Site index in agroforestry systems: age-dependent and age-independent dynamic diameter growth models for *Quercus ilex* in Iberian open oak woodlands

G. Gea-Izquierdo, I. Cañellas, and G. Montero

Abstract: Despite *Quercus ilex* L. being one of the most widespread tree species in the Mediterranean basin, there are no growth models in the literature for this species. In this study, we compare age-dependent and age-independent dynamic diameter growth models and discuss the concept of dominance in open stands. A posteriori dominance was determined to fit potential age-dependent growth models and a site index based on diameter growth was defined. Formulations derived from power decline base models (Korf and Hossfeld) best described diameter growth. The best approach for age-dependent models was a polymorphic and with variable asymptotes generalized algebraic difference approach formulation. Residual errors in trees between 20 and 55 cm ranged from ~7.0% in potential growth models to ~15% in age-independent models expanded by density. Using a unique age-dependent dynamic equation for all trees, regardless of dominance, did not increase the error very much. In age-independent models, the inclusion of the defined site index reduced the prediction error but requires that the age of trees is estimated to determine the site index. The difficulty of estimating *Q. ilex* age makes age-independent models very attractive for system modelling. Age-independent models could be useful in other ecosystems where age estimation is problematic.

Résumé : Bien que *Quercus ilex* L. soit une des essences les plus répandues dans le bassin méditerranéen, la littérature n'offre pas de modèle de croissance pour cette essence. Dans cette étude, nous comparons les modèles dynamiques de croissance diamétrale dépendants et indépendants de l'âge et nous discutons du concept de dominance en peuplements ouverts. Une dominance a posteriori est déterminée pour ajuster les modèles de croissance potentielle dépendants de l'âge. En outre, un indice de qualité de station basé sur la croissance diamétrale est développé. Les formulations mathématiques dérivées des équations à puissance décroissante (Korf et Hossfeld) décrivent le mieux la croissance diamétrale. La meilleure approche pour les modèles dépendants de l'âge est celle de la formulation polymorphique à asymptote variable par la méthode de la différence algébrique généralisée. L'erreur résiduelle pour les arbres de 20 à 55 cm varie d'environ 7 % pour les modèles de croissance potentielle à environ 15 % pour les modèles indépendants de l'âge avec l'ajout de la densité. L'emploi d'une équation unique dépendante de l'âge pour tous les arbres, sans égard à leur dominance, ne fait pas beaucoup augmenter l'erreur. L'inclusion de l'indice de qualité de station dans les modèles indépendants de l'âge réduit l'erreur de prévision, mais requiert l'estimation de l'âge des arbres pour déterminer l'indice de qualité de station. La difficulté à estimer l'âge de *Q. ilex* rend les modèles indépendants de l'âge très attrayants pour modéliser sa croissance. Les modèles indépendants de l'âge pourraient être utiles dans d'autres écosystèmes où l'âge est difficile à évaluer.

[Traduit par la Rédaction]

Introduction

Agroforestry systems share the presence of a woody component, commonly trees, and occupy large expanses across the world (Mosquera et al. 2005). Agrosilvopastoral and silvopastoral systems are different types of agroforestry systems having in common the presence of grazing animals. Management of these systems differs from that of classical forestry systems. Usually, timber is not the most important output, which is the reason why tree growth has not been paid as much attention as in traditional forest systems. Yet, understanding past tree growth is one of the first steps to sustainable management and prediction of future landscape responses to different management or climate change scenarios. Site index models based on the height growth of dominant trees are the classical way of indirectly estimating site quality (mostly a combination of soil fertility and climate) in forestry management (e.g., Carmean 1975; Goelz and Burk 1992; Cieszewski and Bailey 2000). Applying the site index to modelling the tree component in agroforestry systems is not always straightforward. Compared with forests, agroforestry systems are characterized by low tree densities, as other products (e.g., pasture, crops, fruits, cork) are usually of greater economical interest than the timber (Ares and Brauer 2004; Mosquera et al. 2005). Additionally, in some agroforestry systems, trees are pruned (e.g., Balandier and Dupraz 1999) and some of them have originated from fire or thinned "natural" forests or shrublands. This compli-

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G. Gea-Izquierdo,[1] I. Cañellas, and G. Montero. Departamento Sistemas y Recursos Forestales, CIFOR-INIA, Crta. La Coruña km 7.5 28040 Madrid, Spain.

[1] Corresponding author (e-mail: guigeiz@inia.es).

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cates the selection of true life-span dominant individuals. Therefore, the concept of canopy dominance is not directly applicable, as the wide spacing reduces aerial competition, generally resulting in a unique "dominant–codominant" tree stratum. Diameter is more likely to be affected by density than dominant height; however, some studies have used diameter from dominant trees instead of dominant height in systems where dominant height was not available (Carmean 1975; Ares and Brauer 2004).

In Western Iberia, an agrosilvopastoral system of high economical and ecological interest called "dehesa" in Spain and "montado" in Portugal occupies more than 3 000 000 ha (San Miguel 1994; Pulido et al. 2001). This is one of the most famous traditional agroforestry systems in the world, having received much attention in the literature. Dehesas are anthropic savannas mostly dominated by *Quercus* sp., with holm oak (*Quercus ilex* L.) being the most common species followed by *Quercus suber* L. 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 specific management, applied through time, has modelled this landscape. The history of the dehesas is complex and the origin of the current structure uncertain. It is likely that they result from a combination of thinning, conversion by thinning on coppice, acorn sowing, and holm oak selection in what was probably a mixed landscape several thousand years ago. Most authors today (Manuel and Gil 1999; Pulido et al. 2001; Martín-Vicente and Fernández-Ales 2006) suggest that most current dehesas originate from the nineteenth century. Therefore, it is very likely that most of them are still in their first rotation cycle, at least with the open tree structure dominated by holm oak encountered today. As in other agroforestry systems, trees are pruned, usually at regular intervals of 10–20 years (Gómez and Pérez 1996). Lack of tree regeneration is a challenging problem and constitutes a threat for the persistence of these systems (Pulido et al. 2001; Pulido and Díaz 2005).

Holm oak is one of the most important and widespread tree species in the Mediterranean Region (Barbero et al. 1992; Rodá et al. 1999). Despite the importance of the species, and the abundant literature on the ecosystems that it dominates, there are no growth models published. There are several possible explanations: (*i*) it is not a classic timber species, (*ii*) it has been primarily managed to obtain firewood and many holm oak stands are coppice (Rodá et al. 1999), (*iii*) it is very difficult to obtain permission to log tree-like holm oak, and (*iv*) the species' wood anatomy makes it difficult to clearly distinguish annual rings (Gené et al. 1993). The formation of annual rings in holm oak has been described in several dendroecological studies (e.g., Zhang and Romane 1991; Cherubini et al. 2003). However, double rings are sometimes present and because of eccentric growth, absent rings in parts of the circumference are common. It is therefore desirable to analyze whole sections (Gené et al. 1993).

In this study, we discuss the concepts of dominance and site index in low tree density agroforestry systems where trees are pruned using the agrosilvopastoral system called "dehesa" and holm oak as an example. Dynamic age-dependent models are used to define a site index and their fit and applicability are compared with recently proposed age-independent dynamic formulations (Tomé et al. 2006). In addition, the role played by current density in holm oak diameter dynamic growth is analyzed. The main objective is twofold: (*i*) to discuss the concept of dominant growth in low-density agroforestry systems and (*ii*) to compare age-dependent and age-independent formulations for modelling holm oak diameter growth. To do so, we structured our study into three consecutive steps: (1) we fit age-dependent dominant diameter growth models to study the definition of a site index for these woodlands, (2) we discuss the concept of dominance within this low-density system and the possibility of fitting a single dynamic age-dependent growth model for all trees independent of dominance, and (3) we compare the behaviour of age-dependent models with that of age-independent models as proposed by Tomé et al. (2006) and discuss the role of current density as a proxy to management of stands throughout their history and the suitability of the defined site index.

Materials and methods

Study site and sampling methods

Quercus ilex tree samples were collected in central-western Spain close to the border with Portugal (40°37′N, 6°40′W, 700 m above sea level). The trees were included within a belt of ~50 m × 9 km clearcut to construct a freeway. The ecosystem is a typical dehesa under a continental–mediterranean climate with mean annual precipitation of ~600 mm and summer drought. The clearcut belt belonged to a large patch of almost pure holm oak woodland of variable density with sparse *Quercus faginea* Lam. and shrubs such as *Cytisus multiflorus* (L'Hér.) Sweet, *Cistus clusii* Dunal, or *Cistus ladanifer* L. intermixed. Soils in the study area were sandy and of granitic origin, with a few plots located on slate.

Data

During the summer of 2005, we set up 25 plots of variable radius that included 10 trees each. The plots were selected to include stands of different densities (from 39.2 to 210.4 trees/ha with a mean of 129.9 ± 37.9 trees/ha corresponding to 9.5 ± 3.9 m^2/ha) and trees from all diameter classes. The five central trees of each plot (i.e., a total of 125 trees) were pushed down with a bulldozer and sections at 1.30 m and at the base were collected. From the 125 trees felled, 115 presented at least one readable radius (absence of rot). Stem discs were air-dried and then sanded and polished (60–1200 grit). Annual growth was measured with TSAP software and LINTAB (Rinntech 2003). To ascertain that we were measuring annual rings, two or three radii were crossdated in a set of subsamples (Fritts 1976). In addition, all sections at 1.30 m had lower age than discs at the base, resulting in the following model: $\text{age}_{\text{basal}} = 11.82 + 1.01\text{age}_{\text{DBH}}$; $R^2 = 0.93$, residual root mean square error (RMSE) = 7.67. All analyses in this study refer to growth without bark (bark thickness (mm) = 0.02 × diameter at breast height (DBH) (cm) + 0.39; $R^2 = 0.55$, RMSE = 0.24). Annual diameter increments were averaged at 5-year intervals to reduce autocorrelation and minimize possible measuring errors. Whether the estimated tree ages from basal sections are "real ages" or "stem ages" from an older stump is not possible to ascertain. Nevertheless, when the trees were felled, the stumps were not swollen, nor did they present more than one stem, what could suggest an origin from seedlings.

To fit holm oak diameter "potential" growth site index models, tree dominance (assuming in principle that dominance existed) had to be defined a posteriori. We accepted that, under the current densities, within each plot at least two of the five trees were exhibiting potential growth. The growth measurements by plot were plotted on a graph and trees showing apparent suppression were removed. From a total of 88 selected dominant–codominant trees, two to five trees per plot were averaged to build 25 plot series. We used these 25 series to fit potential growth (dominant) models, whereas general age-dependent models for all trees and age-independent models were fitted using the individual 115-tree growth series.

Models and analysis

Four three-parameter base models among the most commonly used in the literature were selected from a larger set of integral growth models preliminary compared. These models were used to formulate both age-dependent and age-independent equations. Two base models belonged to the power decline group (Hossfeld IV and Korf), whereas the other two belonged to the exponential decline group (Richards in all cases and Weibull when parameter $c > 1$ (Zeide 1993; Shvets and Zeide 1996; Kiviste et al. 2002)). All of the selected integral models are differentiable and share the desirable characteristics for site index models (e.g., Cieszewski and Bailey 2000), namely (*i*) polymorphism, (*ii*) inflection point, (*iii*) horizontal asymptote as a biological limit to growth, (*iv*) theoretical basis, (*v*) logical behaviour, and (*vi*) simplicity. Throughout this study, age-dependent models are referred as E*i* and age-independent models as T*i*.

To develop age-dependent models, we used generalized algebraic difference approach (GADA) formulations of the base models (Cieszewski and Bailey 2000; Cieszewski 2004), a generalization of the algebraic difference approach (ADA) by Bailey and Clutter (1974). ADA is a particular type of GADA where only one parameter varies with site. Therefore, E1, E2, E4, E7, E10, and E11 are equivalent to polymorphic ADA, E3 is an anamorphic GADA (equivalent to the models discussed in Cieszewski (2002) and Cieszewski et al. (2006)), and the rest (E5, E6, E8, and E9) are polymorphic with variable asymptotes GADA. Some of these models have been used in other forestry applications (e.g., Barrio-Anta et al. 2006; Cieszewski et al. 2006; Diéguez-Aranda et al. 2006; Tomé et al. 2006). Base-age invariance was achieved by fitting GADA models using the dummy variables method (Cieszewski et al. 2000; Cieszewski 2003). The unobservable theoretical variable X represents the site productivity dimension. Variable X is an unknown function of management regimes, soil conditions, and ecological and climatic factors, which cannot be reliably measured or even functionally defined (Cieszewski 2002). This variable might be of particular interest in this study, as we expect the unknown plot management regime to be very influential on diameter growth. GADAs were used for both potential growth models and general age-dependent models for all trees. All analyses were programmed using the MODEL procedure in SAS 9.1 (SAS Institute Inc. 2004).

Dynamic growth models are usually age dependent. However, age estimation can be very challenging or even impossible for some tree species like the holm oak and many tropical tree species. For this reason, the age-independent formulation proposed by Tomé et al. (2006) appears to be an attractive alternative for species or forest stands where age estimation is not possible (like uneven-age stands). Age independence is achieved by solving the base equations for age in t_1 and then substituting in t_2 expressed as $t_2 = t_{1+\mathrm{dif}}$, where "dif" is the projection length. To generate a family of curves, at least one of the parameters needs to be expressed as a function of site variables and (or) stand characteristics (Tomé et al. 2006). In this study, we use current density to expand the parameters at first approach and then compare this with age-independent models that were expanded by the previously defined site index and density. Formulations based on site index are not really age independent, as some estimation of age is needed to estimate site index.

To remove serial correlation, we graphically compared several stationary autocorrelation structures (processes AR(x) and ARMA(x, 1)) by plotting autocorrelation functions (ACF) of residuals (data not shown). The most parsimonious autoregressive structure that removed autocorrelation was AR(2) ($\varepsilon_i = \rho_1\varepsilon_{i-1} + \rho_2\varepsilon_{i-2}$, where ε_i is the residual for observation i and ρ_1 and ρ_2 are autocorrelation parameters), which was used in all cases. Possible heterokedasticity was examined visually by plotting the residuals against predicted values. When residuals were heterokedastic, the models were fitted using generalized nonlinear least squares weighted by $1/\mathrm{Var}(\varepsilon_i)$, with $\mathrm{Var}(\varepsilon_i)$ being the variance function estimated for the residuals.

Diameter growth was analyzed in three consecutive approaches using dynamic forms derived from the four integral models selected.

(*i*) Potential growth dynamic age-dependent models. We used the 25 series to define a site index based on holm oak diameter growth and analyzed the biological potential growth of the species. Models, designated from E1 to E11, are shown in Table 1.

(*ii*) Tree diameter dynamic age-dependent growth models. We considered two hypothesis concerning crown competition and dominance shared by many other agroforestry systems: (1) in the most open stands, this competition is almost nil, and hence the stands are mostly a combination of free-grown trees or a dominant–codominant unique canopy layer and (2) if dominance is expressed in the more dense stands, it is not a continuous feature of trees because after each pruning rotation, trees need to rebuild their crowns. To answer these hypotheses and their applications to dynamic growth, we analyzed the effect of current density (expanding parameters a or b in models E3d and E5d to compare with E3_2, E5_2, and E9_2, which are nonexpanded) as a proxy to stand history. Generally, current density is not a good covariate to use in dynamic models, as it is likely to change through time. However, in dehesas, as a consequence of history and management, the tree stratum can be considered as almost "static", with few changes in the stand structure (but a slow decline in oak numbers) at least since the 1950s (García del Barrio et al. 2004). It might be hypothesized that the trees remaining today were the healthy, dominant trees from the ancient woodland (if we accept that healthier, dominant trees produce more acorns and firewood) or at least that these would not have been selectively removed, as timber has always been a sec-

Table 1. Base models and difference equations considered to develop the age-dependent growth equations.

Base equation	Parameter related to site	Solution for X	Dynamic equation	ID
Hosfeld IV 1822, cited in Peschel 1938:	$b = X$	$X_0 = t_1^c\left(\frac{1}{y_1} - a\right)$	$y_2 = t_2^c/(X_0 + at_2^c)$	E1
$y = t^c/(b + at^c)$	$c = X$	$X_0 = \ln\left(\frac{y_1 b}{1 - y_1 a}\right)/\ln(t_1)$	$y_2 = t_2^{X_0}/\left(b + at_2^{X_0}\right)$	E2
	$a = X$ $b = b_1X$	$X_0 = (t_1^c/y_1)/(b_1 + t_1^c)$	$y_2 = t_2^c/X_0(b_1 + t_2^c)$	E3
Korf 1939, cited in Lundqvist 1957:	$b = X$	$X_0 = -\ln(y_1/a)/t_1^{-c}$	$y_2 = a(y_1/a)^{(t_1/t_2)^c}$	E4
$y = a\exp(-bt^{-c})$	$a = \exp(X)$ $b = b_1 + (b_2/X)$	$X_0 = 0.5[b_1t_1^{-c} + \ln(y_1) + F_0]$ $F_0 = \sqrt{\{[b_1t_1^{-c} + \ln(y_1)]^2 + 4b_2t_1^{-c}\}}$	$y_2 = \exp(X_0)\exp\{-[b_1 + (b_2/X_0)]t_2^{-c}\}$	E5
	$a = \exp(a_2X)$ $b = X$	$X_0 = \ln(y_1)/(a_2 - t_1^{-c})$	$y_2 = \exp(a_2X_0)\exp(-X_0t_2^{-c})$	E6
von Bertalanffy 1957; Richards 1959:	$b = X$	$X_0 = -\ln\left(1 - \sqrt[c]{y_1/a}\right)/t_1$	$y_2 = a\left\{1 - \left[1 - \sqrt[c]{(y_1/a)}\right]^{t_2/t_1}\right\}^c$	E7
$y = a[1 - \exp(-bt)]^c$	$a = \exp(X)$ $c = c_1 + (1/X)$	$X_0 = 0.5\left\{\ln(y_1) - c_1F_0 + \sqrt{[c_1F_0 - \ln(y_1)]^2 - 4F_0}\right\}$ $F_0 = \ln[1 - \exp(-bt_1)]$	$y_2 = \exp(X_0)[1 - \exp(-bt_2)]^{[c_1 + (1/X_0)]}$	E8
	$a = \exp(a_2X)$ $c = X$	$X_0 = \ln(y_1)/(a_2 + F_0)$ $F_0 = \ln[1 - \exp(-bt_1)]$	$y_2 = \exp(a_2X_0)[1 - \exp(-bt_2)]^{(X_0)}$	E9
Weibull 1951; Yang et al. 1978:	$b = X$	$X_0 = -\ln[1 - (y_1/a)]/t_1^c$	$y_2 = a\{1 - [1 - (y_1/a)]^{(t_2/t_1)^c}\}$	E10
$y = a[1 - \exp(-bt^c)]$	$c = X$	$X_0 = \ln\{-\ln[1 - (y_1/a)]/b\}/\ln(t_1)$	$y_2 = a[1 - \exp(-bt_2^{X_0})]$	E11

ondary product in relation to firewood, acorn production, and pasture. As it is not possible to determine dominance in the field (pruning, open stands), we fitted age–diameter dynamic models for the whole data set (115 trees). These models can be applied to any tree of known age. They are formulated as shown in Table 1, but we add the subindex "d" or "2" to distinguish that they are fitted for the whole data set either expanded by density ("d") or not ("2").

(*iii*) Tree diameter age-independent dynamic growth models. In age-independent formulations (Tomé et al. 2006), parameters a and (or) b were first expanded by density. We did not expand the model parameters with climate or soil variables because we did not have soil analyses and climate was homogeneous through the study area. Finally, we fitted "pseudo-age-independent'' models expanding the same model parameters by density and the previously defined site index. Expansion of the model with the defined site index allowed us to test its validity and discuss our results in relation to Tomé et al.'s (2006). Age-independent models were derived from Hossfeld and Korf base models: T1, T2, and T3 are models expanded only by density (age independent), while T4s is expanded by site index and T5s by site index and density as follows.

Hossfeld IV age-independent models, including T1, T2, T4s, and T5s, were expansions from the expression

$$y_2 = \frac{\left[\sqrt[c]{\frac{y_1\times b}{(1-a\times y_1)}}+\text{dif}\right]^c}{b+a\times\left[\sqrt[c]{\frac{y_1\times b}{(1-a\times y_1)}}+\text{dif}\right]^c}$$

Particularly, a, b, and c are expanded as b = ($b_1\times$ density) in T1, a = (a_1/density) and b = ($b_1\times$ density) in T2, b = (b_{S1}/SI) and a = ($a_{S1}\times$ SI) in T4s, and b = ((b_{S1}/SI) + $b_{d1}\times$ density) and a = (($a_{S1}\times$ SI) + (a_{d1}/density)) in T5s, where a_{S1}, a_{d1}, b_{S1}, and b_{d1} are parameters. The projection length (dif) is the number of years between the known diameter and the one to be predicted. The site index SI is defined by the potential growth models expressed in centimetres (see the Results and Discussion sections).

Korf age-independent equations were used in model T3, where b = ($b_1\times$ density):

$$y_2 = a\times\exp\left\{-b\times\frac{1}{\left[\left(\frac{-b}{\log(y_1/a)}\right)^{1/c}+\text{dif}\right]^c}\right\}$$

The following statistics were used to compare models.

Root mean square error (RMSE):

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

where est is estimated values, obs is observed values, n is the number of observations, and p is the number of parameters when calculating RMSE for a fitted model and p = 1 when calculating RMSE for an age or diameter class. To obtain relative RMSE, we divided the previous expression by the mean observed DBH: $\text{RMSE}\ (\%) = 100\times(\text{RMSE}/\bar{Y})$.

Coefficient of determination (estimation) or efficiency (EF) (validation):

$$R^2 \approx \text{EF} = 1-\frac{\sum_{i=1}^{n}(\text{est}_i-\text{obs}_i)^2}{\sum_{i=1}^{n}(\text{obs}_i-\text{obs}_{\text{mean}})^2}$$

Mean residual (bias):

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

Akaike's information criterion differences (AICd) (Burnham and Anderson 2004):

$$\text{AICd} = n\ln\bar{\sigma}^2+2k-\min(n\ln\bar{\sigma}^2+2k)$$

where

$$\bar{\sigma}^2 = \frac{\sum_{i=1}^{n}(Y_i-\bar{Y}_i)^2}{n}$$

The asymptotic behaviour and DBH at 350 years (DBHwb_{350}) (used as a "naïve" estimate of maximum potential diameter rather than the asymptote) were also used as a criterion for model selection, comparing it with the highest diameter values found in the literature. The largest trees reported in the literature for holm oak do not usually exceed 120 cm DBH, although it is possible to find exceptions that reach almost 150 cm DBH (DGB 1999). As we lacked an independent data set for validation purposes, and despite that some authors consider that cross-validation usually reports the same information as fitting with the whole data set (Kozak and Kozak 2003), we carried out a cross-validation (jackknife) to each model. To do so, the models were fitted n times (n being either the number of plots for "potential models" or the number of trees for the rest) for n fitting data sets obtained from setting aside one plot or tree each time. Then, the prediction residuals were calculated for the observations split from the fitting data set obtaining a set of prediction residuals from the n fits to calculate the validation statistics (Myers 1990). Finally, to test for significance in the selected age–diameter general model between expanded and nonexpanded, we used the Lakkis–Jones test, $L = (\text{SS}_\text{f}/\text{SS}_\text{r})^{m/2}$, where SS_f and SS_r are the error sum of squares for full and reduced models, respectively, and m is the total number of trees; –2 ln(L) converges to a χ^2 distribution (Khattree and Naik 1995).

Results

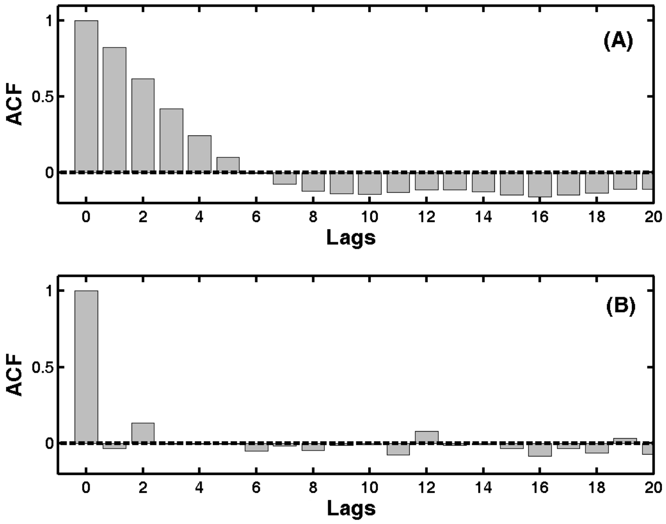
The mean DBH with bark from the 115 *Q. ilex* trees included in our sample was 30.8 ± 13.0 cm, ranging from 10.3 to 68.4 cm. The mean age was 89 ± 29 years, corresponding to estimated tree ages from 26 to 175 years. Mean tree height was 6.3 ± 1.8 m (maximum by plot 8.3 ± 2.3 m),

Table 2. Age-dependent potential growth (25 series) estimation and evaluation goodness-of-fit statistics for the best candidate models (ADA and GADA).

	Estimation			Model evaluation (jackknife)					
ID	RMSE (cm)	Adjusted R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd	DBHwb$_{350}$ (cm) (SI = I)	Asymptote (cm) (SI = I)
E1	0.7890	0.9967	32.0	0.3593	2.5445	0.9654	47.2	88.5	104.6
E2	0.7646	0.9969	0.0	0.1899	2.4496	0.9679	8.5	81.2	95.6
E3	0.7703	0.9968	7.6	0.0716	2.7467	0.9596	124.8	105.9	133.3
E4	0.7901	0.9967	33.3	0.4147	2.6169	0.9634	75.7	128.0	1679.9
E5	0.7687	0.9968	6.4	0.1189	2.6005	0.9639	68.2	141.5	1564.7
E6	0.7720	0.9968	9.8	0.2326	2.9601	0.9533	197.8	151.1	1944.7
E7	0.7896	0.9967	32.7	0.3804	2.5377	0.9656	41.4	74.8	75.1
E8	0.7745	0.9968	13.1	0.1082	2.7793	0.9586	139.9	96.2	98.8
E9	0.7773	0.9968	16.7	0.1129	3.2070	0.9450	282.2	104.2	107.4
E10	0.7906	0.9967	33.9	0.4047	2.5412	0.9655	45.8	71.2	71.3
E11	0.7666	0.9969	2.6	0.2468	2.4291	0.9685	0.0	67.1	67.1

Note: RMSE, residual root mean square error; AICd, Akaike's information criterion differences; MBias, residual mean bias (error); EF, efficiency; DBHwb$_{350}$, DBH without bark predicted at the age of 350 years for site class I. The asymptote is also calculated for class I.

Fig. 1. Autocorrelation function (ACF) of (A) E5 residuals (i.e., predicted–observed) for the 25 plot series without taking into account autocorrelation and (B) E5 residuals for the 25 plot series with AR(2) error structure.



mean stem height was 2.1 ± 0.3 m, and mean crown diameter was 6.4 ± 2.3 m. The thickest tree (68.4 cm) was 93 years old and had a mean crown diameter of 14.4 m, also the largest in the sample. It averaged 0.411 cm/year in radial growth, while the total mean annual radial growth for all samples was 0.175 cm.

Holm oak age-dependent diameter potential growth

In this study (Tables 1 and 2), we have shown only the best models (i.e., the most parsimonious, with a "logical" graphical behaviour) from many different parameterizations tried. The AR(2) error structure eliminated serial autocorrelation (Fig. 1), and the fitting residuals in potential growth models were homocedastic (Fig. 2A). All models had similar statistics, differing in the behaviour in the highest DBH classes. In the fitting step, the estimated RMSE and R^2 were similar in all models (the differences in RMSE are ±0.01 cm, smaller than the measuring error), and AIC pointed in the same direction as RMSE (Table 2). The validation statistics showed that ADA formulations were slightly biased compared with GADA formulations, whereas RMSE and EF were similar among models, with small differences around ±0.1 cm in RMSE. E11 was the best model in terms of RMSE and EF both in the estimation and in the prediction steps. However, its asymptote and diameter at 350 years were too low to be considered as the best model. Formulations derived from Richards and Weibull functions had very low asymptotes and predicted diameters unrealistic in the highest diameter classes, whereas models derived from Hossfeld and especially Korf base models best predicted diameters in the highest classes (DBH at 350 years; Table 2). Among GADA, E3 and E5 were the best: E5 was slightly superior in the goodness-of-fit statistics (the difference in AIC was greater than 10; Burnham and Anderson 2004) and had the advantage of being polymorphic with multiple asymptotes, in opposition to E3, which is anamorphic (Cieszewski 2002; Cieszewski et al. 2006). The predicted DBH$_{350}$ is in accordance with the National Forest Inventory (DGB 1999).

The final model expression was

$$[1]\quad \mathrm{DBH}_2 = \exp(X_0)\exp \times\left\{-[14.77073 + (-37.6516/X_0)]t_2^{-0.237368}\right\}$$

where

$$X_0 = 0.5\left[14.77073t_1^{-0.237368} + \ln(\mathrm{DBH}_1) + F_0\right]$$

where

$$F_0 = \sqrt{\left\{[14.77073t_1^{-0.237368} + \ln(\mathrm{DBH}_1)]^2 + 4(-37.6516)t_1^{-0.237368}\right\}}$$

Fig. 2. Estimation residuals (predicted–observed) versus predicted DBH as an illustration of potential heterokedasticity for the E5 growth model: (A) E5 for the 25 series and (B) $E5_2$ for the 115 series, variance for each diameter class and estimated variance function (i.e., weight, w_i) applied.

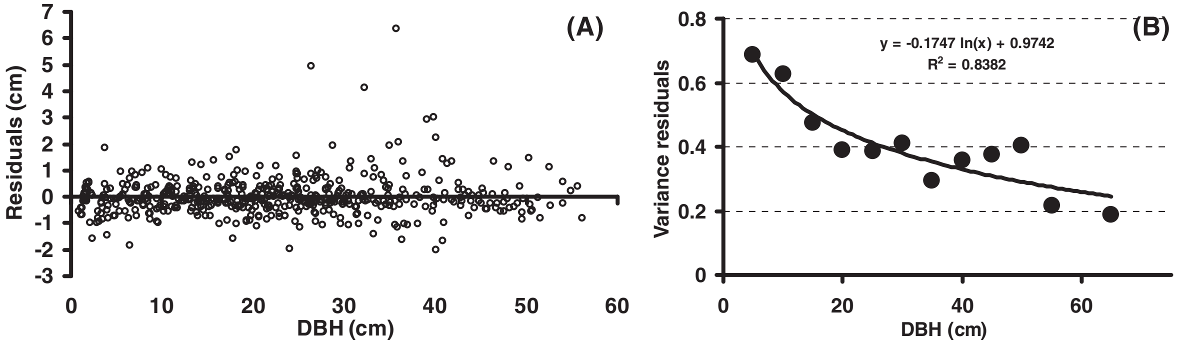


Fig. 3. (A) Mean relative error (RE) in DBH prediction and sample size (*n* = number of observations) according to different choice of reference age for E5 by five years classes and (B) consistency of site index over age estimated using E5 for the 25 series.

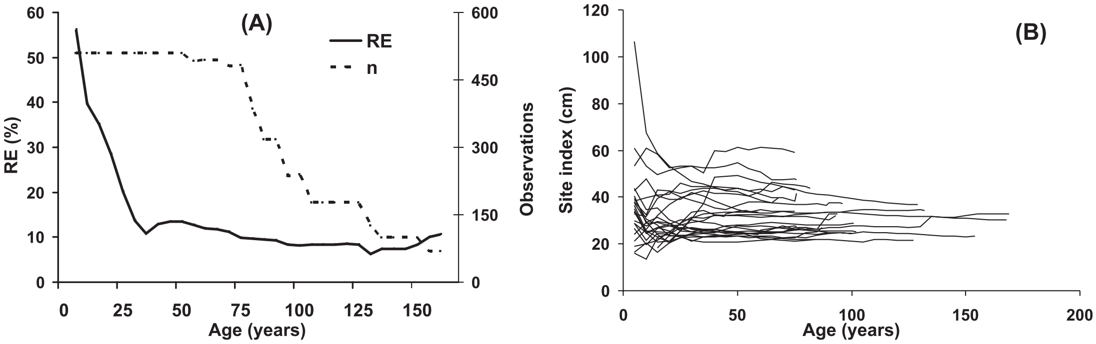
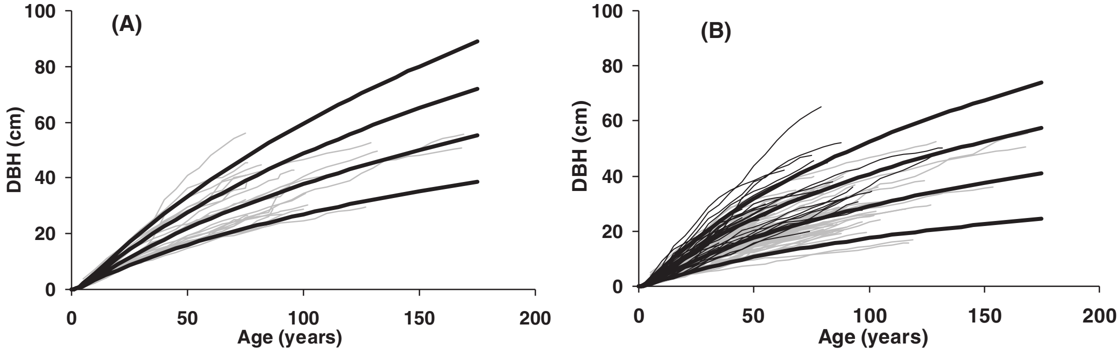


Fig. 4. Age-dependent dynamic models: (A) GADA E5 (Korf base model) potential growth curves (25 series) for site indexes 50, 41, 32, and 23 cm at a reference age of 80 years and (B) GADA $E5_2$ (Korf base model) diameter growth curves, 115 trees. The curves were graphed for DBH 45, 35, 25, and 15 cm at 80 years; the thin black lines correspond to trees growing at a density of ≤100 trees/ha, whereas grey lines correspond to trees growing at a density of >100 trees/ha.



(b_1: SE = 2.374, $p > |t| < 0.001$; b_2: SE = 16.415, $p > |t| < 0.022$; c: SE = 0.027, $p > |t| < 0.001$; coefficients as in Table 2 for E5). From eq. 1, we defined a site index based on diameter growth. Figure 3A suggested the selection of site index from the ages of 30 to 75–80 years, as after 80 years, the number of observations decreased significantly. There are different opinions as to whether reference ages should be greater or lower (Álvarez et al. 2004). We considered 80 years the optimum, as it was the highest age where the error was small and the number of observations was still around 400 (Fig. 3A) and for comparable purposes with the site index selected for *Q. suber* in Sánchez-González et al. (2005). The four site indexes corresponded to 50 cm (class I), 41 cm (class II), 32 cm (class III), and 23 cm (class IV). The individual plots to compare the behaviour of site index in different age classes (Fig. 3B), which remained almost constant over the age of approximately 30 years, also demonstrate that the indexes selected were appropriate. The original data of the 25 series and the selected potential model are shown in Fig. 4A. The error in prediction was around 7% in "dominant" trees from 10 to 45 cm (Fig. 5). Predictive error followed the typical increase in the smallest classes and the proposed model was unbiased in all diameter classes except for trees over 55 cm because of lack of data

Fig. 5. Relative mean root square error (RMSE) and bias in diameter prediction by diameter class for E5 (solid line), E5$_2$ (broken line), T2 (circles), and T5s (triangles).

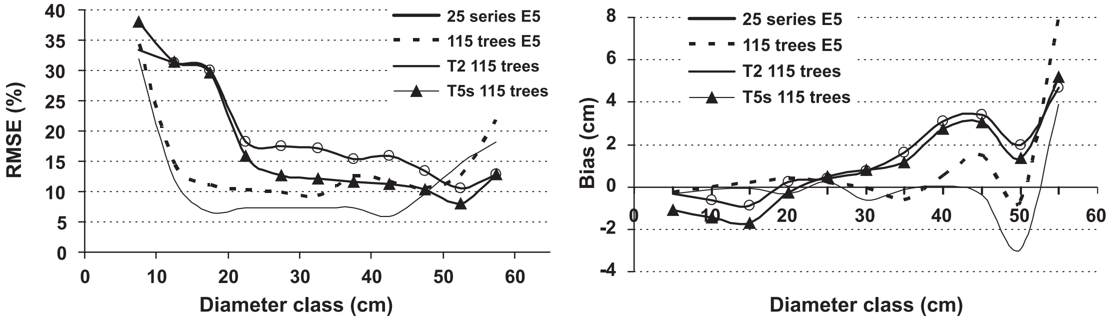
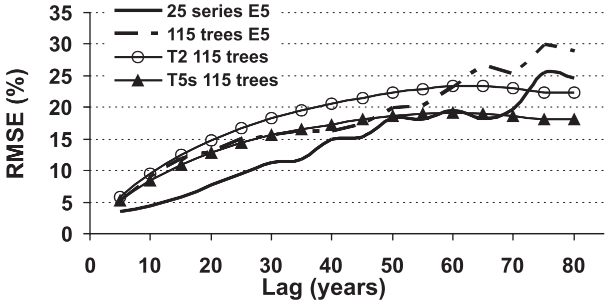


Fig. 6. Relative root mean square error (RMSE) by lag of prediction for E5 (solid line), E5$_2$ (broken line), T2 (circles) and T5s (triangles).



from trees over that size (Fig. 5). As expected, the longer the prediction interval, the larger the error in prediction (Fig. 6). The mean predictive error was lower than 15% for lags shorter than 45 years and only 3.5% for 5 years.

Holm oak age-dependent diameter growth in relation to management

As the data set was different (115 trees instead of 25 series), we compared again some of the best models (GADA) used for potential growth (Table 1) expanding them by density. We did not compare any Weibull models, as they were very similar to Richards but with lower, unrealistic predictions in the highest DBH classes. The residuals were heterocedastic; therefore, a weighting factor was applied in the regression (see Fig. 2B). Again, GADA E5$_2$ formulations from the Korf base model were the best (E5$_2$ and E5d; Table 3). When comparing E5d (model with parameter *b* expanded by density) with E5$_2$ (formulation without expanding parameters), E5d did not increase significantly the information explained by E5$_2$ (Table 3). This was confirmed when we further tested the significance of the expanded parameter: the Lakkis–Jones test comparing E5$_2$ and E5d was not significant (χ^2 = 0.075, p = 1.000). Yet when plotting the nonexpanded model E5$_2$ in Fig. 4B, the fastest growing trees occurred in plots with density below 100 trees/ha (darkest thin lines).

The model finally selected (GADA E5, unique for all trees regardless of density) has the expression

$$[2] \qquad \mathrm{DBH}_2 = \exp(X_0)\exp\left\{-[8.310178 + (1/X_0)]t_2^{-0.264597}\right\}$$

where

$$X_0 = 0.5\left[8.310178t_1^{-0.264597} + \ln(\mathrm{DBH}_1) + F_0\right]$$

where

$$F_0 = \sqrt{\left\{\left[8.310178t_1^{-0.264597} + \ln(\mathrm{DBH}_1)\right]^2 + 4t_1^{-0.264597}\right\}}$$

(b$_1$: SE = 0.118, $p > |t| < 0.001$; c: SE = 0.016, $p > |t| < 0.001$). The residual error increased compared with models built for the 25 series (Table 3; Figs. 5 and 6), as might be expected from the inclusion of suppressed trees. Still, the error is acceptable (~10% for trees 10 cm < DBH < 50 cm), increasing in the smallest and the largest diameter classes in the same way as in potential models. Again, the longer the prediction interval, the larger the error. The mean predictive error was lower than 15% for lags shorter than 25 years and 5.2% for 5 years (Fig. 6).

Holm oak diameter growth in relation to management: age-independent dynamic models

Age-independent models shown were only derived from Hossfeld IV and Korf base models, as formulations from these base models behaved better than Richards'. As in general models for all trees, residuals were again not homocedastic (Fig. 7); therefore, a weighting factor was applied when fitting the models. Age-independent models based on the Hossfeld growth function were the best (Table 4).

T1, T2, and T3 were only expanded by density; thus, they were really independent of age. Among these three models, T2, an age-independent Hossfeld IV model with *a* inversely related and *b* directly related to quantitative density (greater asymptotes in low densities; Fig. 8), was best in the validation statistics (Table 4). Its expression is

$$[3] \qquad \mathrm{DBH}_2 = \frac{(F + \mathrm{dif})^{1.007868}}{(0.023114 \times \mathrm{density}) + \left(\frac{0.465367}{\mathrm{density}}\right)(F + \mathrm{dif})^{1.007868}}$$

with

$$F = t_1 = \sqrt[1.007868]{\frac{\mathrm{DBH}_1(0.023114 \times \mathrm{density})}{\left[1 - \left(\frac{0.465367}{\mathrm{density}}\right)\mathrm{DBH}_1\right]}}$$

where dif is projection length (i.e., $T_2 - T_1$) (a$_1$: SE = 0.010,

Table 3. Parameter estimates and goodness-of-fit statistics for the age-dependent models for 115 trees (parameters expanded and nonexpanded by density).

	Estimation			Model evaluation (jackknife)			
ID	RMSE (cm)	R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd
$E3_2$	0.7234	0.9926	8.5	0.0670	2.6532	0.9508	89.2
$E5_2$	0.7217	0.9927	0.0	–0.0492	2.5887	0.9532	0.0
$E9_2$	0.7327	0.9924	54.4	0.0827	3.0584	0.9347	603.3
E3d	0.7234	0.9926	10.3	0.0767	2.6787	0.9499	122.7
E5d	0.7217	0.9927	1.7	–0.0386	2.6031	0.9527	19.1

Note: Estimation statistics were calculated using the weighted residuals. In E3d, $b = (b_1 + b_d \times \text{density})X$; in E5d, $b = (b_1 + b_d \times \text{density}) + (1/X)$.

$p > |t| < 0.001$; b_1: SE = 0.001, $p > |t| < 0.001$; c: SE = 0.088, $p > |t| < 0.001$). Contrary to GADA age-dependent models, age-independent models only expanded by density were slightly biased in the validation phase, and their RMSE increased 80% as compared with the age-dependent models (Table 4). In Figs. 5 and 6, the relationship between the predicted errors and diameter class or lag of interval prediction are shown: the lag interval below 15% error was 20 years, the error increasing as usual with lag length.

When expanding the age-independent formulations also by site index, the error greatly decreased compared with real age-independent models T1, T2, and T3. In addition, models T4s and T5s were almost unbiased (Table 4; Figs. 5 and 6). The inclusion of the site index reduced in T5s the mean residual by 17% and the mean bias to around 75% compared with age-independent T2. The lag of prediction with error below 15% increased to 25 years (Fig. 6). The model (T5s) expression is

$$[4] \qquad \mathrm{DBH}_2 = \frac{(F+\mathrm{dif})^{0.859611}}{(0.002797\times\mathrm{density}+31.4296/\mathrm{SI})+\left[\left(\frac{-0.06588}{\mathrm{density}}\right)+0.000123\times\mathrm{SI}\right](F+\mathrm{dif})^{0.859611}}$$

with

$$F = \sqrt[0.859611]{\frac{\mathrm{DBH}_1\times(0.002797\times\mathrm{density}+31.4296/\mathrm{SI})}{\left\{1-\left[\left(\frac{-0.06588}{\mathrm{density}}\right)+0.000123\times\mathrm{SI}\right]\mathrm{DBH}_1\right\}}}$$

where dif is projection length and SI is site index in cm (a_1: SE = 0.000, $p > |t| < 0.001$; a_{d1}: SE = 0.0275, $p > |t| < 0.017$; b_1: SE = 1.426, $p > |t| < 0.001$; b_{d1}: SE = 0.000, $p > |t| < 0.001$; c: SE = 0.0084, $p > |t| < 0.001$). Both models 3 and 4 are polymorphic and with variable asymptotes for different densities and site indexes (Fig. 8).

Discussion

This study is the first attempt to model diameter growth in holm oak tree like woodlands. Fitting growth models to this species in this ecosystem is challenging for its particular management and uncertain history. Despite the versatility of the species to thrive in a variety of climates and soils, the historical isolation of tree formations to marginal soils has probably reduced the presence of the species to the worst soil conditions. Nevertheless, it is very likely that trees analyzed exhibit near maximal growth for holm oak in this area, as humans, who probably selected the best trees, enforced the current structure, with low tree densities. Holm oak has been traditionally considered a slow-growth species (Ibáñez et al. 1999). In our results, mean growth is slightly slower than that of other Mediterranean oaks such as *Q. suber* (Sánchez-González et al. 2005; Tomé et al. 2006) and *Quercus pyrenaica* Willd. (Adame et al. 2007). Diameter growth is expected to be greater in low-density agroforestry systems than in forests (Balandier and Dupraz 1999). The young age range found in this study, and in other analyzed samples not included here (partly described in Plieninger et al. 2003), where the maximum age was also below 200 years, agree with the hypothesis that most dehesas originated since the early nineteenth century, mostly after the 1850s and the first half of the twentieth century (Manuel and Gil 1999; Pulido et al. 2001; Martín Vicente and Fernández Ales 2006).

Formulations derived from power decline base models (Korf and Hossfeld) rather than exponential decline (Richards, Weibull when $c > 1$ (Kiviste et al. 2002)) best described diameter growth in all cases, as stated in the literature (Zeide 1989, 1993; Shvets and Zeide 1996). The analysis of “potential growth” describes how species grow and provides tools that can be applied in system models (Porte and Bartelink 2002). What we consider here as “potential growth” could be more accurately denominated “maximum diameter growth under traditional ‘dehesa’ management”. As in other previous studies, GADA formulations had a slightly better fit than simpler ADA (e.g., Cieszewski 2002; Barrio-Anta et al. 2006). The model selected (E5), polymorphic and with variable asymptotes GADA formula-

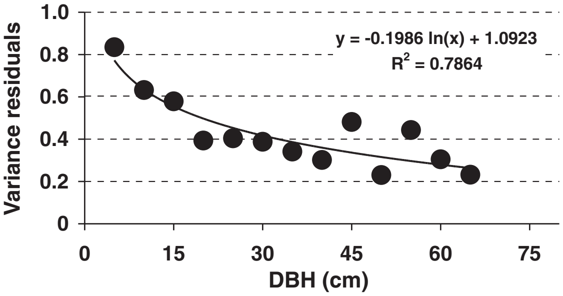


Fig. 7. Estimation residuals (predicted-observed) versus predicted DBH as an illustration of potential heterokedasticity for age independent formulations. Residual variance by diameter class and estimated variance function (i.e., weigth, w_i) applied in T2 and T5s.

tion derived from the Korf growth function, fit the data with a reduced RMSE of 2.6 cm and 7% in DBH classes from 10 to 45, coinciding with the diameter range within which most trees of the dehesas are found (Pulido et al. 2001). The errors yielded (Tables 2–4; Figs. 5 and 6) are in accordance with site dynamic growth studies for other tree species (e.g., Barrio-Anta et al. 2006; Diéguez-Aranda et al. 2006).

The wide range of densities included in our plots makes possible the comparison between "potential models" and the effect of density in general models for all trees regardless of their social position within the stand. Although density was not included in the models, the most open stands coincided with the most productive (Fig. 4B); the reason could be that humans thinned the most productive sites more intensively, and in turn, this has produced better pastures. Thus, the positive effect of low density and fertile sites is likely to be combined in these anthropic woodlands. The small increase in the error with respect to "potential growth" models and the similarity between the model for 25 series and the model for 115 trees would support the hypothesis of codominance of most trees. This could have been expected, as only 23.5% of trees had been considered "suppressed" in the graphical analysis, meaning that the five trees analyzed per plot generally exhibited very similar growth. Our results support the use of a single model for all densities and for any tree in the system, as the error does not increase significantly. An average tree would reach ~15 cm DBH after 30 years, which is in accordance with the approximate age suggested for cattle exclusion on regenerated sites (San Miguel 1994). This mean tree would reach around 27 cm at 60 years and 35 cm at 90 years (see Fig. 4B).

Model 2 can be applied to any tree in the system without defining dominance. However, accurately estimating tree age in holm oak is extremely difficult. This is the reason why we compared age-independent formulations (Tomé et al. 2006) with the previous age-dependent dynamic models. When expanding only by density, the models where slightly biased and increased the error except in prediction lags greater than 50–60 years, where age-independent models were better. Yet this increase was acceptable, especially bearing in mind the advantage of neglecting age. Additionally, the highest errors in models 3 and 4 coincided with the smallest and greatest diameter classes. This is a normal feature in growth models that results from a lack of data in the largest classes and worse predictive ability in the youngest ages. When expanding also by site index (model 4), the error significantly decreased, with a behaviour similar to that of the general age-dependent model 2, especially when analyzing the mean error by lag of prediction. In both models, the smallest error was again centred in diameter classes from 20 to 50 cm (Fig. 5), which are the most abundant in the system today (Pulido et al. 2001). In T5s, density explained less variance than site index, which is in accordance with the noninclusion of density in $E5_2$. Although T5s is not totally "age independent", as site index must be estimated, it enabled us to test the validity of the defined site index and compare our results with those of Tomé et al.'s (2006) original paper. The aforementioned increase in error with respect to age-dependent dynamic models found in our analysis is not totally compatible with the results of Tomé et al. (2006) for *Q. suber* age-independent formulations in a similar system. In that study, age-independent models had a slight better fit than age-dependent ones. Nevertheless, we consider our results reasonable: when significant covariates are added to an equation ("age" in this case), the error is likely to decrease and the goodness-of-fit increase. In addition, T5s would likely improve if soil and climatic data were available. Although we believe that it is unlikely to explain such a great difference in the increase in error with respect to that study, the increase in error found in our models might result from the use of a site index derived from diameter rather than from height. Acknowledging the previous shortcomings and from the tremendous advantage of neglecting age, we believe that the error yielded is acceptable in the middle diameter classes, which are the most common in these woodlands, as discussed. Age-independent models are an alternative to model growth in tree species that do not form annual rings, including many species in the tropics (Verheyden et al. 2005), and can be applied to other agroforestry systems, particularly in Mediterranean climates (e.g., Jackson et al. 1990; Ovalle et al. 1990), and to uneven-aged stands (Tomé et al. 2006).

The site index based on diameter growth proposed was significant in T5s. This would support the definition of site indexes based on diameter growth in open stands. It is supported by an ecological basis, if we accept that when canopies are competing for light, trees tend to focus growth in height, whereas isolated trees focus growth in increasing their canopies and stem diameter (Hasenauer 1997). Therefore, in open stands, we could consider diameter growth as potential at least in terms of competition for light. Finally, the fact that current density was included in age-independent life-span models might reflect the human influence upon these systems: the current woodland structure and density were modified decades ago and the stands are static except for tree death, which is gradually reducing the tree stock.

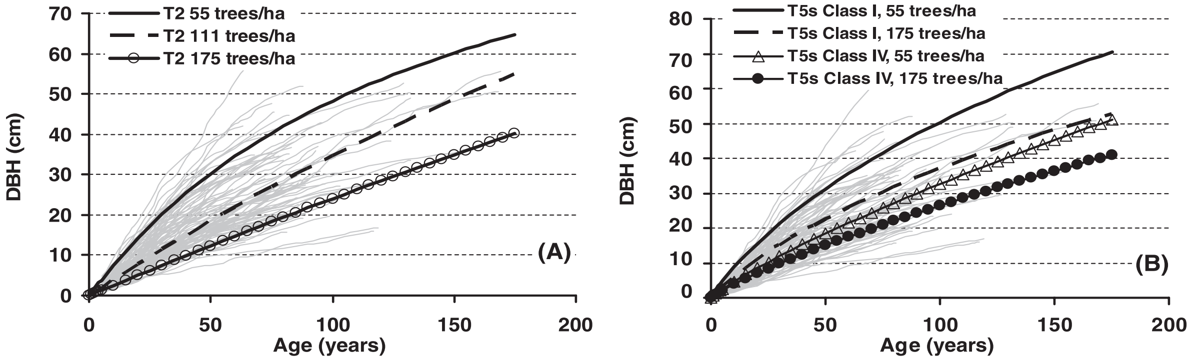
In this study, we offer different possibilities to model diameter growth in holm oak open woodlands. It would be interesting to study the difference comparing the implementation of a site index based on a general equation for all trees with a site index based on potential growth series, particularly when soil and climate variables are available. Whether these models, based on past growth, are appropriate to predict diameter under different future climatic scenarios is something that should be studied.

Table 4. Age-independent holm oak diameter growth dynamic models with parameters expanded by stand density (T1, T2, and T3) and (or) site index (T4s and T5s).

	Estimation			Model evaluation (jackknife)			
ID	RMSE (cm)	R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd
T1	0.6762	0.9927	900.0	–0.4007	4.7340	0.8333	6240.8
T2	0.6781	0.9927	981.2	–0.5587	4.6274	0.8407	5549.2
T3	0.6856	0.9925	1317.7	–0.4495	4.7475	0.8323	6327.3
T4s	0.6632	0.9930	307.7	–0.0742	4.0366	0.8788	1400.5
T5s	0.6565	0.9931	0.0	–0.1413	3.8545	0.8895	0.0

Note: Estimation statistics were calculated using the weighted residuals.

Fig. 8. Age independent models: (A) T2 for densities 55, 111 and 175 trees/ha; (B) T5s for site index 50 (Class I) and 23 (Class IV), densities 55 and 175 trees/ha.



Conclusions

The "potential growth" equations were unbiased and with an error of around 7% in the most abundant diameter classes encountered in the system, modelling the data and the asymptotic growth tendency of the species very well. The general age-dependent model selected, applicable to any tree within any stand density knowing its age, did not increase the error (which was around 10% in DBH from 10 to 50 cm) much compared with the "potential" models. Density did not provide much information in the age-dependent models, whereas in age-independent models, in spite of being significant, the residual errors decreased when the site index proposed was used to expand the parameters. The inclusion of the defined site index in the models increased the accuracy of age-independent formulations, although it added the same limitation that age must be estimated to define the site index. Age-independent models including site index were similar to general age-dependent models in the most abundant diameter classes in the system (20–55 cm). The discussion of age-independent dynamic models offers managers and researchers of other agroforestry systems and tropical forests new alternatives for modelling dynamic growth in highly altered tree systems and in species or stands where the determination of age is cumbersome.

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