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Original article

Individual-tree growth and mortality models for Scots pine (*Pinus sylvestris* L.) in north-east Spain

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Abstract – A distance-independent diameter growth model, a static height model and mortality models for *Pinus sylvestris* L. in north-east Spain were developed based on 24 permanent sample plots established in 1964 by the Instituto Nacional de Investigaciones Agrarias (INIA). The model set enables the simulation of stand development on an individual tree basis. To predict mortality, two types of models were prepared – a model of the self-thinning limit and two logistic models for the probability of a tree to survive the coming 5-year-period. The plots ranged in site index from 13 to 26 m (dominant height at 100 years), and were measured an average of 5 times. The data for the diameter growth model consisted of 10 843 observations and ranged in age from 33 to 132 years. The relative bias for the diameter growth model was 1.2%. The relative biases for the height and self-thinning models were 0.10 and 0.23%, respectively. The relative RMSE values were 64.1, 8.29 and 17%, respectively, for the diameter growth, height and self-thinning models. The two tree-level survival functions used the past average growth, basal area of trees larger than the subject tree and the past 5-year growth as predictors.

growth and yield / mixed models / simulation / *Pinus sylvestris* L.

Résumé – **Modèles individuels de croissance et de mortalité pour le pin (*Pinus sylvestris* L.) dans le nord-est de l'Espagne.** Un modèle non spatialisé de croissance en diamètre, un modèle statique de hauteur et des modèles de mortalité pour *Pinus sylvestris* L. en Espagne du Nord ont été développés, à partir de 24 placettes permanentes établies en 1964 par l'Instituto Nacional de Investigaciones Agrarias (INIA). Cet ensemble de modèles permet de simuler le développement du peuplement au niveau de l'arbre individuel. L'indice de fertilité des différentes placettes variait de 13 à 26 m (hauteur dominante à 100 ans). Les placettes ont été mesurées 5 fois en moyenne. Pour prévoir la mortalité, deux types de modèles ont été établis – un modèle de densité limite (auto-éclaricie par mortalité naturelle) et deux modèles pour la probabilité de survie pendant la période des 5 années suivantes. Les données pour le modèle de croissance en diamètre correspondent à 10 843 observations, dans une gamme d'âge de 33 à 132 ans. Le biais relatif pour le modèle de la croissance en diamètre était 1,2 %. Les biais relatifs pour les modèles de hauteur et d'auto-éclaircie étaient de 0,10 et 0,23 % respectivement. Les valeurs relatives du RMSE étaient de 64,1, 8,29 et 17 %, respectivement, pour les modèles de croissance en diamètre, de hauteur et d'auto-éclaircie. Les prédicteurs dans les fonctions de survie établies étaient: la croissance moyenne passée, la surface terrière des arbres plus grands que l'arbre sujet et la croissance des cinq années passées.

croissance et production / modèles mixtes / simulation / *Pinus sylvestris* L.

1. INTRODUCTION

Scots pine (*Pinus sylvestris* L.) forms large forests in most of the mountainous areas of Spain, occupying an area of 1 280 000 ha [17]. It is very important to Spanish forestry because of its economic, ecological and social roles. One of the major needs in forest management planning is to predict forest stand development under different treatment alternatives. In the case of Spain, these predictions have been traditionally taken from yield tables – tabular records showing the expected volume of wood per hectare by combinations of measurable characteristics of the forest stand (age, site quality and stand density).

Yield tables are static models that usually apply to fully stocked or normal stands. Efficient forest management calls for the use of forest growth modelling expressed as mathematical equations or systems of interrelating equations that can predict future stand development with any desired combination of inputs. In view of the importance of *P. sylvestris* in Spain, there is a need for a reliable system of growth and yield

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Table I. Mean, standard deviation (S.D.) and range of main characteristics in the study material[a].

Variable	N	Mean	S.D.	Minimum	Maximum
Diameter growth model (Eq. 1)					
id5 (cm per 5 years)	10843	1.0	0.7	–1.6	5.0
dbh (cm)	10843	20.8	7.7	5.0	55.6
BAL (m^2 ha^{-1})	10843	24.3	12.8	0.0	60.7
G (m^2 ha^{-1})	128	42.8	9.3	22.6	65.1
T (years)	128	64.0	22.7	33.0	132.0
SI (m)	24	19.9	3.3	13.7	25.8
Height model (Eq. 2)					
h (m)	3525	14.5	3.5	4.8	27.2
dbh (cm)	3525	24.1	9.0	5.1	61.0
H_{dom} (m)	113	15.7	3.2	7.8	24.6
D_{dom} (cm)	113	31.7	7.5	14.3	51.8
T (years)	113	69.0	24.6	36.0	148.0
Self-thinning model (Eq. 3)					
N_{max} (trees per hectare)	18	1869.2	1498.0	674.9	5519.5
D (cm)	18	22.8	7.0	8.9	31.6
SI (m)	10	18.5	3.2	13.7	23.3
Mortality model 1 (Eq. 4)					
P (survive)	11119	0.9	0.1	0.0	1.0
dbh (cm)	11119	20.7	7.7	5.0	55.6
BAL (m^2 ha^{-1})	11119	24.5	12.9	0.0	60.7
T (years)	128	64.0	22.7	33.0	132.0
Mortality model 2 (Eq. 5)					
P (survive)	11119	0.9	0.1	0.0	1.0
id5 (cm per 5 years)	11119	1.0	0.7	–1.6	5.0
BAL (m^2 ha^{-1})	11119	24.5	12.9	0.0	60.7

[a] N: the number of observations at tree-, plot-measurement-, and plot-level; id5: 5-year diameter increment; dbh: diameter at breast height; BAL: competition index; G: stand basal area; T: stand age; SI: site index; h: tree height; H_{dom}: dominant height; D_{dom}: dominant tree diameter; N_{max}: the self-thinning limit; D: mean square diameter; *P* (survive): probability of a tree surviving.

predictions that, with appropriate economic parameters and ecological models, would support decision making in the management of Scots pine forests.

Munro [18] suggested the following classification for growth models:

1. Stand-level models.
2. Distance-independent tree-level models.
3. Distance-dependent tree-level models.

Stand-level models use stand variables (e.g., age, site index, basal area per hectare and number of trees per hectare) as inputs, while at least some of the predictor variables in a tree-level model are individual tree characteristics. In the case of distance-independent (non-spatial) tree-level models, the individual tree characteristics do not require any information on the spatial distribution of the trees. Distance-dependent (spatial) tree-level models, on the other hand, include a spatial competition measure. Competition is often expressed as a function of the distance between the subject tree and its neighbours as well as the size of the neighbours. Distance-independent models do not use spatial information to express competition, but they can use predictors which measure stand density (for example, stand basal area) and thus express the overall competition in a stand [15]. When individual tree information for a stand is available, tree-level models enable a more detailed description of the stand structure and its dynamics than stand-level models [15]. Examples of tree-level models (spatial and non-spatial) are many [1, 4, 15, 20–22, 28, 31, 35, 37]. Spanish studies on growth, mortality and regeneration dynamics of Scots pine stands are for instance: Rio [24], Rio et al. [25] and González and Bravo [9].

The objective of this study is to develop a model set, which enables tree-level distance-independent simulation of the development of *P. sylvestris* stands in north-east Spain. The system consists of a diameter growth model, a static height model, and models for the self-thinning limit and the probability of a tree to survive for the coming 5-year-period.

2. MATERIALS AND METHODS

2.1. Data

The data were measured in 24 permanent sample plots (*table I*) established in 1964 by the Instituto Nacional de Investigaciones

Agrarias (INIA) to represent most Scots pine sites in north-east Spain. The plots were located in the provinces of Huesca, Lérida and Tarragona. The plots were naturally regenerated and thinned after the second measurement. The sites ranged in site index (at an index age of 100 years) from 14 to 26 m. The site index for each site was determined using the site index model of Palahí et al. [19]. The mean plot area was 0.1 ha. The plots were measured at 5-year-intervals, except for the last measurement where the interval varied from 10 to 16 years. The last measurement was conducted during the year 2000. At each measurement, tree diameter at 1.3 meters height (dbh) from all trees thicker than 5 cm, and tree heights of a sample of at least 20 trees per plot were recorded. Dead trees were recorded at each measurement. This resulted in 3525 diameter/height observations and 10843 five-year diameter growth observations (*table I*). At each measurement the stand characteristics were computed from the individual-tree measurements of the plots.

Most plots were thinned after the first measurement. Many of the removed trees were dying or already dead when the thinning was carried out. Because it was not known whether a removed tree was living or dead the thinned trees were not used as observations.

2.2. Diameter increment

A diameter growth model was prepared using tree-level (diameter and basal area of larger trees) and stand-level (site, basal area and age) characteristics and their transformations as predictors. The predicted variable was the five-year diameter growth. This was obtained as a difference between two successive diameter measurements. The last growth observation (10 to 16 years growth) was converted into five-year growth by dividing the diameter increment by the time interval between the two measurements and multiplying the result by 5. Due to errors in measuring accurately dbh, several growths were negative. Therefore, it was not possible to model the logarithmic transformation of the predicted variable. The final model, thus, described the linear relationship between the dependent and the independent variables (Eq. (1)). All predictors had to be significant at the 0.05 level without any systematic errors in the residuals.

Due to the hierarchical structure of the data (i.e. there are several observations from the same trees, trees are grouped into plots, and plots are grouped into provinces), the generalised least-squares (GLS) technique was applied to fit a mixed linear model. The linear models were estimated using the maximum likelihood procedure of the computer software PROC MIXED [27].

The diameter growth model was as follows:

$$id5_{lkjt} = \beta_0 + \beta_1 \times dbh_{lkjt} + \beta_2 \times \frac{1}{dbh_{lkjt}} + \beta_3 \times \frac{dbh_{lkjt}}{T_{lkt}} + \beta_4 \times BAL + \beta_5 \times \ln(G_{lkt}) + \beta_6 \times SI_{lk} + u_{lk} + u_{lkj} + e_{lkjt} \quad (1)$$

where *id5* is future diameter growth (cm per 5 years); *dbh* is diameter at breast height (cm), *BAL* competition index measuring the total basal area of larger trees; *T*, *G* and *SI* are stand age (years), basal area (m^2 ha^{-1}) and site index (m) at an index age of 100 years, respectively. Subscripts refer to province: *l*; plot: *k*; tree: *j*; and measurement: *t*. u_{lk}, u_{lkj} and e_{lkjt} are independent and identically distributed random between-plot, between-tree and within-tree factors with a mean of 0 and constant variances of σ^2_{pl}, σ^2_{tr}, σ^2_{e}, respectively. These variances and the parameters β_i were estimated using the GLS method. At first, random between-province and between-measurement factors were also included in the model but they were not significant.

2.3. Height model

Since the height sample trees in each measurement were different, the observations in the estimation data (*table I*) did not allow for the estimation of a height growth model. A static height model was therefore estimated. For this purpose, two candidate models were evaluated; a non-linear height model used by e.g., Hynynen [12] and Mabvurira and Miina [15] and a linear height model proposed by Eerikäinen [7]. Both model types were estimated with and without random parameters, which can take into account the random between-plot and between-measurement factors. Because the models with random parameters did not outperform the simpler model, the non-linear height model was estimated using a nonlinear least squares (NLS) technique in SPSS [29]. The SPSS software uses the Levenberg-Marquart algorithm to obtain the final parameter estimates. The loss function was defined as the sum of squared residuals (observed minus predicted values). This model enables the estimation of tree heights when only stand age, tree diameters and stand dominant height are measured (as is the normal case in forest inventory).

The non-linear height model was as follows:

$$h_{lkjt} = 1.3 + (H_{dom,\,lkt} - 1.3) \times \left(\frac{dbh_{lkjt}}{D_{dom,\,lkt}}\right)^{\left(\beta_0 + \beta_1 \times \left(\frac{dbh_{lkjt}}{D_{dom,\,lkt}}\right) + \beta_2 \times T_{lkt}\right)} + e_{lkjt} \quad (2)$$

where *h* is tree height (m); H_{dom} and D_{dom} are dominant height (m) and dominant diameter (cm) of the stand, respectively.

2.4. Mortality

To account for mortality, two types of models – a model of the self-thinning limit and a model for the probability of a tree to survive the coming growth period – were developed. According to Reineke's expression [23] and the –3/2 power rule of self-thinning [34], a log-log plot of the average tree size and stem density will give a straight self-thinning line of a constant slope. Nevertheless, the suitability of these two theoretical relations for describing the self-thinning process has been called into question by various authors in the last three decades [3, 6, 11, 13, 22, 35, 36]. According to Hynynen's study [11] the slope of the line varies for different tree species, while the intercept of the self-thinning line varies within tree species according to site index. In this study, the self-thinning model was developed from data obtained from 10 plots (*table I*). These plots were selected by dividing all plots of the study into three major site classes ($SI \le 17$ m, $SI >$ 17–21 m and $SI > 21$ m) and then choosing for each site class those plots and measurement occasions, which were considered to be at the self-thinning limit (*figure 3*). The influence of site quality on the intercept of the self-thinning line was examined by adding the site index to the model as an independent variable. The following model for the self-thinning limit was estimated using ordinary least squares (OLS) method.

$$\log(N_{max,\,lkt}) = \beta_0 + \beta_1 \times \log(D_{lkt}) + \beta_2 \times SI_{lk} + e_{lkt} \quad (3)$$

in which N_{max} is the highest possible number of trees per hectare, *D* is the mean square diameter (cm), and *SI* is the site index (m). The mean square diameter is calculated from $D = \sqrt{40\,000/\pi} * G/N$, and log stands for the 10-base logarithm.

Individual tree survival models predict the probability of survival for each tree involved in the growth projection [5]. Conceptually, the individual survival probability should be within [0, 1]. Of the functions with this property, logistic regression is the most widely employed [2, 4, 10, 14, 16, 32, 37]. Probability of survival is usually determined by some function of tree size and competition index [16]. The probability is then compared with a threshold value, usually a uniform random deviate. Mortality occurs if the deviate exceeds the predetermined probability of surviving. The data for estimating the probability of a tree surviving the next growth period, as a function of tree and stand characteristics were obtained from the whole data set including all plots and measurements (*table I*). Individual tree records were coded as either live or dead at the end of each growing period. This resulted in 10 843 records classified as live and 276 classified as dead.

Monserud [16] demonstrated that growth was an important explanatory variable in mortality determination. Actual growth, however, is not always available. Therefore, two different models were fitted that can be used according to the information available. The first of these models (Eq. (4)) uses the average tree diameter growth as one of the predictors, while the other (Eq. (5)) uses the actual tree diameter growth during the past 5 years as a predictor. The following mortality models were estimated using the Binary Logistic procedure in SPSS [29].

$$P(survive)_{lkjt} = \frac{1}{1+\exp\left(-\left(\beta_0+\beta_1\times BAL_{lkjt}+\beta_2\times\dfrac{dbh_{lkjt}}{T_{lkt}}\right)\right)}+e_{lkjt} \quad (4)$$

$$P(survive)_{lkjt} = \frac{1}{1+\exp(-(\beta_0+\beta_1\times BAL_{lkjt}+\beta_2\times id5_{lkjt}))}+e_{lkjt} \quad (5)$$

in which P(survive) is the probability of a tree surviving for the next 5-year-period.

2.5. Model evaluation

2.5.1. Fitting statistics

The models were evaluated quantitatively by examining the magnitude and distribution of residuals for all possible combinations of variables. The aim was to detect any obvious dependencies or patterns that indicate systematic discrepancies. To determine the accuracy of model predictions, bias and precision of the models were tested [8, 19, 30, 33]. Absolute and relative biases and root mean square error (RMSE) were calculated as follows:

$$bias = \frac{\sum(y_i-\hat{y}_i)}{n} \quad (6)$$

$$bias\% = 100\times\frac{\sum(y_i-\hat{y}_i)/n}{\sum\hat{y}_i/n} \quad (7)$$

$$RMSE = \sqrt{\frac{\sum(y_i-\hat{y}_i)^2}{n-1}} \quad (8)$$

$$RMSE\% = 100\times\sqrt{\frac{\sum(y_i-\hat{y}_i)^2/(n-1)}{\sum\hat{y}_i/n}} \quad (9)$$

where n is the number of observations; and y_i and $\hat{y}_i$ are observed and predicted values, respectively.

2.5.2. Simulations

In addition, the models were further evaluated by graphical comparisons between measured and simulated stand development. The simulations were based on the models developed in this study. The simulation of one 5-year-time step consisted of the following steps:

1. For each tree, add the 5-year diameter increment (Eq. (1)) to the diameter, and increment tree ages by 5 years.

2. Multiply the frequency of each tree (number of trees per hectare that a tree represents) by the 5-year survival probability. The survival probability was calculated by equation (4). Use of equation (4) corresponds better to the practical situation than using equation (5) because past growth is usually unknown.

3. Calculate stand dominant height from the site index and incremented stand age using the Hossfeld equation of Palahí et al. [19], and calculate the dominant diameter from incremented tree diameters.

4. Calculate tree heights using equation (2).

5. Calculate the self-thinning limit (Eq. (3)). If the limit is exceeded, remove trees until the self-thinning limit is reached, starting with the trees with the lowest survival probability (Eq. (4)).

Table II. Estimates of the parameters and variance components of the diameter growth model (Eq. (1)), height model (Eq. (2)) and self-thinning model (Eq. (3)).

Parameter	Diameter growth model (Eq. 1)	Height model (Eq. 2)	Self-thinning model (Eq. 3)
β_0	4.1786	0.5546	5.2060
β_1	–0.0070	–0.3317	–1.8150
β_2	–8.0476	–0.0015	0.0212
β_3	0.6945	-	-
β_4	–0.0042	-	-
β_5	–1.1092	-	-
β_6	0.0764	-	-
σ^2_{pl}	0.0206	-	-
σ^2_{tr}	0.0821	-	-
σ^2_e	0.3373	1.4553	0.0030
R^2	0.2400	0.8900	0.9700

The growth of four plots representing different site indices and stand ages were simulated over the whole observation period. In addition all growth intervals of all plots were simulated and the simulated 5-year change in stand characteristics was compared to the measured change. The measured mean height was calculated from tree heights obtained as follows [19]: a height curve was fitted separately for each plot and measurement and missing tree heights were obtained from this curve.

3. RESULTS

3.1. Diameter growth and height models

All parameter estimates of the diameter growth model are logical and significant at the 0.001 level (*table II*). The coefficient of determination (R^2) was 0.24. Increasing competition (*BAL*) and stand basal area decreased the diameter growth of a tree. High average past growth (dbh/age) and site index increased diameter growth. Both the untransformed dbh and the transformation 1/dbh were significant predictors that describe the non-linear pattern between diameter increment and dbh. The transformation dbh/age describes the influence of age on the relationship between dbh and diameter increment. The absolute and relative biases in the diameter growth model were 0.0124 cm per 5-year-period and 1.2%, respectively (*table III*).

The bias of the fixed part of the diameter growth model was examined by plotting the residuals as a function of the predicted variable and predictors of the model (*figure 1*). The residuals of the fixed model part are correlated within each

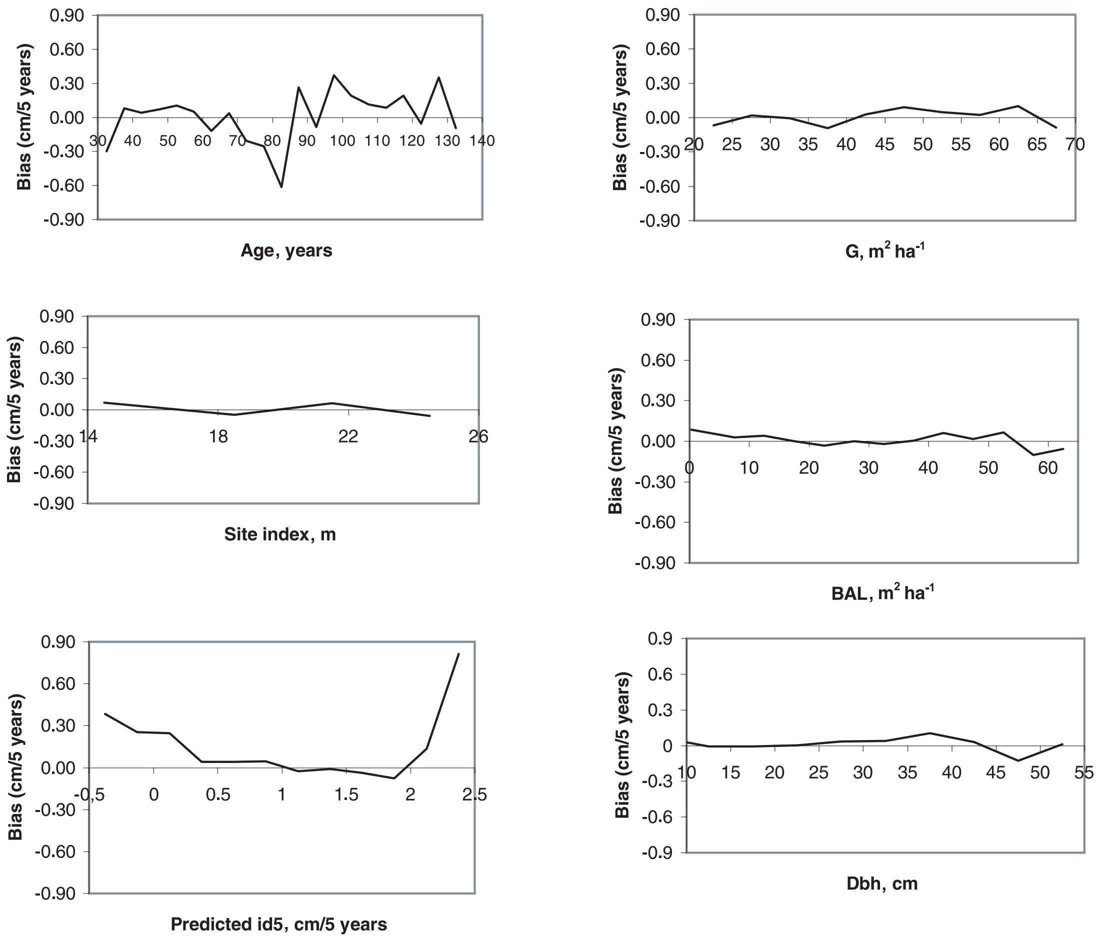

Figure 1. Mean residuals (bias) of the diameter growth model as a function of stand age, basal area, site index, competition index (*BAL*), predicted diameter growth and tree diameter.

Table III. Absolute and relative biases and RMSEs of the diameter growth model (Eq. (1)), height model (Eq. (2)) and self-thinning model (Eq. (3)).

Criteria	Diameter growth model (Eq. 1)	Height model (Eq. 2)	Self-thinning model (Eq. 3)
Bias	0.0124 cm $5yr^{-1}$	0.0153 m	4.30 trees ha^{-1}
Bias %	1.2	0.10	0.23
RMSE	0.6600 cm $5yr^{-1}$	1.2000 m	325 trees ha^{-1}
RMSE %	64.1	8.29	17.00

plot and tree (part of the residual variation is explained by random plot and tree factor). This should be taken into account when analysing *figure 1*. However, no obvious dependencies or patterns that indicate systematic trends between the residuals and the independent variable can be found. The bias showed a positive trend only when the predicted diameter growth exceeded 2 cm per 5-year-period (*figure 1*), but diameter growth greater than 2 cm is very rare. The relative RMSE value for the diameter growth model was 64.1%.

The estimated height model describes tree height as a function of diameter at breast height, age, dominant height and dominant diameter (Eq. (2)). Due to the form of equation (2), the height of a tree with dominant diameter is equal to the dominant height of the stand. Furthermore, when the age of the stand increases the height differences between dominant trees and the other trees in the stand are less pronounced. The estimated height model had a R^2 value of 0.89. The relative bias for the height model was 0.10% and the RMSE was 8.29% (*table III*). There were no obvious trends in the bias of the height model (*figure 2*).

3.2. Mortality models

The self-thinning model describes the relationship between the square mean diameter and number of trees per hectare in a stand (Eq. (3)). The R^2 value was 0.97, with an RMSE of 0.003 (*table III*). According to the model, the better the site the higher the stocking level of the stand with differences between sites being more pronounced in young stands (*figure 3*). The relative bias and RMSE value for the self-thinning model were 0.23 and 17%, respectively. Owing to the logarithmic transformation of the predicted variable, a correction factor $\sigma_{st}^2/2$ should be added to the constant of equation (3).

The probability of a tree in *P. sylvestris* stands to survive the next 5 years was estimated by two different models (Eqs. (4)

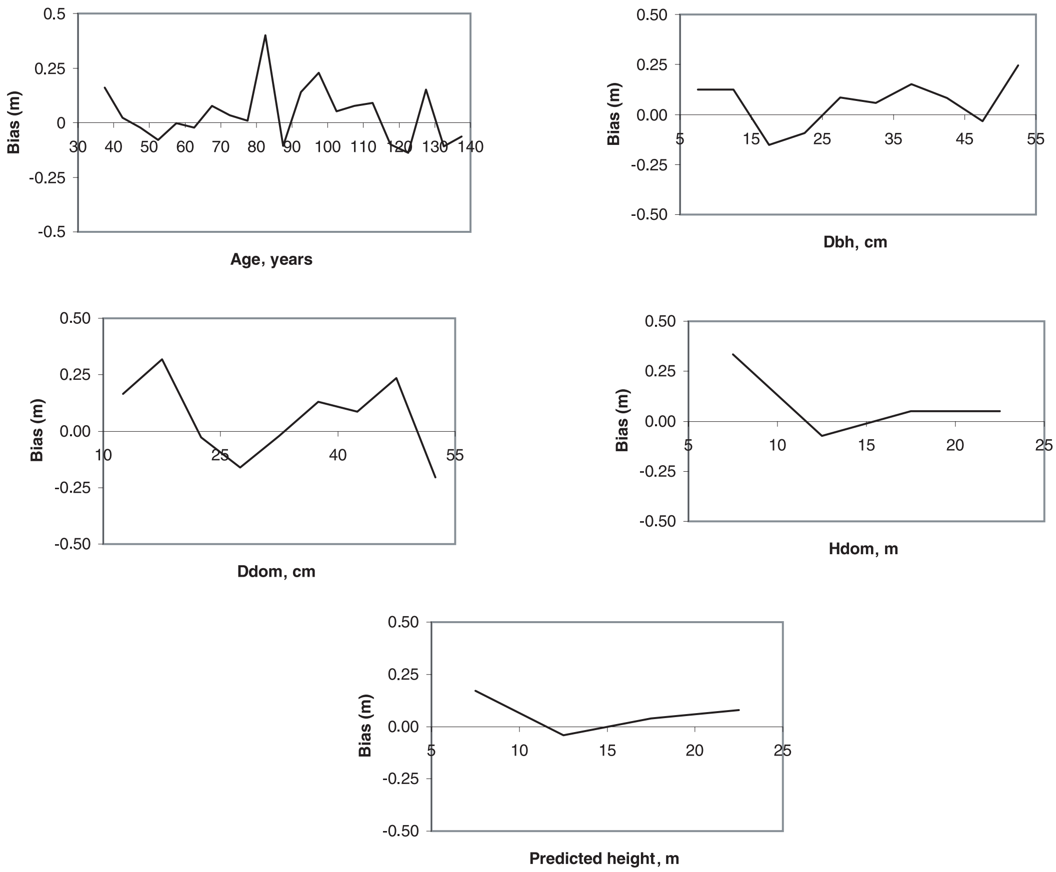

Figure 2. Mean residuals (bias) of the height model as a function of stand age, dominant height, dominant diameter, tree diameter and predicted tree height.

Table IV. Estimated parameters, their standard errors (S.E.), statistical significance and odds ratios for the logistic mortality models (Eqs. (4) and (5))[a].

Parameter	Estimate	S.E	Wald statistics	Significance	Odds ratio (exp(β))
Mortality model 1 (Eq. 4)					
β_0	3.954	0.286	190.821	0.000	-
β_1	–0.035	0.005	43.788	0.000	0.965
β_2	2.297	0.613	14.021	0.000	9.943
χ^2-value	94.039				
Mortality model 2 (Eq. 5)					
β_0	2.938	0.175	280.530	0.000	-
β_1	–0.020	0.005	15.010	0.000	0.980
β_2	2.719	0.139	382.350	0.000	15.160
χ^2-value	620.180				

[a] χ^2: Chi-square value.

and (5)) for two different situations. Equation 5 is used when information on the past 5-year diameter growth of the subject tree is available. Equation 4 is used when only average diameter growth is available for the subject tree. The probability of a tree surviving is best explained by its past diameter growth and its competition index (Eqs. (4) and (5), *table IV*). The Wald tests show that the parameter estimates of equations (4) and (5) are significant ($P < 0.05$) (*table IV*). By analysing equations (4) and (5) it can be deduced that the more suppressed the tree is (the greater the competition index), the smaller is the survival probability. The greater is the past diameter growth (average growth or past 5 years growth), the

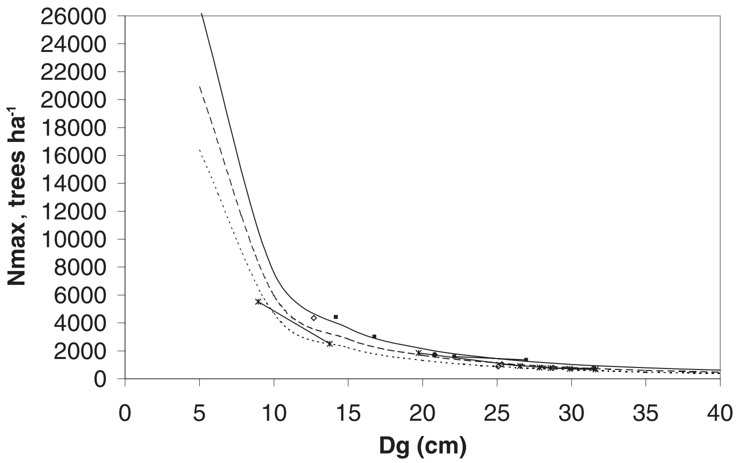

Figure 3. Actual and predicted maximum number of living trees per hectare as a function of mean square diameter (D) estimated using the self-thinning model (Eq. (3)). Each curve indicates the self-thinning limit for a different site. The points from the same plot are joined. Plots from the same site class have the same symbol.

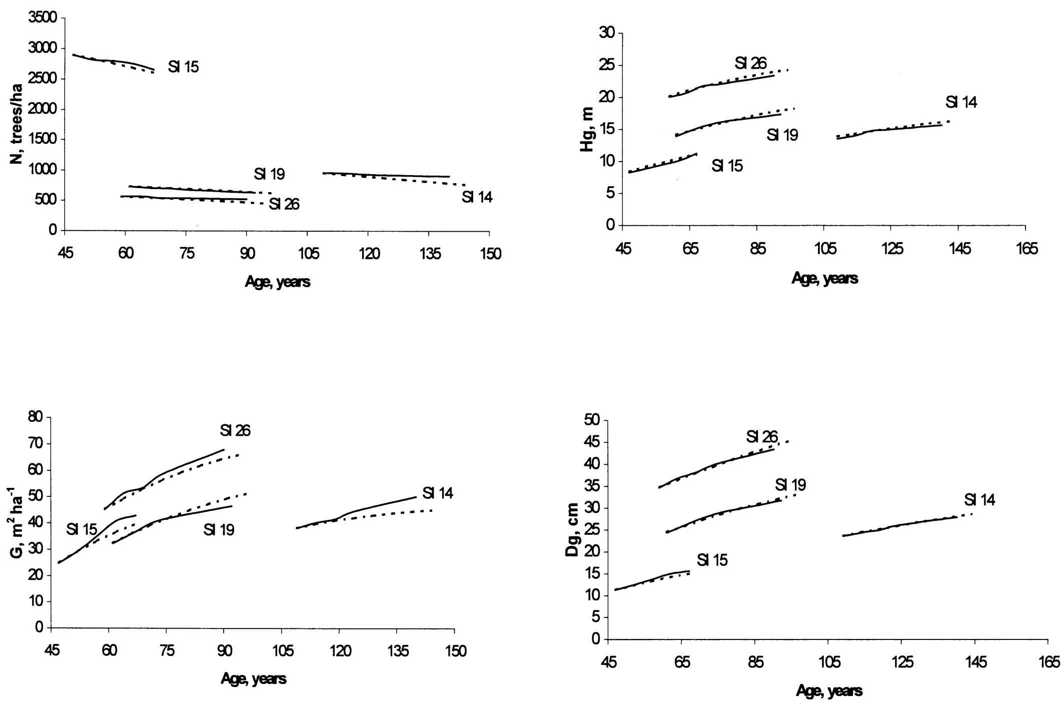

Figure 4. Measured and simulated stand development in four sample plots with site indexes 14, 15, 19 and 26 m at 100 years. The solid line is the measured development and the dashed line is the simulated development. N is number of trees per hectare; G is basal area; H_g is basal-area-weighted mean height and D_g is basal-area-weighted mean diameter.

greater is the probability of a tree surviving. The probability ratios of the covariates show that the past growth (Eq. (4)) and 5-year diameter growth (Eq. (5)) have the strongest relative effect on the probability of a tree surviving. With continuous variables, the probability ratio describes the change of probability per one unit change of covariate. This means for instance that the probability of survival becomes 15 times higher (Eq. (5)) with 1 cm increase in the past 5-year diameter growth.

3.3. Simulation results

Figure 4 shows examples of actual and simulated stand development for four stands with site indices 26, 19, 14 and 15 m at 100 years, respectively. The four selected plots cover the range of variation in site index and stand age among the plots used to develop the growth and mortality models. *Figure 4* shows that the model set developed in this study enables a very accurate long-term simulation of stand development for the four selected stands.

Figure 5 shows the measured and predicted changes of different stand variables for all plots in all the measurements. It is evident from these figures that there is no bias in the predictions by the model set. However, the predicted range of variation in the 5-year change in basal area, mean diameter and mean height is smaller than the observed change. This is mainly due to the fact that the diameter growth model explains

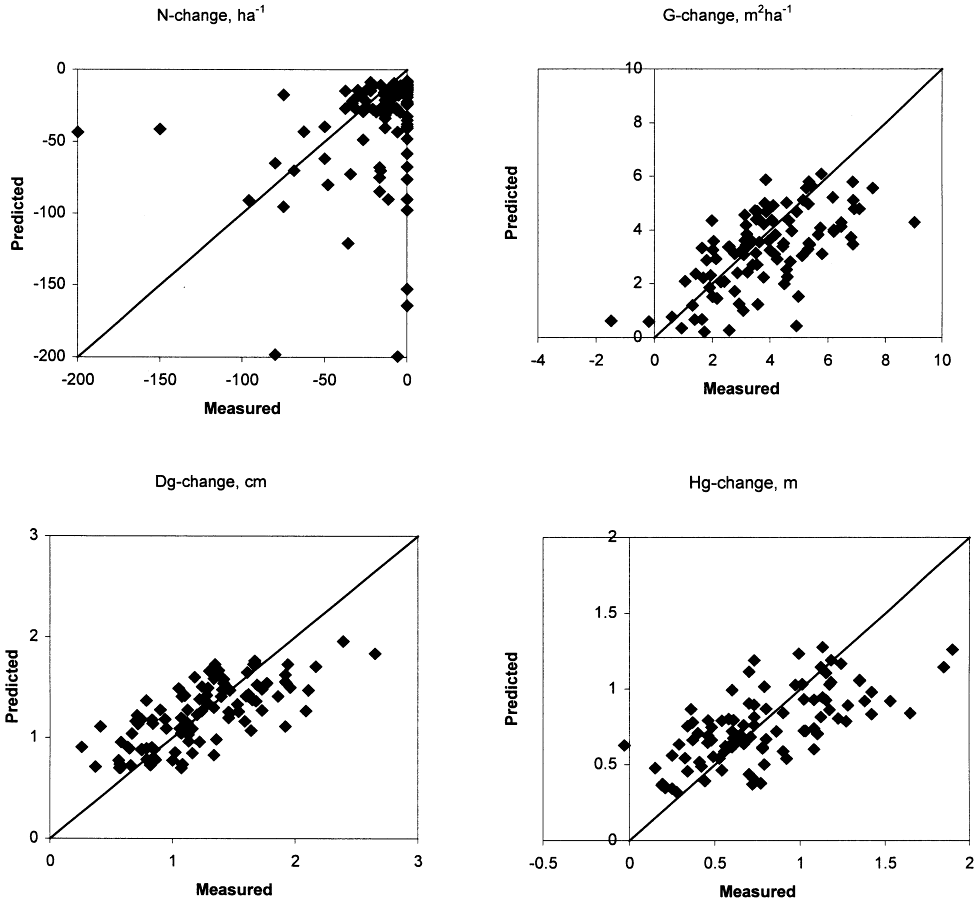

Figure 5. Measured and predicted 5-year changes of all plots for all measurement intervals. N is number of trees per hectare; G is basal area; H_g is basal-area-weighted mean height and D_g is basal-area-weighted mean diameter.

only part of the variation in diameter increment. It should also be noticed that the growth was simulated by using only the fixed part of equation (1).

4. DISCUSSION

This study presented individual-tree models for *P. sylvestris* stands in north-east Spain based on permanent sample plots measured an average of 5 times and ranging in site index from 14 to 26 m at 100 years. In fitting the models, both measured dominant height and site index were used as predictors. The site index model developed by Palahí et al. [19] can be used to obtain dominant height when applying the models in simulations. To predict mortality below the self-thinning limit, the logistic survival functions may be used. When the self-thinning limit is reached the logistic mortality functions may be used to select the dead trees (those trees with the lowest survival probability).

In this study the slope (–1.815) of the self-thinning line is different from the one given by Reineke [23] (–1.605), but it is very similar to the slope obtained for Scots pine by Rojo and Montero [26] in the Sistema Central (–1.836) and by Rio et al. [25] for stands in the Sistema Ibérico and Central (–1.829) in Spain. Hynynen [11] obtained for Scots pine in Finland a slope equal to –1.844. This reflects a rather constant value for this species in spite of changing environmental conditions. According to this study, the intercept of the self-thinning line was found to vary according to site index. This is in accordance with the results obtained by Hynynen [11] for Scots pine in Finland.

The data set in this study had limitations, which caused problems in the modelling work and that can affect the model predictions. The total number of plots available was only 24. However, a good feature of the data was that the development of plots was observed for a long time, up to 36 years. The data did not have a representation of very young stands (under 33 years) and there was not much data from stands beyond the normal rotation age (only 3 plots were measured at ages older than 100 years). In addition, human errors associated with diameter measurements were common. The breast height diameter may not have been measured at exactly the same height, and the direction of the diameter measurement may have been different. This resulted in low precision of the diameter increment observations, which are differences of two successive dbh measurements. This is reflected in the value of the coefficient of determination (0.24). The precision of the diameter growth predictions, therefore, needs to be viewed within the data constraints exposed above.

Height growth models could not be developed because there were not enough sample tree heights per plot measured more than once. The height model developed in this study is useful for predicting tree heights, for instance in inventory situations when the dominant height and tree diameters are measured, but all trees are not measured by height. The model predicts tree height accurately and, therefore, it can be used for growth simulation as well.

Examples of simulated stand development were used to demonstrate how the equations work together in long-term simulations. Simulation results were presented for four stands, which represent the range in site index (from 14 to 26 m at 100 years) of the data set. The system of equations developed in this study appeared to provide accurate predictions of stand development (*figure 4*). Therefore, the tree-level models reported in this study could confidently be used to predict the growth of different *P. sylvestris* stands on several sites in Spain.

This study is the first, known by the authors, on individual-tree growth models for Scots pine in Spain. Scots pine in Spain is a species of great economic, ecological and social importance and the models presented in this study can provide valuable information for further studies on optimising the management and evaluating alternative management regimes for the species.

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