Analysis of Holm Oak Intraspecific Competition Using Gamma Regression

Guillermo Gea-Izquierdo and Isabel Cañellas

Abstract: Analysis of plant competition is a major issue in ecology and forestry, as it influences plant growth and plant-environment interactions. Competition is expected to be lower in the sparse tree stratum of open woodlands and agroforestry systems than in closed forests. We have analyzed competition in open woodlands of *Quercus ilex* in the Iberian Peninsula by studying a 10-year diameter growth increment from collected samples and from consecutive National Forest Inventories. Density was the competition index selected in all models, outperforming more complex distance-dependent indices. The models showed that competition is playing a role in growth but that the covariate most correlated with growth is age or dbh as a surrogate of age. Therefore, below-ground competition is likely to be limiting tree growth, but below-ground competition is lower in open woodlands compared with that in denser forests and thus potential growth (which is strongly linked to age) is almost expressed. Model behavior was improved when data were fitted directly using generalized linear models, which do not require transforming of the dependent variable. Our results showed that modeling growth with the gamma probability distribution resulted in better models compared with Gaussian linear models. Gamma regression offers a great potential for many forestry applications. FOR. SCI. 55(4):310–322.

Keywords: dehesa, *Quercus ilex*, diameter increment growth, generalized linear model

THERE ARE MANY STUDIES analyzing competition among trees in closed forests (e.g., Biging and Dobbertin 1995, Canham et al. 2006), where density is usually greater than in agroforestry systems and open woodlands. All agroforestry systems have a low-density woody stratum, in which trees are likely to compete with each other and with the herbaceous and/or shrub layers for below-ground resources. Below-ground interactions are complex and poorly understood. Despite this potential source of competition, low-density trees are generally thought to exhibit free growth, which in traditional forestry would be considered as potential growth (Hasenauer 1997).

Agrosilvopastoral systems are one special type of agroforestry system; these include the *Quercus* spp.-dominated open woodlands of West Iberia (called "dehesas" in Spain) that cover more than 3,000,000 ha. *Quercus ilex* L. (holm oak) is the most common tree species in the ecosystem and probably the most important and widespread tree species in the Mediterranean Region (Barbero et al. 1992). These oak stands are not suitable for traditional, intensive forestry because of the poor sandy soils and Mediterranean variable dry climate in which they thrive. The origin and history of the dehesas are complex. The specific management applied through time has modeled the landscape, resulting in the low-density, open tree stratum encountered today. As in other agroforestry systems, trees are regularly pruned (San Miguel 1994).

Diameter increment is mostly related to three factors: age, site index (as a surrogate of fertility), and competition (Lessard et al. 2001). Competition can be defined in various ways, emphasizing different variables. If one bears in mind that competition is never totally symmetric or asymmetric, it can be broadly classified as either asymmetric or symmetric. These classifications are usually applied to competition for light and soil resources, namely nutrients and water (Schwinning and Weiner 1998). In crowded systems, asymmetric competition for light is, in general, the primary cause of size inequality. In agroforestry systems the tree stratum is not crowded; therefore, symmetric competition (soil moisture) is likely to be the most important competitive factor affecting tree growth. In particular, in Mediterranean ecosystems, below-ground competition for water is generally more likely to be a principal growth-limiting factor than crown competition for light or competition for nutrients (e.g., Mayor and Rodá 1994, Ogaya and Peñuelas 2007). Competition among species is not symmetrical, with different species competing distinctly for soil resources (Canham et al. 2006). Competition can also influence the way trees respond to climate (e.g., Cescatti and Piutti 1998); thus, analysis of competition is interesting not only from a commercial point of view but also for conservation.

The most commonly used competition indices assume that there is a relationship between the size and proximity of competitor trees and the distribution of resources (Larocque 2002). Tree competition indices used in forestry can be generally classified as distance dependent or distance independent. Distance-dependent indices can be further subclassified as area overlap indices, point-density indices, distance-weighted size ratio indices, and area-potentially-available indices (Tomé and Burkhart 1989, Biging and

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Dobbertin 1995, Larocque 2002). Many authors' results suggest that more complex distance-dependent indices are not better than distance-independent indices (e.g., Martin and Ek 1984, Biging and Dobbertin 1995) although there are exceptions (e.g., Mailly et al. 2003, Stadt et al. 2007). The search radius to decide whether a neighbor is competing or not can be a crucial issue (Biging and Dobbertin 1992). Often indices calculated from crown features are very much correlated with growth (Biging and Dobbertin 1992, 1995, Miina and Pukkala 2000), but those cannot be reliably calculated in pruned stands, common in some agroforestry systems. The conclusion from the numerous studies analyzing competition is that there is no superior competition index (Tomé and Burkhart 1989, Biging and Dobbertin 1995), but, depending on the stand structure and particular environment, certain indices will be better than others.

There is a wide variety of different models in the literature to describe diameter growth, which is a key variable in forestry modeling (Porte and Bartelink 2002). Most individual tree diameter models used can be ascribed to two categories, namely empirical or semiempirical (Vanclay 1994). Examples of empirical models can be found in Miina (1993), Andreassen and Tomter (2003), and Mailly et al. (2003), whereas semiempirical examples are found in Biging and Dobbertin (1995), Canham et al. (2006), and Stadt et al. (2007). Empirical models are generally linear in their parameters, although usually linearity is achieved after some transformation (most often logarithmic) to achieve normality and mimic the nonlinear, sigmoid shape of plant growth (Wykoff 1990, Schwinning and Weiner 1998). Semiempirical models have the advantage that their foundations are in biological theory, but they require the estimation of potential growth, which is difficult and adds an extra source of error (Wykoff 1990, Vanclay 1994). Semiempirical models are more complex than empirical models because they are nonlinear. In addition, e.g., Martin and Ek (1984) and Sánchez-González et al. (2006) did not detect an improvement in accuracy using semiempirical models. Other statistical methods (generalized additive models, classification and regression tree analysis, and artificial neural networks) used in ecological modeling (Guisan and Zimmermann 2000) have been used for modeling stand characteristics in Inventory data (Moisen and Frescino 2002). Generally, they were not an improvement on classic linear models, but we do not know of any study using them to model diameter increment. Generalized linear models (GLMs) are a class of linear models that relax the Gaussian assumption. Therefore, GLMs are able to fit different shapes of data, including data with heterogeneous variances and probability distributions such as the Gaussian (normal), Poisson, gamma, and negative binomial (McCullagh and Nelder 1989). Gaussian and Poisson models are frequently used in forestry and ecology, but gamma and negative binomial models, although have been used in other biological sciences, are not yet very common in studies of ecology and forestry (e.g., Guisan and Zimmermann 2000, Gea-Izquierdo et al. 2007, Salway and Wakefield 2007).

The objectives of this study were to analyze whether it is true that holm oaks in this system exhibit free growth and to what extent competition affects diameter growth; to compare different empirical models and discuss whether modeling growth directly with gamma distributions results in better models than classic log-transformed Gaussian models; and to check the possibility of using the Spanish National Forest Inventory (IFN) for holm oak growth modeling, as these data are a cheap (for the user) and interesting source of information (Moisen and Frescino 2002).

Materials and Methods

Study Area and Data
Sampled Data

The two directly sampled study areas were typical dehesas with acidic bedrock (granites, slates, and cuarcites) under a Continental Mediterranean climate with mean annual precipitation of approximately 600 mm and summer drought. Mean annual temperatures at the study areas were 16.0°C at Cáceres (southern most sampled area) and 13.2°C in Salamanca. Sampled data were collected from 37 plots generally including 10 trees: 25 plots in Salamanca (40°37′N, 6°40′W, 700 m above see level) and 12 plots in Cáceres (39°28′N, 6°11′W, 393 m above see level) (Figure 1). These plots were all included in different holm oak woodland belts clearcut to construct two freeways. For each of the 10 trees, we measured distance and azimuth to the center of the plot, two perpendicular crown radii, total height and height to crown base, and two perpendicular
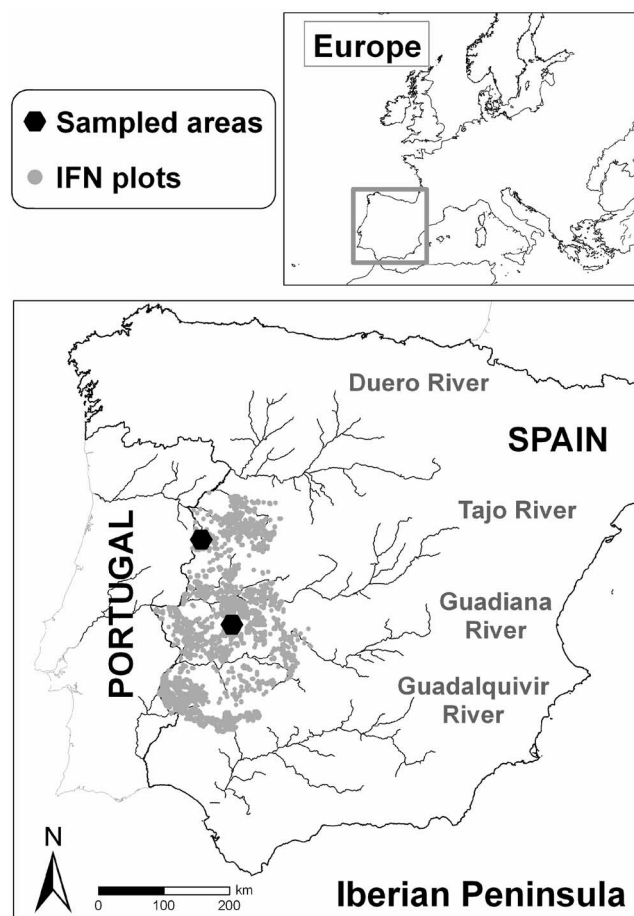

Figure 1.   Location of the study plots.

diameters at 1.30 m (dbh). We sampled all holm oaks, including shrubs which, when calculating indices, were considered as competing trees having a dbh equal to that of a treelike holm oak of equivalent crown. This assumption was made because there were no signs of pruning in recent years at Cáceres. To reduce bias from sampling design we corrected the plot radius (R_i) for calculations using $R_i = r_i + l_i$, where $l_i = 0.5 \cdot (r_i/n)$, where n is the number of trees in the plot, and r_i is the distance of the last tree within plot i (Cañadas 2000).

To estimate growth, the five central trees of each plot were pushed down with a bulldozer, and sections at 1.30 m and at the base were collected. Data are likely to be slightly biased away from individuals with the widest diameters (and, hence, probably greatest ages) as the oldest and thickest trees tended to be rotten, and only trees with at least one readable radius were included in the analysis. In total, 168 trees, 115 from Salamanca and 53 from Cáceres, were included in the analyses (Figure 2). Annual ring width was estimated as explained in Gea-Izquierdo et al. (2008) and the sum of the period 1995–2004 (hereafter Incdbh$_{10}$) was used as the dependent variable. We considered bark growth to be negligible compared with dbh growth and hence it was not taken into account in the analyses. Covariates were calculated from plot attributes, site index was calculated from Gea-Izquierdo et al. (2008), and competition indices were calculated as explained below (Table 1). Covariates analyzed included dbh^2, as growth is likely to be a paraboloid with an inflection point (Wykoff 1990).

As a consequence of the previously described characteristics of the system, we only tested competition indices that do not depend on crown features, i.e., those based on distances, crowding, and/or tree diameters. A total of 18 distance-dependent and distance-independent indices were studied (Table 2). The distance of influence (the distance within which neighbors are considered to be competing) used for each index was determined in a preliminary study (Gea-Izquierdo 2008) comparing fixed distances with relative distances (from 40 to 140 times the dbh). Density has not changed much during the last decades in the dehesas (García del Barrio et al. 2004), and there were no signs of recent logging in the study area, so we assume that density was constant during the last 10 years.

IFN Data

In the IFN plots are located systematically in a 1-km grid and are measured with a periodicity of 10 years. Plots are circular with four different radii (from 5 to 25 m) where different tree sizes are sampled. For this study we only used data from the 10-m radius, analyzing trees with dbh > 12.5 cm. Other studies with similar inventory design have also selected specific subplots (Canham et al. 2006). By using only this subset of the data we avoided biases from sampling different sizes in the contiguous radii and we reduced within-plot data spatial correlation. Because of the differences in plot design, data collection, and processing we decided to compare the results derived from fitting models to our data and those derived from fitting models to the IFN data independently without mixing the two data sets.

Plots from the provinces of Salamanca, Cáceres, and Badajoz (Figure 1) were selected. Plots were only selected if they were holm oak monospecific and of a density lower than 500 trees/ha. Decreasing density limits (500, 250, and 150 trees/ha) were compared to avoid as much as possible shrub formations from coppice. Following the previous criteria and deleting negative increments (5% of the total), we analyzed 2,819 trees from 1,566 plots (Figure 1). The difference between dbh in the second and third inventories was used as a dependent variable, taking as covariates the plot density, basal area, tree height, Universal Transverse Mercator (UTM) coordinates, slope, meteorological data (Sánchez-Palomares et al. 1999), and river basin (the three last covariates were estimated using a geographic information system). No other competition indices were calculated from the plot design and the inventory data limitations already described. The holm oak data in IFN are not as complete as those for other species, as past diameter increments from increment borers are not available, reducing modeling possibilities (Trasobares et al. 2004).

Models and statistical analyses

A flow chart is shown in Figure 3 to ease tracking analyses flow and models comparison. Models were fitted to 10-year increments for two reasons: to compare with IFN data and to reduce climatic variability and measuring error,
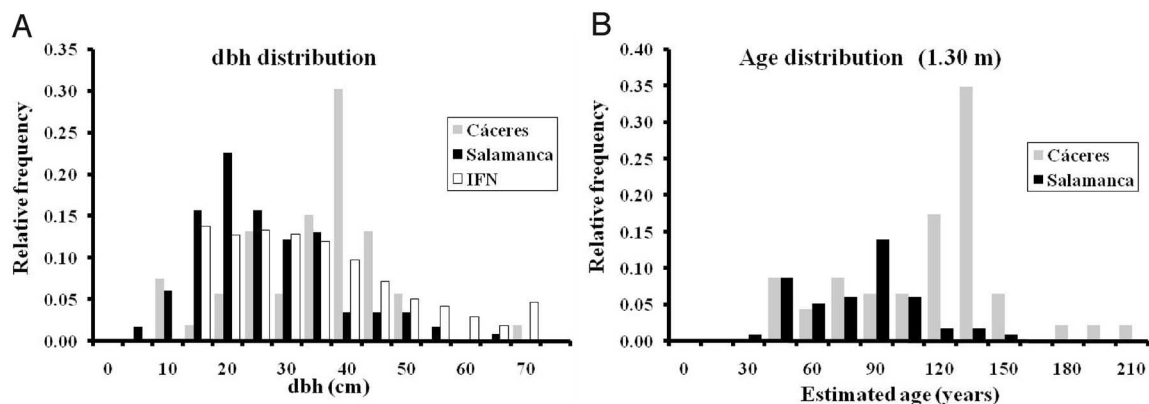

Figure 2. A, diameter distribution of plots: (i) Cáceres plots in gray bars; (ii) Salamanca plots in black bars; and (iii) IFN plots in white bars. B, age distribution at 1.30 m.

Table 1. Sample characteristics

	Ciudad Rodrigo				Cáceres				IFN*		
	dbh (cm)	Age	Density (trees/ha)	BA (m²/ha)	dbh (cm)	Age	Density (trees/ha)	BA (m²/ha)	dbh (cm)	Density (trees/ha)	BA (m²/ha)
Mean	28.9	88	117.8	8.5	39.6	116	45.6	5.8	36.8	73.8	5.7
CV (%)	38.8	32.3	39.2	41.9	33.1	31.4	44.3	37.0	44.6	101.2	64.1
Minimum	10.2	26	35.8	4.1	13.9	42	15.3	3.1	13.4	5.1	0.4
Maximum	68.4	175	190.8	16.2	96.8	212	87.3	9.6	108.2	489.6	31.4
n	115	110	25	25	53	46	12	12	2,819	1,566	1,566

dbh, diameter at breast height (1.30 m); BA, plot basal area; age, estimated age in the base; n, sample size; CV, coefficient of variation.
* Data from IFN3: plot radius = 10 m, dbh trees > 12.5 cm, density < 500 trees/ha.

Table 2. List of competition indices used in the study

Index	Name	Expression	Reference
Distance-independent indices			
CII1	Plot density (Nn)	n/plot area (in trees/ha)	
CII2	BA	$\sum_{i=1}^{n} \pi \cdot (\text{dbh}_i/2)^2$	
CII3	ddg	dbh_i/Dmc	
CII4	Glover	$\text{dbh}_i^2/\overline{\text{dbh}}^2$	Glover and Hool (1979)
CII5	BAL	$\sum_{j=1}^{n-1} \pi \cdot (\text{dbh}_j/2)^2$ when $\text{dbh}_j > \text{dbh}_i$	
CII6r	Number of competitors within r meters (N_r)		Moravie et al. (1999) cited in Paulo et al. (2002)
CII7r	Number of competitors within r meters such that $\text{dbh}_j > \text{dbh}_i$		Moravie et al. (1999) cited in Paulo et al. (2002)
CII8r	Sum of size of trees within r meters	$\sum \text{dbh}_j$	Steneker and Jarvis (1963) cited in Paulo et al. (2002)
CII9r	Size ratio	$\text{dbh}_i/\sum_{i=1}^{n} \text{dbh}_i$	Daniels et al. (1986) cited in Paulo et al. (2002)
Distance-dependent indices			
CID10	Clark-Evans	$(\sum_{i=1}^{n} \min(\text{dist}_{ij})/n)(2 \cdot \sqrt{Nn})$ (Nn in trees/m²)	Clark and Evans (1954)
CID11	Distance to nearest tree (NN)		Moravie et al. (1999) cited in Paulo et al. (2002)
CID12	Distance to NN such that $\text{dbh}_j > \text{dbh}_i$		Moravie et al. (1999) cited in Paulo et al. (2002)
CID13r	Size ratio proportional to distance	$\sum_{i=1}^{n} (\text{dbh}_j/\text{dbh}_i) \cdot [1/(\text{dist}_{ij} + 1)]$	Hegyi (1974) cited in Biging and Dobbertin (1995)
CID14r	Size difference proportional to distance	$\sum_{i=1}^{n} [(\text{dbh}_j - \text{dbh}_i)/(\text{dist}_{ij} + 1)]$	Moravie et al. (1999) cited in Paulo et al. (2002)
CID15r	Negative exponential size ratio	$\sum_{i=1}^{n} (\text{dbh}_j/\text{dbh}_i) \cdot [1/\exp(\text{dist}_{ij} + 1)]$	
CID16r	Negative exponential weighted size ratio	$\sum_{i=1}^{n} (\text{dbh}_j/\text{dbh}_i) \cdot \exp[(-\text{dist}_{ij} + 1)/(\text{dbh}_i + \text{dbh}_j)]$	Martin and Ek (1984)
CID17r	Lorimer	$\sum_{i=1}^{n} \cdot [(\text{dbh}_j/\text{dbh}_i)/(\sqrt{\text{dist}_{ij}/r})]$	Lorimer (1983) cited in Mailly et al. (2003)
CID18r	Crowding	$\sum_{i=1}^{n} (\text{dbh}_j/\text{dist}_{ij})^\gamma$; with $\gamma = 1$	Miina and Pukkala (2000); Stadt et al. (2007)

The index i refers to the subject tree, j refers to a competitor, dist_{ij} = distance between i and j, BA = plot basal area, Dmc = $2 \cdot (\sqrt{\text{BA}/Nn \cdot \pi})$, n = number of trees in plot k, dbh_i = dbh of tree i, BA_i = basal area of tree i, and r = search radius.

as the species is slow-growing. Diameter increment was approached in two ways: age-dependent models and age-independent models. This double approach was done to study the role played by age in the models (potential diameter growth would imply age explaining the most variance with null competition) as age estimation in holm oak is generally impossible for managers. As discussed in the Introduction, we decided to use empirical models. Exponential or power models are biologically sound if fitted for the data range over the growth inflection point (or even before in some cases [Wykoff 1990]), which is usually located at early ages, at least in holm oak (Gea-Izquierdo et al. 2008).
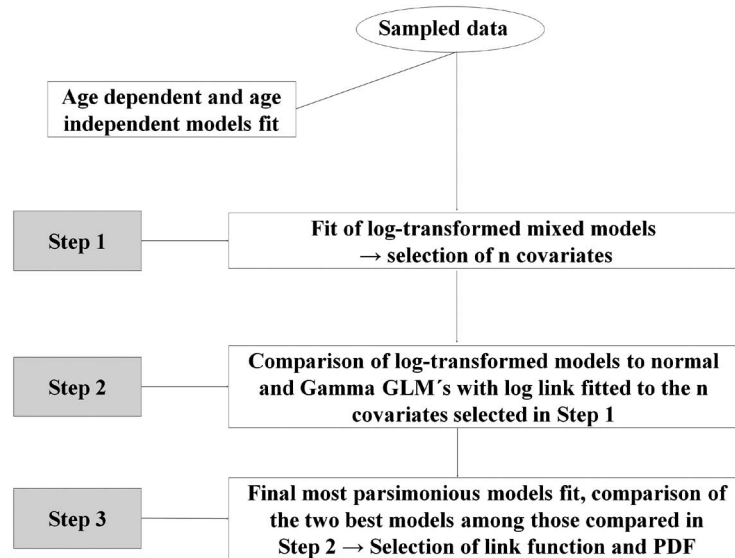
Figure 3. Flow chart of the steps followed in the study for model fitting and validation: for both age-dependent and -independent models only for sampled data.

Similarly, log transformation has been widely used (e.g., Wykoff 1990, Andreassen and Tomter 2003, Trasobares et al. 2004) because it results in a negative exponential shape close to biological growth. However, transformation alters the error structure, resulting in biases that must be corrected (Myers 1990). In the study, we used the correction proposed by Snowdon (1991) to correct residuals from log-transformed models.

After log transformation, researchers generally obtain a linear model with normal errors (i.e., the data are lognormal), and this has been the classic approach to diameter empiric growth models. Classic general linear models with a normal distribution are extended into GLMs that, using maximum likelihood theory, are able to fit linear models to any probability distribution included in the exponential family (McCullagh and Nelder 1989). Therefore, data fitted by GLMs belong to $f_Y(y; \theta, \phi) = \exp\{(y\theta - b(\theta))/a(\phi) + c(y, \phi)\}$ where θ and ϕ are the canonical and dispersion parameters, respectively. GLMs include probability distributions such as the normal (where variance $= \phi = \sigma^2$) or the gamma functions (where variance $= \mu^2 \cdot \phi$) (McCullagh and Nelder 1989). GLMs directly fit the expected mean of the dependent variable, hence avoiding biases included in transformed general models (McCullagh and Nelder 1989). They have the generic expression $E(Y_i) = \mu_i = g^{-1}(\eta_i)$, with Y_i being the random component or dependent variable (belonging to the exponential family), $g(\cdot)$ being the link function, and η_i being the linear predictor (McCullagh and Nelder 1989). General linear models are a particular type of GLM with identity link and Gaussian distribution, whereas a log-transformed model is the same as a lognormal GLM with an identity link. The gamma function can be used to fit variables with constant coefficient of variation and is usually used either with identity, log, or reciprocal links (Halekoh and Højsgaard 2007).

GLMs and general linear models share the same assumptions of independence among observations. In general linear models, correlations within the data can be modeled to obtain more robust and accurate estimates by using linear mixed models. These models include both fixed and random effects and can model correlation in the residual variance-covariance structure (Verbeke and Mohlenbergs 2000). An extension of linear Gaussian mixed models are generalized linear mixed models (GLMMs), similar to normal mixed models in structure, in which G (random effects covariate structure) and R (residual covariate structure) can be modeled and with expression (Diggle et al. 2002, Mohlenberghs and Verbeke 2005):

$$f_i(y_{ij}|b_i, \beta, \varphi) = \exp\{\varphi^{-1}[y_{ij}\theta_{ij} - \varphi(\theta_{ij})] + c(y_{ij}, \varphi)\}, \quad (1)$$

$$\mu_{ij} = E(Y_{ij}|b_i) = g^{-1}(x'_{ij}\beta + z'_{ij}b_i), \quad (2)$$

where $g(\cdot)$ is the link function, x_{ij} and z_{ij} are matrixes of known covariates, β is a p-dimensional vector of fixed effects, and b_i is a q-dimensional vector of random effects, $b_i \sim N(0, G)$. Y_{ij} are observations from any distribution of the exponential family, with covariance matrix V, where φ is the scale parameter and θ is the natural parameter (Diggle et al. 2002, Molenberghs and Verbeke 2005).

In this study we compared linear log-transformed general models with GLMs with normal and gamma probability density functions (PDFs) and their ability to select significant covariates in parsimonious models. Covariates were selected by comparing nested models fitted using maximum likelihood methods by log-likelihood ratio tests compared with a χ^2 distribution (Verbeke and Mohlenberghs 2000), whereas significance of covariates in GLMs was tested using analyses of residual deviance (McCullagh and Nelder 1989). The covariates having the lowest asymptotic t values where tested first in the next nested fit. Random effects were accepted when the SE was at least two times smaller than the estimated mean. To check for multicollinearity in linear normal models we calculated the variance inflation factor (Myers 1990) using PROC REG. The other analyses were performed

using PROC MIXED for linear mixed models, PROC GEN-MOD for GLMs, and PROC GLIMMIX for GLMMs, all in SAS 9.1 (SAS Institute, Inc. 2004). We did not have an independent data set, and the sample size was too small to be split so we carried out an autovalidation (jackknife), leaving out one plot each time and calculating the goodness-of-fit statistics to the residuals obtained (Myers 1990).

To compare behavior between models we calculated the following goodness of fit statistics:

—Mean residual bias (bias)

$$\text{Bias} = \frac{\sum_{i=1}^{n}(\text{est}_i - \text{obs}_i)}{n} \quad (3)$$

—Root mean square error (RMSE)

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\text{est}_i - \text{obs}_i)^2}{n - p}}, \quad (4)$$

—Adjusted coefficient of determination (Mittlböck and Heinzl 2002) for general normal linear models,

$$R_{ss}^2 = 1 - \frac{(n - k - 1)^{-1} \cdot \sum_{i=1}^{n}(y_i - \hat{\mu}_i)^2}{(n - 1)^{-1} \cdot \sum_{i=1}^{n}(y_i - \bar{\mu})^2} \quad (5)$$

and for GLMs (both Gaussian and Gamma),

$$R_D^2 = 1 - \frac{(n - k - 1)^{-1} \cdot D(y; \hat{\mu})}{(n - 1)^{-1} \cdot D(y; \bar{\mu})}, \quad (6)$$

with n representing sample size and k representing the number of fitted parameters. The R^2 calculated in the autovalidation is called efficiency (EF), and it is the same as R_{SS}^2 without the correction for the degrees of freedom (in all models EF $= 1 - [\sum_{i=1}^{n}(y_i - \hat{\mu}_i)^2/(\sum_{i=1}^{n}(y_i - \bar{\mu}_i)^2)]$). All R^2 and EF values are calculated for residuals obtained using only the mean response (i.e., the fixed effects, if any random effects exist in the model). To check for systematic departures in GLMs, McCullagh and Nelder (1989) recommend plotting standardized deviance residuals against predicted values and covariates. We decided to plot raw residuals (observed − predicted) to ease the interpretation and comparison with general models.

Results

At the landscape scale dehesas are a mosaic of different plant assemblages; in contrast, at the plot scale trees tended to be displaced following an uniform pattern (1.400 ± 0.214) (Clark and Evans 1954). Plot summary statistics are shown in Table 1, and the distributions of age and dbh can be seen in Figure 2. These distributions are skewed and non-normal, with samples from Salamanca being younger with a smaller mean dbh.

Competition in Age-Dependent Diameter Increment Models

In Table 3 we show the selected covariates using log-likelihood ratio tests for the log-transformed mixed model (Verbeke and Mohlenbergs 2000). In Table 4 we compare the log-transformed models and the GLMs with log links including extra covariates as selected from Table 3 to ease the comparison between models. Five covariates were selected in the age-dependent log-transformed model (excluding those that were collinear with the previously selected covariates [not shown]); age was the covariate explaining the most variance, followed by density (CII1) and ddg

Table 3. Selection of covariates in linear mixed model

	Variables added	$-2LL$	$p(\chi^2)$	EF (%)	Max VIF (x)
Age-dependent models [$\log(\text{Incdbh}_{10}) = f(x_c)$]					
1	Age	160.2	<0.0001 (55.5)**	33.19	1.000
2	Density (CII1)	151.1	0.0026 (9.10)**	44.69	1.037
3	ddg (CII3)	134.6	<0.0001 (16.5)**	50.01	1.608 (age)
4	(1/dbh)	126.6	0.0050 (8.0)**	51.81	2.607 (1/dbh)
5	CID15$_{50}$	119.1	0.0062 (7.5)**	53.09	2.608 (1/dbh)
Age-independent models (own data) [$\log(\text{Incdbh}_{10} + 1) = f(x_c)$]					
1	(1/dbh)	79.1	<0.0001 (24.0)**	13.47	1.000
2	Density (CII1)	68.1	0.0009 (11.0)**	21.57	1.04
3	DumCac	57.9	0.0014 (10.2)**	26.98	1.83 (DumCac)
4	CID15$_{50}$	50.9	0.0081 (7.0)**	29.88	1.85 (DumCac)
5	CII7$_{50}$	45.9	0.0253 (5.0)**	30.98	2.00 (CII7)
6	dbh	41.7	0.0404 (4.20)**	33.42	3.69 (dbh)
Age-independent models (IFN) [$\log(\text{Incdbh}_{10} + 1) = f(x_c)$]					
1	Y UTM (km)	2,643.2	<0.0001 (29.7)**	1.407	1.00
2	Slope	2,611.9	<0.0001 (31.3)**	3.170	1.04
3	Density	2,606.7	0.0226 (5.2)**	3.649	1.07 (slope)
4	dbh	2,600.6	0.0135 (6.1)**	3.763	1.23 (density)
5	Height	2,589.0	0.0066 (11.7)**	4.306	1.72 (dbh)
6	Tmin	2,583.8	0.0226 (5.2)**	4.685	3.89 (Tmin)
7	DumGuad	2,577.6	0.0128 (6.20)**	4.906	4.04 (Tmin)

Models were fitted using maximum likelihood estimation (Verbeke and Mohlenberghs 2000). $-2LL$, -2 times residual log-likelihood; $p(\chi^2)$, log-likelihood ratio test, probability associated to the χ^2 distribution; EF, efficiency calculated for the residuals without back-transforming; Max VIF, maximum variance inflation factor corresponding to covariate x; DumCac, dummy variable for Cáceres data; Tmin, mean of minimum temperatures of the coldest month; DumGaud, dummy variable for the Guadiana and Guadalquivir river basins. Basic model: $(\text{Incdbh}_{10ij}) = f(x) + b_i + \varepsilon_{ij}$; for plot i, tree j, linear relationship of fixed effects $f(x)$, and random intercept plot effect b_i.
** Significant at $\alpha = 0.05$.

Table 4. Model comparisons

	Estimation					Validation (jackknife)		
Model	$-2LL$	Mean bias (cm)	RMSE (cm)	R^2_{SS}	R^2_D	Mean bias (cm)	RMSE (cm)	EF (%)
Age-dependent models								
Log-transformed Gaussian LM ($\approx$lognormal GLM)	—	0.0244	1.0303	50.599	—	0.0145	1.0964	45.737
Gaussian GLM with a log link	−236.5	0.0083	1.0176	51.787	51.787	−0.0105	1.1422	41.112
Gamma GLM with log link ($1/\mu$)	−204.0	0.0042	1.0261	50.977	53.929	−0.0035	1.0899	46.378
Age-independent models								
Log-transformed Gaussian LM ($\approx$lognormal GLM)	—	<0.0001	1.2084	30.807	—	−0.0153	1.3021	22.059
Gaussian GLM with a log link	−264.1	0.0216	1.1690	35.249	35.249	0.0252	1.2344	29.952
Gamma GLM with a log link ($1/\mu$)	−241.8	0.0093	1.1965	32.163	28.718	−0.0049	1.2808	24.598

The fitting statistics for the log-transformed linear model (LM) are calculated using the corrected predictions: $pred_{corr} = \hat{y}$ CF (Snowdon 1991); $-2LL$, -2 times residual log-likelihood. All models include only fixed effects (see text for nonsignificant tests for random effects). All age-dependent models include the five covariates selected in Table 3 for the log-transformed linear model, whereas age-independent models include the six covariates selected in Table 3 except 1/dbh (see text for details).

(CII3). The previous three covariates were negatively correlated with growth, reflecting the existence of competition. The log-transformed mixed model explained >50% of the variance of the back-transformed dependent variable (Table 4). Among GLMs, the log-likelihood maximized in gamma models both with the reciprocal link (−203.8: the maximum; hence, the link used in the final model shown in Table 5) and the log link (−204.0) compared with the Gaussian model with a log link (−236.5). Gamma models were better than log-transformed models (equivalent to a lognormal GLM) and Gaussian GLMs with log link (identical to a nonlinear exponential model), particularly in terms of the validation statistics and, as mentioned, they maximized the likelihood.

In Table 5 we show the estimates of the gamma model with inverse (=reciprocal) link and log-transformed. The gamma model reduced the significant covariates to density and age, which were the covariates with the strongest correlation (negative) from the beginning, both in the statistics and graphic analysis (not shown). It can be seen how using the Gaussian PDF overinflates the coefficient of determination from the excessive number of covariates selected. The final age-dependent model is a gamma GLM including an intercept, age at 1.30 m, and density, with no random coefficients (the random coefficient in the GLMM was nonsignificant) (Table 5), and it had the expression

$$\text{Inc}10_i = \hat{\mu}_i = \frac{1}{\left\{\begin{array}{c} 0.05331 + 0.003097 \cdot \text{Age}_{dbh} \\ + 0.000979 \cdot \text{Density} \end{array}\right\}} + \varepsilon_i, \quad (7)$$

with $\varepsilon_i \sim G(\mu, \mu^2/8.6828)$. Because age was closely related to dbh and estimating age in holm oak is extremely difficult, it would be very useful to estimate ages from dbh (Plieninger et al. 2003). The relationship obtained was

$$\text{Age}_{ij} = 21.0457[32578]$$
$$+ (2.3742[01518] + b_i) \cdot \text{dbh}_{ij} + \varepsilon_{ij}, \quad (8)$$

with $\varepsilon_i \sim G(\mu, \mu^2 \cdot 0.02820[0.003433])$, $b_i \sim N(0, 0.3347[0.09466])$, MBias = −0.120, RMSE = 23.41, and $R^2_{SS} = 47.24$ (SEs of parameters are shown in brackets).

Distribution of residuals against predicted values and covariates are shown in Figures 4 and 5.

Competition in Age-Independent Diameter Increment Models

Six covariates were first selected in the log-transformed model (Table 3), among which density, the inverse of dbh, and a dummy variable for the Cáceres data were most strongly related to diameter increment. However, we used only five covariates to compare models in Table 4, excluding (1/dbh), because although this covariate was significantly selected in the estimation phase, the autovalidation statistics were better in all models without its inclusion (not shown), and models depicted more realistic fits. All age-independent GLMs in Table 4 were also fitted using the log-link for comparative purposes. Both untransformed GLMs were better than the log-transformed classic model. Although the Gaussian GLM had the best goodness-of-fit statistics (Table 4), it can be seen in Table 5 that the gamma model was the best as it reduced the number of selected covariates significantly. Thus, it resulted in more parsimonious models depicting the real relationship between covariates and the dependent variable, despite increasing the RMSE slightly. The log-likelihood was maximized in gamma models both with a reciprocal link (−238.9) and with a log link (−241.8), compared with the Gaussian model with a log link (−264.1) and a reciprocal link (−256.7). As the reciprocal maximized the likelihood with both PDFs, we used the reciprocal link to fit final normal and gamma age-independent GLMs (Table 5). The variables finally selected in the gamma model with an inverse link were again density and dbh (in lieu of age) and a dummy for the Cáceres province. These three variables were negatively correlated with diameter increment (i.e., positive estimates using a reciprocal link). The final expression was

$$\text{Inc}10_i = \hat{\mu}_i = \frac{1}{\left\{\begin{array}{c} 0.1070 \cdot \text{DumCac} \\ + 0.005572 \cdot \text{dbh} + 0.001858 \cdot \text{Density} \end{array}\right\}}$$
$$+ \varepsilon_i, \quad (9)$$

Table 5. Model parameter estimates and confidence intervals

| | Age-dependent models | | | Age-independent models | | | |
| | Log-transformed Gaussian linear model | Gamma GLM with reciprocal link | | Gaussian GLM with reciprocal link | | Gamma GLM with reciprocal link | |
Parameter/statistic	Estimate (SE)	Estimate (SE)	P (χ^2 value)	Estimate (SE)	P (χ^2 value)	Estimate (SE)	P (χ^2 value)
Intercept	1.3098 (0.1969)	0.05331 (0.02383)	0.0207 (5.35)**	−0.2402 (0.04891)	<0.0001 (21.49)**	—	0.4670 (0.53)
Age 1.30 m	−0.01074 (0.001191)	0.003097 (0.000288)	<0.0001 (16.13)**	—	—	—	—
Density	−0.00408 (0.000630)	0.000979 (0.000191)	0.0661 (3.38)*	0.002175 (0.000239)	<0.0001 (102.20)**	0.001858 0.000170	<0.0001 (22.99)**
ddg	0.7070 (0.1318)	—	0.1470 (2.10)	—	—	—	—
$CID15_{50}$	1.9658 (0.7896)	—	0.5341 (0.39)	−0.6320 (0.08063)	0.0006 (11.76)**	—	0.3329 (0.94)
(1/dbh)	3.8485 (1.7124)	—	0.6502 (0.21)	—	0.8670 (0.03)	—	0.6031 (0.27)
$CII7_{50}$	—	—	—	0.02329 (0.005016)	0.0114 (6.40)**	—	0.3792 (0.77)
dbh	—	—	—	0.009817 (0.000793)	<0.0001 (73.03)**	0.005572 (0.000697)	0.0003 (13.29)**
Dummy Cáceres	—	—	—	0.1145 (0.02128)	0.0006 (11.76)**	0.1070 (0.02606)	0.0857 (2.95)*
ϕ (SE)	—	8.6828 (0.9381)		1.1159 (0.0609)		6.3170 (0.6718)	
Mean bias (cm)	0.0244	<0.0001		0.0211		−0.0304	
RMSE (cm)	1.0313	1.0595		1.1193		1.2291	
R^2_{ss} (R^2_D)	50.506	48.697 (46.632)		40.637 (40.637)		29.293 (24.830)	
σ^2_i	0.01426 (0.01006)*	0.000 (—)		0.000 (—)		0.000 (—)	

p values are for the analysis of deviance test compared to the χ^2 distribution (McCullagh and Nelder 1989). For the sake of clarity, tests are only shown for those covariates selected in Table 3. For test of hypothesis (log-likelihood ratio tests) of log-transformed model, see Table 4. ϕ, dispersion parameter in GLM; σ^2_i, variance estimate of random intercept effect for GLMM with the same fixed parameters as the corresponding GLM. The SE of prediction is shown in parentheses. Goodness-of-fit statistics in the transformed model were calculated with the back-transformed corrected residuals (see text for details).

* Significant at α = 0.10.
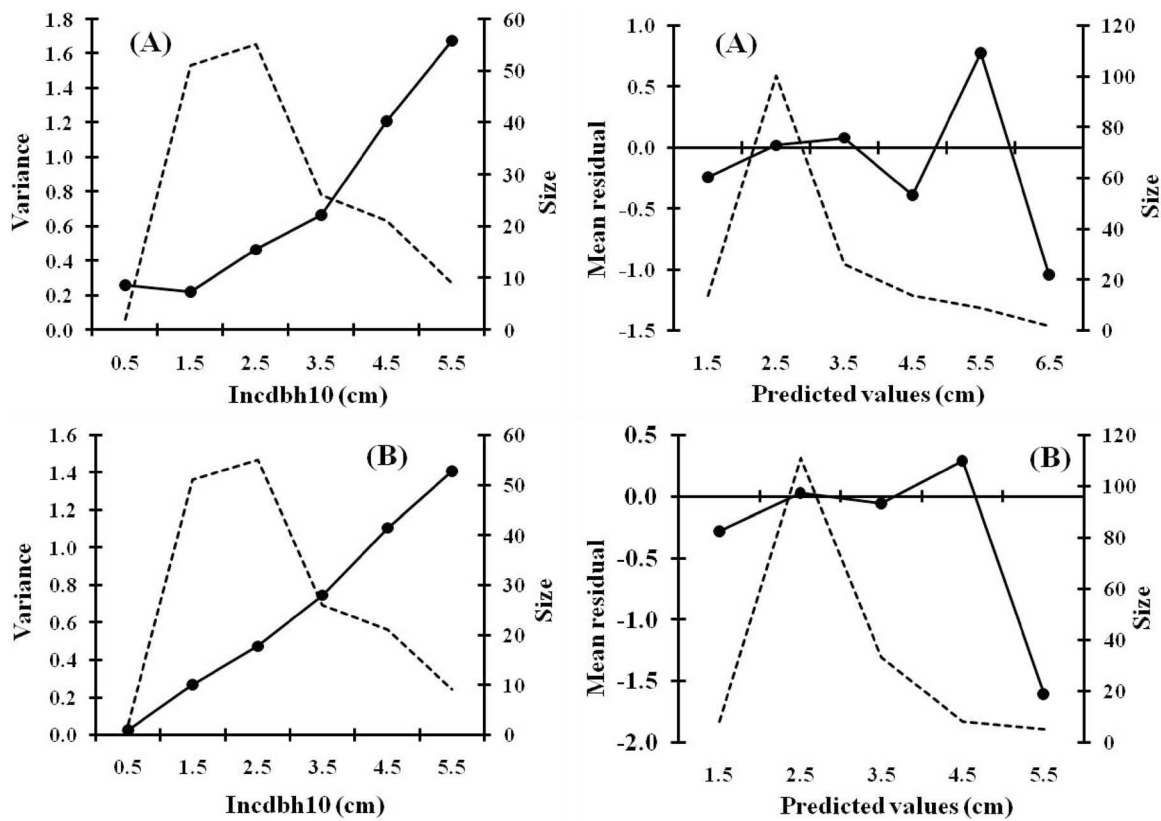
** Significant at α = 0.05.

Figure 4.   Variance function of residuals and residuals against predicted values: A, age-dependent models; B, age-independent models. Thick lines with dark circles correspond to variance function or mean residual and dashed line to sample size.
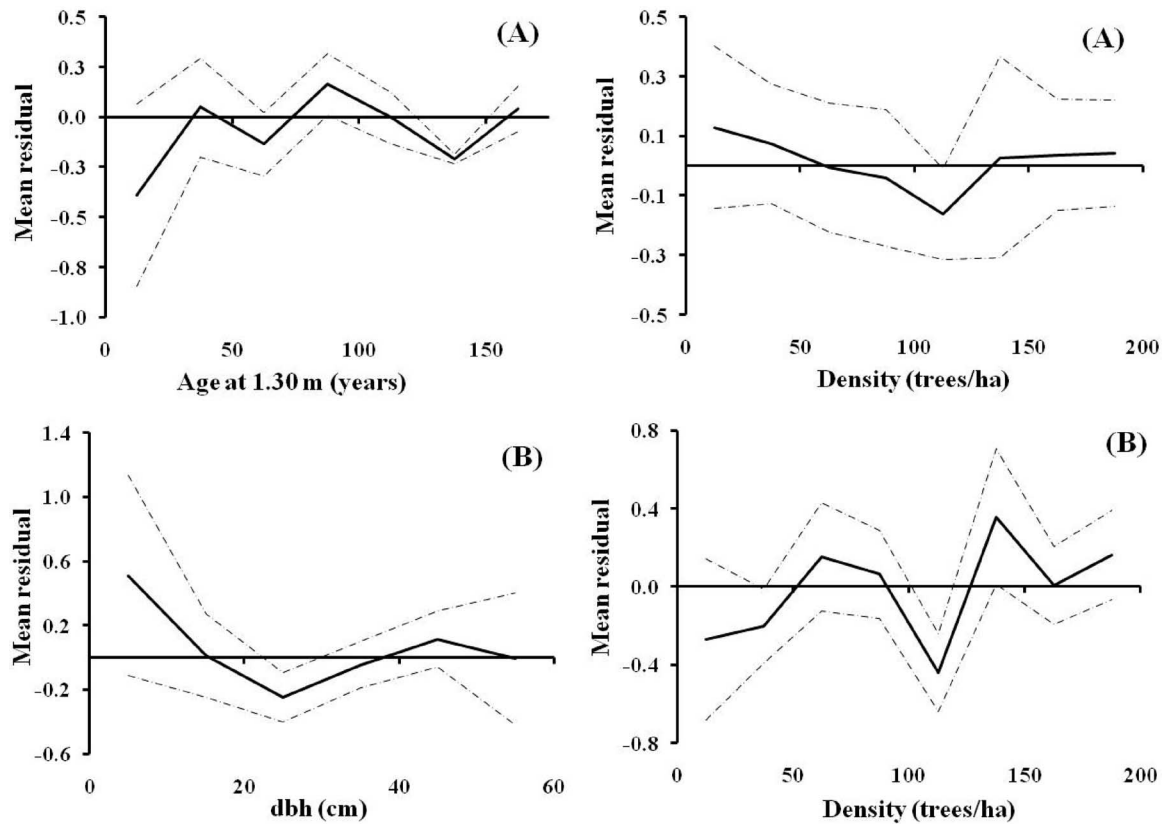

Figure 5.   Plots of residuals against selected covariates in the final models: A, age-dependent models; B, age-independent models. Dark lines correspond to mean residuals and dashed lines to standard error of the mean.

where $\varepsilon_i \sim G(\mu, \mu^2/6.3170)$. A random intercept effect was not significant (Table 5). Distribution of residuals against predicted values and covariates is shown in Figures 4 and 5.

Applicability of the IFN to Model Holm Oak Diameter Growth

For IFN data we fitted a log-transformed model (Table 3) as data and residuals were less skewed than in the sampled set and to ease comparison with other published studies. Density was also selected in this model; however, the covariates that explained the most variance were slope and the Y UTM (Table 3). The final model included six covariates, and its expression was

$$\text{Inc10} = \text{CF} \cdot (\exp(-4.0376 + 0.001175 \cdot \text{Y UTM}$$
$$- 0.00448 \cdot \text{Slope} - 0.00038 \cdot \text{Density}$$
$$- 0.00234 \cdot \text{dbh} + 0.02329 \cdot \text{Height}$$
$$+ 0.02842 \cdot \text{T}_{\min}$$
$$+ 0.08161 \cdot \text{DumGuad} + b_i \varepsilon_i) - 1) \quad (10)$$

with $\varepsilon_i \sim N(0, 0.1032[0.004409])$ and $b_i \sim N(0, 0.05348[0.004484])$. CF is the correction factor (1.11614 with our data [Snowdon 1991]), Y UTM is expressed in km, slope is in %, density is in trees/ha, dbh is in cm, and height is in m. $\text{T}_{\min}$ is the mean of minimum temperatures in the coldest month, and DumGuad is a dummy variable for the Guadiana and Guadalquivir river basins, which are the southernmost basins in the study area (Figure 1), with $\text{M}_{\text{Bias}} = 0.000$, RMSE = 1.548, and R^2 = 3.931. Results were similar if only plots with a density of <250 trees/ha were analyzed: 2,667 observations, $\text{M}_{\text{Bias}} = 0.000$, RMSE = 1.551, and R^2 = 4.130. Finally, if only plots with density of <150 trees/ha were used, the model fit was worse (2,429 obs., $\text{M}_{\text{Bias}} = 0.000$, RMSE = 1.559, and R^2 = 3.369).

Discussion
Holm Oak Intraspecific Competition

Our results show that competition does exist, but age is clearly the most influential covariate, probably because the trees are not competing for light (at least in the lowest densities), as they are in closed forests. As found in many other studies (e.g., Martin and Ek 1984, Biging and Dobbertin 1995, Wimberly and Bare 1996) distance-dependent indices did not outperform distance-independent indices (which are considered to reflect symmetric competition) and thus we do not expand more on the discussion of this issue here. Plot density is the best competition index, which might be expected from the uniformity of the stands (Biging and Dobbertin 1992). In semiarid woodlands, competition for water is likely to be more important than competition for light. Competition for below-ground resources can occur over greater distances than competition for light (Schwinning and Weiner 1998); hence, holm oak trees could be prospecting large areas (both in depth and topsoil) outside of their own crown projection (Canadell et al. 1996, Jackson et al. 1996, Moreno et al. 2005).

Holm Oak Diameter Increment Models and Growth Prediction

The first conclusion that can be extracted from the model comparison is that untransformed GLMs, both with the normal and gamma PDFs, fitted the data better than the classic transformed models (Table 4). Mixed models and GLMs rely on maximum likelihood estimation, and it can be seen how models with inverse link function and PDFs that maximize the likelihood resulted in the most parsimonious models. Models fitted with the Gaussian PDF selected too many covariates, overinflating the coefficient of determination. Age and density were negatively correlated with growth in age-dependent models. Gamma models were the best, and they are of interest for two main reasons: we are directly modeling the raw dependent variable because this avoids biases from transformation and makes the models easier to use for managers and researchers and we are using a flexible PDF that is able to model departures from normality, particularly increasing variance with increasing scores of the dependent variable (Figure 4), and thus weighted regression is not required.

Age-independent models also show how selecting the appropriate PDF results in more parsimonious models with a lower number of significant covariates, enabling a clearer discussion of the relationship between covariates and the dependent variable. In normal models $R_D^2 = R_{SS}^2$ is calculated identically (McCullagh and Nelder 1989, p. 34), whereas in gamma models the deviance is calculated as $2\sum[-\log(y/\hat{\mu}) + (y - \hat{\mu})\hat{\mu}]$, which makes direct comparison of this statistic less straightforward. However, the decrease in R_D^2 compared with R_{SS}^2 in gamma models was unexpected (Mittlböck and Heinzl 2002). As the analysis of deviance is more restrictive in gamma models than in Gaussian models, because of the way the deviance is calculated and from the best fit of the dependent data, we decided to accept covariates at $\alpha = 0.10$ (Table 5). Again, density was negatively correlated with growth, and dbh was also significant. The dummy for Cáceres is added to dbh as an estimate of older age in that location (Table 1; Figure 2), as it is deduced from its only inclusion in the age-independent model. The same could be thought of dbh: as it is only included in age-independent models, it seems that it is, in fact, being selected mostly as an indirect estimate of age in the system. The IFN data and our observations when measuring the whole life growth of both samples (unpublished observations) points toward less growth in the southernmost holm oaks from Cáceres compared with those in Salamanca, but sample age may be a confounding variable.

In some studies the square dbh enters in the final models (e.g., Wykoff 1990, Larocque 2002) to fit the biological point of inflection expected in growth. In our model it was not selected, probably because the inflection point is reached at a very young age (smaller than 10 cm dbh) (Gea-Izquierdo et al. 2008) or because it was not included sufficiently in the sampled plots (Table 1) or in the ecosystem in general (Pulido et al. 2001). Age-independent models explained less of the variation in the dependent variable ($>29\%$), but efficiencies were similar to those of other studies (e.g., Lessard et al. 2001, Sánchez-González et al.

2006, Stadt et al. 2007). The inclusion of age reduced the model error and almost doubled efficiency ($R^2 = 48.7$) (Table 5). This result reflects the high correlation between growth and age that was especially noticeable in the lowest density stands, as a consequence of reduced or nil competition. We did not find such a close relationship between dbh and age as that in Plieninger et al. (2003), but it is still good enough to give an estimate, bearing in mind the general difficulty of estimating ages from dbh (Cook and Kairiukstis 1990). The dbh-age relationship has possibly occurred because aerial competition is reduced to the minimum, particularly in low-density stands. This relationship is likely to vary in other holm oak formations, especially if they are not as homogeneous as our stands.

In the sampled plots we only characterized holm oak shrubs, although some plots included high densities of *Cytisus multiflorus* (L'Hér.) and *Cistus* spp. This could be, along with the different parent materials, another reason for differences between plots that were not included in the models. In addition, we did not sample the holm oak shrubland, which results from logging or coppicing, as seen in Cáceres (unpublished observations). Some of this unexplained variability was expected to have been explained by random effects. However, no random parameters were significant in the final models (neither in log-transformed models nor in GLMs); therefore, with the model proposed it is not possible to perform climatic, spatial, or plotwise random effects calibrations to improve prediction accuracy (Lappi 1991, Miina 1993, 2000). Other diameter increment models usually include random components (Miina 1993, Miina and Pukkala 2000, Calama and Montero 2005); the reasons that random plot parameters were not included in our models could be related to the open stands and management of the areas studied. Larger data sets might provide more insights into improving model accuracy.

Finally, when growth models are fitted, the question arises as to whether estimations based on past growth are applicable to future growth, especially under the current conditions of climate change. It has been shown that tree growth responds to climate change, and this is expected to be more patent in tree species growing at the limit of their distribution areas or under climates where limiting factors mean that the vegetation type is on the border between treelike formations and, for instance, steppe or shrubland. This is the case for the continental Mediterranean climate ecosystems of our study area. Problems could arise if changes in aridity, for instance, changed this tendency, especially in stands such as those in Mediterranean ecosystems where timber is not the principal product and where close stands are likely to be crucial for regeneration and forest preservation (Pulido et al. 2001). These issues should be addressed in future studies, particularly with this species and ecosystem, for which preservation of the ecosystem integrity (e.g., topsoil, humidity levels) with treelike formations should be the principal goal. Climate-growth interactions in climate change scenarios and their inclusion in diameter increment models are a must for the future. The effect of competition on growth could be also modified if climate changes (Cescatti and Piutti 1998, Yeh and Wensel 2000).

Use of the IFN to Model Holm Oak Diameter Growth

The IFN data do not seem to be appropriate for modeling individual tree diameter growth in *Quercus ilex*. We found very poor correlations between covariates and growth ($R^2 < 4\%$), even when compared with other forest inventory studies in which R^2 does not tend to be very high, but in all cases greater than our results (usually >20%; e.g., Lessard et al. 2001, Andreassen and Tomter 2003, Trasobares et al. 2004, Canham et al. 2006). This can be explained by (1) the heterogeneity of holm oak stands, including coppice and seedlings, shrubs, and treelike oaks; (2) the stem profile, which makes it difficult to clearly define the dbh at 1.30 and, hence, remeasure it at the same point in different samples; (3) management of the stands, including pruning and clearing; and (4) assumption of a constant error in IFN sampling, independent of the target species, which should not be assumed, as the slower the growth of the species, the greater the expected relative error.

The IFN models presented are log-transformed linear mixed models. Moisen and Frescino (2002) observed that linear models fit Inventory data as well as other more complex techniques. Many covariates were selected, but as seen in Table 3, latitude (calculated as the Y UTM) and slope were the regressors that explained most of the variation and are the only correlations we would consider as hypotheses for further investigations. It is impossible to conclude whether this trend is real because the model explains too little variance. However, the relationship with latitude and slope seems logical from a climatic and edaphic point of view. In general, the southern most plots would be expected to experience more water stress, especially considering the changes in patterns of precipitation and increases in temperature that have occurred during the last decades (e.g., Esteban-Parra et al. 1998; Intergovernmental Panel on Climate Change 2007). The stem diameter increment in holm oak coppices has been shown to be strongly correlated with water availability (e.g., Mayor and Rodá 1994, Ogaya and Peñuelas 2007). In addition, higher slopes have shallower, poorer soils that retain less water (Puerto and Rico 1992). Density was also selected in IFN models, confirming the fact that density affects growth in these open woodlands. Although tree height is not a reliable covariate in this ecosystem, it was included in the models. We allowed the inclusion of tree height to show the best possible fit, but assumed that this equation will not be used for predictive purposes, but only to support what we have discussed about data modeling.

Conclusions

Although often considered as free grown, we have shown that competition limits holm oak growth to some extent in Iberian open woodlands. Thus, free growth might also be exhibited only in the lowest densities. Age-dependent models explained approximately 50% of diameter increment variation, whereas the most parsimonious age-independent models explained approximately 30%. Age was the covariate most correlated with growth, which reflects the reduced

competition for light with increased age. This finding was also supported by the substitution of age by dbh (if we accept that it is closely related to age in the absence of competition) in age-independent models. The analyses of different competition indices showed that density (a simple distance-independent index) outperformed more complex distance-dependent indices perhaps because below-ground competition is limiting holm oak growth in these uniform stands, although competition appears to be reduced compared with that in closed forests. Aerial competition is generally minimal as crowns are either isolated or form a unique dominant-codominant layer; however, below-ground competition reduced tree growth.

Finally, modeling diameter growth directly with generalized linear models and with the gamma distribution to fit the natural growth trend of increasing variance with increasing growth resulted in more parsimonious models that explained holm oak diameter increment more clearly. These results suggest that data transformations in future empirical models should be avoided, particularly when data depart much from normality and that data should be modeled directly with the most appropriate PDF. This modeling approach is likely to have great potential for forestry applications.

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