***	+	ns	*

First, it was tested whether there was a significant interaction (I) between family and the covariate. If not, the ANCOVA was repeated without the interaction effect. The sign of the slope (β) of the covariate indicates whether it had a positive (+) or negative (−) effect on tree architecture. When the interaction between family and covariate is significant, then the slope refers to the value for the Fagaceae (which were coded with dummy variable 1). The slope for the Pinaceae was in those cases not significantly different from zero. The results for Family are not shown, as the aim of this analysis was to show whether, apart from Family, wood density, shade tolerance and climate have independent effects on tree architecture

See Table 1 for an explanation of the architectural parameters. PCA_1 and PCA_2 refer to the axis scores of the first and second principal component analysis axes

ns $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Species that rapidly increase their crown length with diameter are species that maintain their lower shaded branches (e.g., *Fagus sylvatica* and *Quercus petraea*), whereas species with a constant crown length (*P. pinaster* and *P. pinea*) either actively or passively abscise their lower branches. Ackerly (1999) found that leaves in the bottom of the crown are abscised when they present a net carbon drain. If the same argument applies to whole branches, then these differences in branch turnover might be explained by species' shade tolerance: for shade-tolerant species with low photosynthetic light compensation points, these lower shaded branches may still contribute to net carbon gain, whereas for the light-demanding species, these shaded branches may present a net carbon drain in terms of maintenance costs.

Architectural trait associations

Species with larger maximum stem diameter (D_{max}) attained also a larger maximum crown diameter (CD_{max}) (Fig. 2a). Wide crowns enhance the ability to intercept light and consequently, thick stems are needed to make trees biomechanically more stable and to provide hydraulic support (sensu Aiba and Nakashizuka 2009).

Pairs of architectural parameters, crown diameter ($CD_{7.5}$ and CD_{slo}) and to a lesser extent, height ($H_{7.5}$ and H_b) were negatively related (Fig. 2a). This could partly be a regression artefact, because regression lines with high slopes may force the intercept (and hence, architecture of 7.5-cm thick trees) to be low. Alternatively, it points to differences in ecological strategy, where some species build saplings with tall slender stems and wide crowns, whereas other species catch up or overtake in later phases, by realizing rapid increases in height and crown diameter with stem diameter growth. This trade-off between architectural intercepts and slopes could reflect the 'pessimistic' versus 'optimistic' strategies of Kohyama (1987) (cf. King 1990), where pessimistic species that persist in the shaded understory show lateral crown spread to optimize current light capture, whereas optimistic species obtain brighter light conditions in the forest canopy by rapidly increasing their tree height and crown size with increasing diameter.
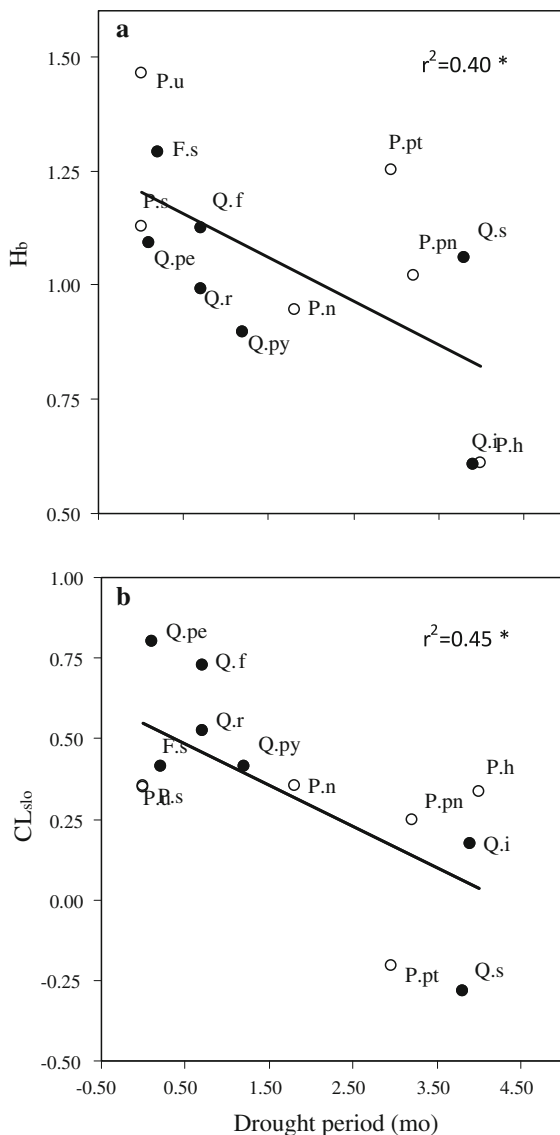
Fig. 5 Relationships between tree architectural parameters and drought period of 13 Spanish canopy tree species. Drought period is the number of those months when the monthly precipitation is less than twice the average monthly temperature. **a** Height slope (H_b), **b** crown length "slope" or power function exponent (CL_{slo}) versus drought. Regression lines, coefficients of determination (r^2) and significance values are shown. *Open symbols* indicate Pinaceae species ($n = 6$) and *closed symbols* indicate Fagaceae species ($n = 7$). See Table 1 for an explanation of species abbreviations. *$P < 0.05$; **$P < 0.01$

Architectural differences between Pinus and Fagaceae

Fagaceae species had the widest crowns (CD_{max}), whereas *Pinus* species tended to have the tallest trees

(H_{asy} and H_{max}) (Fig. 3; Table 1), mirroring the results for angiosperms and gymnosperms in general (Niklas 1994), where angiosperms have larger lateral crown-spread and larger stem diameter to support those crowns as opposed to gymnosperms, which have stronger apical control and invest more in the central trunks and less in branches (Harold and Hocker 1979; Spurr and Barnes 1983). In addition, the Fagaceae had wider crowns as young trees ($CD_{7.5}$; Fig. 3), and higher scores on the first PCA axis that summarizes overall tree architecture (Fig. 2b). This is in line with the suggestion that shade-tolerant species, such as Fagaceae, place preference on current light capture (Givnish 1988). The wider crowns of the Fagaceae might be a consequence of their higher wood density, because high-density wood provides greater mechanical efficiency for horizontal branch expansion (Sterck et al. 2006; Anten and Schieving 2010). Architectural differences between the two groups can also be attributed to the differences in their leaves. Pines have round needles arranged in a bottlebrush around each twig. A single layer of pine foliage is therefore not very effective in intercepting light, which may explain the shade intolerance of pines. Fagaceae have flat leaves, allowing a single horizontal branch to intercept most light. Hence, spreading branches are more effective in *Quercus* species, and especially so in the planar-branched *Fagus* species.

Pinus saplings had similar height compared with Fagaceae saplings at 7.5-cm dbh (Fig. 3a), and a similar height increase with stem diameter (H_b, Fig. 3b), suggesting that they follow in the first part of their life (from 7.5-cm diameter onwards) similar growth trajectories. This contrasts with the results for a temperate forests in Oregon (King 1991), where the gymnosperms (*Tsuga*, *Taxus* and *Abies*) did have a faster height increase with stem diameter than deciduous angiosperms, possibly because they showed little increase in crown width with increasing tree height.

Architectural relations with wood density, shade tolerance and climate

Wood density and length of the drought period emerged as the strongest correlates of interspecific variation in tree architecture (Tables 2 and 3). Wood density explained 61% of the variation in the second PCA axis that describes overall tree architecture (Fig. 4e) and in the ANCOVA, it also explained

variation in the first PCA axis. Wood material properties may therefore have large consequences for tree biomechanics, architecture and design.

Sapling crown diameter was positively related to wood density (Fig. 4b) and shade tolerance (Fig. 4e). Species with dense wood make stronger and narrower branches that are produced at lower horizontal extension cost per unit biomass invested because it provides a better balance in terms of minimizing mass investment and maximizing resistance to rupture and flexibility (Sterck et al. 2006; Anten and Schieving 2010). As a consequence, dense-wooded species produce a wide crown, which enhances light acquisition and reduces self-shading. Such a strategy is especially beneficial for shade-tolerant species that regenerate in the light-limited understory. Indeed, several other studies also found that shade-tolerant species make wider crowns (Sterck et al. 2006; Poorter et al. 2006). In contrast, branches made of low-density wood are weaker, and need therefore to be extra thick to provide sufficient strength (Sterck et al. 2006). This leads to high biomass investments per unit branch length, and light-demanding species make, perhaps for that reason, short branches (Sterck et al. 2006).

We found no relationship between wood density and sapling height at standardized stem diameter, although Iida et al. (2012) found for Malaysian rainforest trees a positive relationship, possibly because dense wood is stronger and stiffer, and allows trees to produce more slender stems. High-density wood seems therefore to have the best of both worlds, in terms of horizontal and vertical expansion. Yet, low wood density species need to invest less *biomass* per unit stem height than high wood density species (cf. Kooyman and Westoby 2009) in order to maintain the same degree of mechanical stability to support the plant's weight (Anten and Schieving 2010). Low wood density species show, therefore, a faster height growth (Muller-Landau 2004; Poorter 2008; King et al. 2005) and a low wood density is therefore especially advantageous for light-demanding species that need to monopolize gaps by growing rapidly in height and complete their life cycle before they are being overtopped by competing neighbouring plants. Wood density is emerging as a core functional trait (Chave et al. 2009), not only because of its importance for tree stability and architecture (King et al. 2006) but also because of its importance for defence against pathogens (Loehle 1988), stem hydraulics and cavitation resistance (Pratt et al. 2007;

Markesteijn et al. 2011), and hence, photosynthetic carbon gain (Santiago et al. 2004). The effect of wood density was largely maintained in the ANCOVA analysis, suggesting that wood density may contribute to architectural variation not only between families but also within families.

We make a reasoned case for the importance of wood density for tree architecture while acknowledging that this study is a correlative study. Correlation does not imply causation as many other species leaf and stem traits may also contribute to the observed architectural differences. However, Iida et al. (2012) found across 145 coexisting angiosperm rainforest tree species a positive relationships between wood density, stem slenderness, crown width and crown length.

The weak correlation amongst architectural traits and species shade tolerance suggests that for the Fagaceae, shade tolerance in the regeneration stage is mainly driven by other factors independent from tree architecture, such as seed size (Sánchez et al. 2006). Shade tolerance of Mediterranean oaks has also been linked to their ability to persist in the understory, e.g., through resprouting, rather than by carbon gain maximization under low light (Retana et al. 1999).

Drought is one of the most important factors driving species segregation in this region (e.g., Montoya et al. 2009) and accordingly, key architectural traits were correlated with length of the drought period, both in the all-species correlation analysis, the ANCOVA analysis, and especially for the Fagaceae. Drought also contributes to architectural variation within families, perhaps because the variation in length of the drought period within families is relatively large (Pinaceae 0–4 and Fagaceae 0.2–3.8 months). Chiefly height increase with stem diameter (H_b) and crown length increase with diameter (CL_{slo}) were negatively related to the length of the drought period (Fig. 5), and similar patterns have been found for height within species in other water-limited communities (Barton 1993; Martinez and López-Portillo 2003). Drought imposes limits to the height of plants (Tilman 1988) and leads to shallow crowns, as instead sufficient biomass has to be invested in roots for water uptake, and in stems to assure water transport and replace embolized vessels. In addition, species in dry environments should be smaller to reduce hydraulic path lengths and to maintain leaf water potentials sufficiently high and avoid cavitation. In contrast, in more perhumid areas, the forests are taller and more closed, and here species

would benefit from a rapid increase in height with stem diameter, to outcompete and overtop their neighbours for light. Patterns of asymptotic height for Fagaceae are therefore consistent with the expectation from mechanistic theory that species from more productive environment should allocate more resources to competition for light (Tilman 1988). Accordingly, species ranking in maximal height for Fagaceae (Q.i < Q.s < Q.f < Q.py < Q.r < Q.pe & F.s) matches species' relative position along a climatic productivity gradient (Montoya et al. 2009) while, for Pinaceae, this ranking is not so clear. Tradeoffs between maximal height and other traits linked to drought tolerance and resprouting (e.g., lignotuber development or root development) may drive Fagaceae species segregation patterns along these gradients (Zavala et al. 2000). In contrast, for shade-intolerant pines, traits linked to fire resistance (Barton 1993), tolerance to drought (Martínez-Vilalta and Piñol 2002) or allometric plasticity to rapidly occupy open spaces (Zavala et al. 2011) might be more relevant to explain species ecological dominance.

Conclusions

The architectural analysis suggests both phylogenetic contingencies as well as differentiated ecological strategies between the two dominant families of Iberian canopy tree species. Fagaceae species had high-density wood, the thickest stems and widest crowns, and were shade tolerant. This would allow them to better acquire light in shaded environments. Pinaceae species had low-density wood and a light-demanding temperament, and reached taller heights by allocating more resources to the formation of the central trunk, rather than allocating resources to branches. Interspecific variation can be explained by differences in wood properties and drought adaptations. Fagaceae species conform to the expectations from mechanistic theory—a larger stature with increasing productivity. Interspecific differences for Pinaceae depart, however, from this model, and might be due to other selective factors such as fire.

Wood density is important for tree biomechanics and may have large consequences for tree architecture. The relationship between shade tolerance and tree architecture might partly be driven by the fact that shade-tolerant species have a higher wood density compared with light-demanding species (Online

Resource 2, cf van Gelder et al. 2006). Wood density is emerging as a core functional trait, not only because it is important for biomechanics but also because it is important for many other plant functions, with important consequences for species segregation and coexistence.

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