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Original article

Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain

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Abstract – A distance-independent diameter growth model, a static height model, an ingrowth model and a survival model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia (north-east Spain) were developed. Separate models were developed for *P. sylvestris* and *P. nigra*. These models enable stand development to be simulated on an individual tree basis. The models are based on 922 permanent sample plots established in 1989 and 1990 and remeasured in 2000 and 2001 by the Spanish National Forest Inventory. The diameter growth models are based on 8058 and 5695 observations, the height models on 8173 and 5721 observations, the ingrowth models on 716 and 618 observations, and the survival models on 7823 and 5244 observations, respectively, for *P. sylvestris* and *P. nigra*. The relative biases for the height models are 6.7% for *P. sylvestris* and 3.3% for *P. nigra*. The biases for the diameter growth models are zero due to the applied Snowdon correction. The biases of the ingrowth models are zero due to the applied fitting method. The relative RMSE values for the *P. sylvestris* and *P. nigra* models, respectively, are 56.4% and 48.6% for diameter growth, 24.0% and 21.7% for height, and 224.3% and 257.3% for ingrowth.

growth and yield / mixed-species stand / uneven-aged stand / mixed models / simulation

Résumé – Modèle de croissance pour des peuplements irréguliers et mélangés de *Pinus sylvestris* L. et *Pinus nigra* Arn. en Catalogne (Nord-Est de l'Espagne). Un modèle non spatialisé de croissance en diamètre, un modèle statique de hauteur, un modèle de développement, et un modèle de survie pour des peuplements irréguliers et mélangés de *Pinus sylvestris* L. et *Pinus nigra* Arn. en Catalogne (Nord-Est de l'Espagne) ont été développés. Des modèles séparés ont été développés pour *P. sylvestris* et *P. nigra*. Cet ensemble de modèles permet de simuler le développement du peuplement au niveau de l'arbre individuel. Les modèles ont été étendus à partir de 922 placettes établies en 1989 et 1990 et remesurées en 2000 et 2001 par l'Inventaire Forestier National Espagnol. Les modèles de croissance en diamètre correspondent à 8058 et 5695 observations, les modèles de hauteur à 8173 et 5721 observations, les modèles de développement à 716 et 618 observations, et les modèles de survie à 7823 et 5244 observations, respectivement. Les biais relatifs pour les modèles de hauteur sont de 6,7 % pour *P. sylvestris* et 3,3 % pour *P. nigra*. Les biais pour les modèles de croissance en diamètre sont zéro en raison de l'appliqué correction de Snowdon. Les biais pour les modèles de développement sont zéro en raison de la méthode d'adaptation appliquée. Les valeurs relatives du RMSE pour les modèles de *P. sylvestris* et *P. nigra*, respectivement, sont de 56,4 % et 48,6 % pour la croissance en diamètre, 24,0 % et 21,7 % pour l'hauteur, et 224,3 % et 257,3 % pour le développement.

croissance et rendement / peuplement mélangé / peuplement irrégulier / modèles mixtes / simulation

1. INTRODUCTION

Pinus sylvestris L. and *Pinus nigra* Arn. ssp. *salmannii* var. *pyrenaica* mixtures form large forests in the *Montane-Mediterranean* vegetation zones of Catalonia (from 600 to 1600 m a.s.l.) [4, 32] occupying an area of 267 000 ha [12, 13]. Both species supply important products such as poles, saw logs and construction timber. The ecological (e.g. biodiversity maintenance, soil protection) and social (e.g. recreation, rural tourism, mushroom collection) functions of the pine mixtures are also significant. Most of the stands are managed using the selection system, which leads to considerable within-stand variation in tree age [11]. *P. sylvestris* is clearly a light demanding species, while *P. nigra* shows a moderate degree of shade tolerance [30], being more adaptable to irregular and multi-layered stand structures.

Management planning methods currently applied in Catalonia predict the yields of stands based on yield tables and increment borings. Yield tables are static models assuming that all stands are fully stocked, pure and even-aged. They do not portray the actual or historical development of individual stands [5]. Increment borings in inventory plots are used to develop simple compartment-wise models to express diameter growth

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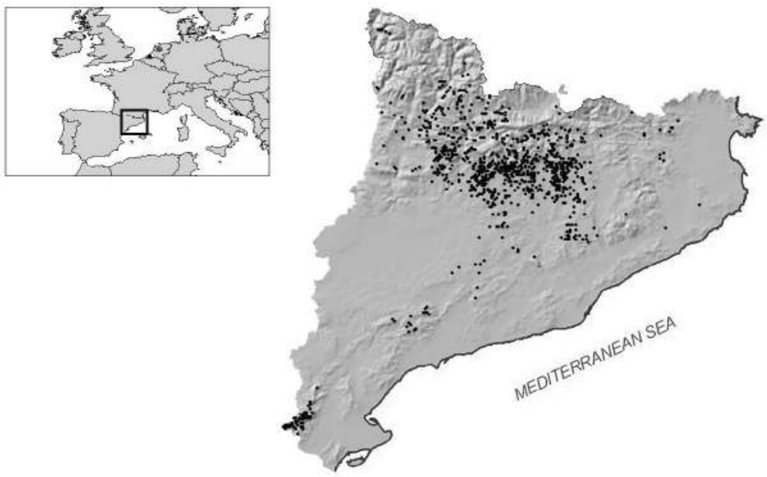

Figure 1. Geographical distribution of sample plots representing pure stands and mixtures of *P. sylvestris* and *P. nigra* in Catalonia.

as a function of diameter. These models cannot be used in long-term simulations. Forest management planning requires growth and yield models that provide a reliable way to examine the effects of silvicultural and harvesting options, to determine the yield of each option, and to inspect the impacts of forest management on the other values of the forest [38].

Growth and yield models can be classified into two major categories: whole stand and individual tree models. Whole stand models use stand parameters such as basal area, volume, and parameters characterising the underlying diameter distribution to simulate the stand growth and yield. Individual tree models use individual trees as the basic unit for simulating tree establishment, growth and mortality; stand level values are calculated by adding the individual tree estimates together [27]. The benefit of using individual-tree models is that the stand can be illustrated much more thoroughly and several treatments simulated more easily than with stand models [29]. Individual-tree models can be distance-dependent or distance-independent. The high cost of obtaining tree coordinates restricts the application of distance-dependent individual-tree models. The expense of such a detailed methodology is seldom warranted, making non-spatial models a more feasible alternative [38]. To date, the only empirical individual-tree growth and yield model available for the Catalan region is the non-spatial model for even-aged Scots pine stands in northeast Spain, developed by Palahí et al. [25].

Some variables such as dominant height, stand age and site index used in even-aged models are not directly applicable to uneven-aged stands [27]. The age of individual trees of an uneven-aged stand is often unknown, which means that neither stand nor tree age is a useful model predictor. An alternative to the use of these variables is to obtain site information from topographic descriptors such as elevation, slope, aspect, location descriptors (latitude), and soil type [2]. Examples of this type of models are PROGNOSIS [36, 39], designed for the Northern Rocky Mountains, PROGNAUS [22] developed for the Austrian forests, and the model developed by Schröder et al. [33] for maritime pine trees in northwestern Spain. An interesting feature of these models is that they may be applied to both uneven-aged and even-aged conditions. Another possibility to accommodate site in the model is to rely on the presence of plant species that indicate site fertility [3].

This study aims at developing a model set, which enables tree-level distance-independent simulation of the development of uneven-aged mixtures of *P. sylvestris* and *P. nigra* in Catalonia. The system consists of a diameter growth model, a static height model, an ingrowth model and a survival model for the coming 10-year period. Separate models are developed for *P. sylvestris* and *P. nigra*. The predictor variables have been restricted to site, stand and tree attributes that can be reliably obtained from stand inventories normally carried out in the region. The model set should apply to any age structure and degree of mixture (including pure stands) of the two pine species.

2. MATERIALS AND METHODS

2.1. Data

The data were provided by the Spanish National Forest Inventory [6, 16–19]. This inventory consists of a systematic sample of permanent plots distributed on a square grid of 1 km, with a 10-year remeasurement interval. From the inventory plots over the whole of Catalonia, 922 plots representing all degrees of mixture (including pure stands) between *P. sylvestris* and *P. nigra* were selected (Fig. 1). The criterion for plot selection was that the occupation of one (pure stands) or two (mixed stands) of the studied species in the stands should be at least 90%. Most of the stands were naturally regenerated. The sample plots were established in 1989 and 1990. The remeasurement was carried out in 2000 and 2001.

A hidden plot design was used: plot centres were marked by an iron stake buried underground; the iron stake was relocated by a metal detector. Trees were recorded by their polar coordinates and marked only temporarily during the measurements. The sampling method used circular plots in which the plot radius depended on the tree's diameter at breast height (dbh, 1.3 m) (Tab. I). At each measurement, the following data were recorded from every sample tree: species, dbh, total height, and distance and azimuth from the plot centre.

In the second measurement, a tree previously measured in the first measurement was identified as: standing, dead or thinned. Trees that entered the first dbh-class (from 7.5 to 12.4 cm) during the growth period were also recorded. The standing and dead trees resulted in 8173 diameter/

Table I. Plot radius for different classes of tree dbh.

dbh	Plot radius, m
75 ≤dbh < 125 mm	5
125 ≤dbh < 225 mm	10
225 ≤dbh < 425 mm	15
dbh ≥ 425 mm	25

height and 8058 diameter growth observations for *P. sylvestris* (Tab. II), and 5721 diameter/height and 5695 diameter growth observations for *P. nigra* (Tab. III). There were also 721 diameter/height and 717 diameter growth observations for other species, referred to as accompanying species. Because it was not known whether a tree removed in thinning was living or dead, the thinned trees were not used as observations. At each measurement the growing stock characteristics were computed from the individual-tree measurements of the plots.

2.2. Diameter increment modelling

A diameter growth model was prepared for both pine species. The predicted variable in the diameter growth models was the logarithmic transformation of 10-year diameter growth. This resulted in a linear relationship between the dependent and independent variables, and enabled the development of multiplicative growth models [9, 15, 21, 22, 33, 39]. Ten-year diameter growth was calculated as a difference between the two existing diameter measurements (years 1989–1990 and 2000–2001). The growth observations (10 to 12 year growth) were converted into 10-year growths by dividing the diameter increment by the time interval between the two measurements and multiplying the result by 10. The predictors were chosen from tree, stand and site characteristics as well as their transformations. All predictors had to be significant at the 0.05 level, and the residuals had to indicate a non-biased model. Due to the hierarchical structure of the data (trees are grouped into plots, and plots are grouped into provinces), the generalised least-squares (GLS) technique was applied to fit the mixed linear models. The residual variation was therefore divided

Table II. Mean, standard deviation (S.D.) and range of the main characteristics in the study material related to *P. sylvestris.*

Variable[a]	N	Mean	S.D.	Minimum	Maximum
Diameter growth model (Eq. (1))					
id10 (cm/10 a)	8058	2.6	1.6	0.1	12.4
dbh (cm)	8058	20.8	8.5	7.5	76.1
BALsyl (m^2 ha^{-1})	8058	10.2	8.9	0	50.0
BALnig+acc (m^2 ha^{-1})	8058	1.7	3.3	0	38.9
BALthin (m^2 ha^{-1})	8058	0.9	2.8	0	35.0
G (m^2 ha^{-1})	645	23.2	11.2	1.3	55.1
Diameter growth plot factor models (Eq. (3)),					
u_{lk} (ln (cm/10 a))	645	–1.3E–06	0.32	–1.39	0.92
ELE (100 m)	645	9.9	3.4	2	19
SLO (%)	645	35.9	9.3	7.5	41.6
Height model (Eq. (5))					
h (m)	8173	12.3	3.5	2.9	26.5
dbh (cm)	8173	23.8	8.7	7.7	77.7
Height plot factor models (Eq. (6))					
u_{lk} (m)	646	2.7E–03	2.26	–5.03	8.72
ELE (100 m)	646	9.9	3.4	2	19
LAT (100 km)	646	46.54	0.44	45.10	47.36
CON (km)	646	86.4	32.0	15.3	186.6
Ingrowth model (Eq. (8))					
ING (trees ha^{-1})	716	64.7	134.2	0	1018.6
G (m^2 ha^{-1})	716	17.4	9.8	1.3	55.1
Gsyl (m^2 ha^{-1})	716	11.2	10.1	0.4	50.9
Ingrowth trees mean dbh model (Eq. (10))					
DIN (cm)	199	9.1	1.0	7.6	11.7
G (m^2 ha^{-1})	199	15.6	8.8	1.6	47.2
ELE (100 m)	199	10.4	3.4	3	18
Survival models (Eq. (12))					
P (*survive*)	7823	0.96	0.19	0.0	1.0
dbh (cm)	7823	20.8	8.7	7.5	76.4
h (m)	7823	10.5	3.4	3	25
BALall (m^2 ha^{-1})	7823	11.9	9.5	0	53.7
ELE (100 m)	544	11.1	3.3	2	19
CON (km)	544	94.3	33.1	15.3	186.6

[a] *N*: number of observations at tree- and stand-level; *id10*: 10-year diameter increment; *dbh*: diameter at breast height; *BALsyl*: competition index of *P. sylvestris*; *BALnig+acc*: competition index of *P. nigra* and accompanying species; *BALthin*: 10-year thinned competition; *G*: stand basal area; *h*: tree height; u_{lk}: random between-plot factor; *ELE*: elevation; *SLO*: slope; *LAT*: latitude; *CON*: continentality; *ING*: stand ingrowth; *Gsyl*: stand basal area of *P. sylvestris*; *DIN*: mean dbh of ingrowth trees; *P* (*survive*): probability of a tree surviving; *BALall*: competition index calculated from all species.

Table III. Mean, standard deviation (S.D.) and range of the main characteristics in the study material related to *P. nigra*.

Variable[a]	N	Mean	S.D.	Minimum	Maximum
Diameter growth model (Eq. (2))					
id10 (cm/10 a)	5695	2.8	1.5	0.1	12.8
dbh (cm)	5695	18.9	8.0	7.5	73.8
BALnig (m^2 ha^{-1})	5695	8.3	7.6	0	53.9
BALsyl+acc (m^2 ha^{-1})	5695	2.0	3.8	0	44.7
BALthin (m^2 ha^{-1})	5695	1.4	3.2	0	38.2
Diameter growth plot factor models (Eq. (4))					
u_{lk} (ln (cm/10 a))	526	5.7E–07	0.30	–1.21	0.72
ELE (100 m)	526	8.1	2.7	2	15
SLO (%)	526	35.1	10.2	1.5	41.6
LAT (100 km)	526	46.42	0.45	45.10	47.07
CON (km)	526	80.7	29.2	15.3	146.2
Height model (Eq. (5))					
h (m)	5721	11.6	3.4	2.1	31.0
dbh (cm)	5721	21.9	8.4	7.8	81.5
Height plot factor models (Eq. (7))					
u_{lk} (m)	528	–3.8E–03	2.19	–6.95	10.34
ELE (100 m)	528	8.1	2.7	2	15
LAT (100 km)	528	46.42	0.45	45.10	47.07
CON (km)	528	80.7	29.2	15.3	146.2
Ingrowth model (Eq. (9))					
ING (trees ha^{-1})	618	69.8	154.9	0	1273.2
G (m^2 ha^{-1})	618	16.4	9.2	1.3	59.4
Gnig (m^2 ha^{-1})	618	10.5	8.5	0.5	59.4
ELE (100 m)	618	7.8	2.6	2	15
CON (km)	618	79.4	27.3	15.3	146.2
Ingrowth trees' mean dbh model (Eq. (11))					
DIN (cm)	169	9.1	0.9	7.5	12.1
G (m^2 ha^{-1})	169	14.4	7.6	1.3	39.7
Survival models (Eq. (13))					
P (*survive*)	5244	0.98	0.10	0	1
dbh (cm)	5244	18.8	8.2	7.5	73.8
BALall (m^2 ha^{-1})	5244	10.0	8.1	0	50.7
G (m^2 ha^{-1})	425	20.1	9.6	1.3	55.1
CON (km)	425	84.3	27.1	15.3	146.2

[a] *N*: number of observations at tree- or stand-level; *id10*: 10-year diameter increment; *dbh*: diameter at breast height; *BALnig*: competition index of *P. nigra*; *BALsyl+acc*: competition index of *P. sylvestris* and accompanying species; *BALthin*: 10-year thinned competition; *G*: stand basal area; *h*: tree height; u_{lk}: random between-plot factor; *ELE*: elevation; *SLO*: slope; *LAT*: latitude; *CON*: continentality; *ING*: stand ingrowth; *Gnig*: stand basal area of *P. nigra*; *DIN*: mean dbh of ingrowth trees; *P* (*survive*): probability of a tree surviving; *BALall*: competition index calculated from all species.

into between-province, between-plot and between-tree components. The linear models were estimated using the maximum likelihood procedure of the computer software PROC MIXED in SAS/STAT [31].

The *P. sylvestris* (Eq. (1)) and *P. nigra* (Eq. (2)) diameter growth models were as follows:

$$\ln(id10_{lkt}) = \beta_0 + \beta_1 \times \frac{1}{dbh_{lkt}} + \beta_2 \times \ln(dbh_{lkt}) + \beta_3 \times \frac{BALsyl_{lk}}{\ln(dbh_{lkt}+1)} + \beta_4 \times \frac{BALnig+acc_{lk}}{\ln(dbh_{lkt}+1)} + \beta_5 \times \frac{BALthin_{lk}}{\ln(dbh_{lkt}+1)} + \beta_6 \times \ln(G_{lk}) + u_l + u_{lk} + e_{lkt} \quad (1)$$

$$\ln(id10_{lkt}) = \beta_0 + \beta_1 \times \frac{1}{dbh_{lkt}} + \beta_2 \times \ln(dbh_{lkt}) + \beta_3 \times \frac{BALnig_{lk}}{\ln(dbh_{lkt}+1)} + \beta_4 \times \frac{BALsyl+acc_{lk}}{\ln(dbh_{lkt}+1)} + \beta_5 \times \frac{BALthin_{lk}}{\ln(dbh_{lkt}+1)} + u_l + u_{lk} + e_{lkt} \quad (2)$$

where *id10* is future diameter growth (cm in 10 years); *dbh* is diameter at breast height (cm), *BALsyl* is the total basal area of *P. sylvestris* trees larger than the subject tree (m^2 ha^{-1}); *BALnig + acc* is the total basal area of trees that are not *P. sylvestris* and are larger than the subject tree (m^2 ha^{-1}); *BALnig* is the total basal area of *P. nigra* trees larger than the subject tree (m^2 ha^{-1}); *BALsyl + acc* is the total basal area of trees other than *P. nigra* and larger than the subject tree (m^2 ha^{-1});

BALthin is the total basal area of trees larger than the subject tree and thinned during the next 10-year period (m^2 ha^{-1}); and *G* is stand basal area (m^2 ha^{-1}). Subscripts *l*, *k* and *t* refer to province *l*, plot *k*, and tree *t*, respectively. u_l, u_{lk} and e_{lkt} are independent and identically distributed random between-province, between-plot and between-tree factors with a mean of 0 and constant variances of σ^2_{prov}, σ^2_{pl}, and σ^2_{tr}, respectively. These variances and the parameters β_i were estimated using the GLS method. At first, all three random factors were included in the model but the between-province factor was not significant, and it was therefore excluded from the models.

The random plot factors (u_{lk}) of the models (Eqs. (1) and (2)) correlated logically with the site factors. In order to include the site effects in the simulations, linear models predicting the random plot factors were developed using the ordinary least squares (OLS) technique in SPSS [35] . The models for the random plot factor of *P. sylvestris* (Eq. (3)) and *P. nigra* (Eq. (4)) were as follows:

$$u_{lk} = \beta_0 + \beta_1 \times ELE_{lk} + \beta_2 \times (ELE_{lk})^2 + \beta_3 \times SLO_{lk} + e_{lk} \quad (3)$$

$$u_{lk} = \beta_0 + \beta_1 \times \ln(ELE_{lk}) + \beta_2 \times SLO_{lk} + \beta_3 \times CON_{lk} + \beta_4 \times LAT_{lk} + e_{lk} \quad (4)$$

where u_{lk} is plot factor predicted by equations (1) or (2); *ELE* is elevation (100 m); *SLO* is slope (%); *CON* is continentality (linear distance to the Mediterranean Sea, km); *LAT* is latitude (y UTM coordinate, 100 km). In simulations, the random plot factor (u_{lk} in Eqs. (1) or (2)) may be replaced by its prediction (Eqs. (3) or (4)). Other site characteristics and their transformations adopted logical signs, namely aspect, soil texture, and humus, but were not significant. Another version of the plot factor models was prepared using the presence of certain plant species in the stand as dummy variables (referred to as species dummies), in addition to variables listed in equations (3) and (4).

To convert the logarithmic predictions of equations (1) and (2) to the arithmetic scale, a multiplicative correction factor suggested by Baskerville [1] was tested ($\exp(s^2/2)$), where s^2 is the total residual variance of the logarithmic regression). However, it resulted in biased back-transformed predictions. Therefore, an empirical ratio estimator for bias correction in logarithmic regression was applied to equations (1) and (2). As suggested by Snowdon [34], the proportional bias in logarithmic regression was estimated from the ratio of the mean diameter growth $\overline{id10}$ and the mean of the back-transformed predicted values from the regression $\overline{\exp[\ln \hat{id}\,10]}$. The ratio estimator was therefore $\overline{id10} / \overline{\exp[\ln \hat{id}\,10]}$.

2.3. Height modelling

Analysis of the height data revealed that there were obvious and large errors in the height measurements of the first measurement occasion. Therefore, height growth models could not be estimated. Consequently, static height models using the second measurement were developed. Models that enable the estimation of total tree heights when only tree diameters and site characteristics are measured (as is the case in forest inventory) were estimated.

Elfving and Kiviste [8] proposed 13 functions having a zero point, being monotonously increasing and having one inflexion point, for approximation of the relationship between stand age and height. These functions were tested as the height model, but dbh was used instead of age as the predictor. A total of 10 two- and three-parameter functions were tested. The models developed by Hossfeld [28] and Verhulst [14] gave the best fit. Out of this these, Hossfeld model (Eq. (5)) was selected because it has been used earlier in Spain [24, 26]. The non-linear height models were estimated using the non-linear mixed procedure (NLMIXED) in SAS/STAT [31]. In the procedure, it is possible to include only two random factors in the model. Because the random between-plot factor was more significant than the random between-province factor, the plot factor was included in the model. The non-linear height models for *P. sylvestris* and *P. nigra* were as follows:

$$h_{lkt} = \frac{\beta_1}{(1 + \beta_2 / \; dbh_{lkt} + \beta_3 \,/\, dbh^2_{lkt})} + u_{lk} + e_{lkt} \quad (5)$$

where *h* is tree height (m); *dbh* diameter at breast height (cm); β_1, β_2, β_3 are parameters. The random plot factors u_{lk} were modelled as a function of site variables. The models for the random plot factor for *P. sylvestris* (Eq. (6)) and *P. nigra* (Eq. (7)) were developed using the ordinary least squares (OLS) technique in SPSS [35]:

$$u_{lk} = \beta_0 + \beta_1 \times ELE_{lk} + \beta_2 \times LAT_{lk} + \beta_3 \times CON_{lk} + \beta_4 \times \ln(CON_{lk}) + \beta_5 \times (CON_{lk})^2 + e_{lk} \quad (6)$$

$$u_{lk} = \beta_0 + \beta_1 \times ELE_{lk} + \beta_2 \times LAT_{lk} + \beta_3 \times (CON_{lk})^2 + \beta_4 \times \frac{1}{CON_{lk}} + e_{lk} \quad (7)$$

where u_{lk} is random plot factor of the related height model. Other site characteristics and their transformations such as aspect, slope and soil texture were not significant in the final version of the models. Another version of the models was prepared using species dummies as additional predictors.

2.4. Ingrowth modelling

A linear model predicting the number of trees per hectare entering the first dbh-class (from 7.5 to 12.4 cm) during a 10-year growth period was prepared for each species. The predictors were chosen from stand and site characteristics and their transformations. Mixed linear models were estimated first, but the random between-province factor was not significant. Thus, ingrowth models for *P. sylvestris* (Eq. (8)) and *P. nigra* (Eq. (9)) were estimated using the ordinary least squares (OLS) method in SPSS [35]:

$$ING_{lk} = \beta_0 + \beta_1 \times G_{lk} + \beta_2 \times \frac{1}{G_{lk}} + \beta_3 \times \frac{Gsyl_{lk}}{G_{lk}} + e_{lk} \quad (8)$$

$$ING_{lk} = \beta_0 + \beta_1 \times G_{lk} + \beta_2 \times \frac{Gnig_{lk}}{G_{lk}} + \beta_3 \times \frac{CON_{lk}}{ELE_{lk}} + e_{lk} \quad (9)$$

where *ING* is ingrowth (number of trees ha^{-1}) at the end of a 10-year growth period; *Gsyl* and *Gnig* are stand basal area of *P. sylvestris* and *P. nigra*, respectively (m^2 ha^{-1}). The mean dbh of the ingrowth trees of *P. sylvestris* (Eq. (10)) and *P. nigra* (Eq. (11)) was modelled as well. The models were estimated using the ordinary least squares (OLS) method:

$$DIN_{lk} = \beta_0 + \beta_1 \times G_{lk} + \beta_2 \times ELE_{lk} + e_{lk} \quad (10)$$

$$DIN_{lk} = \beta_0 + \beta_1 \times G_{lk} + e_{lk} \quad (11)$$

where *DIN* is the mean dhh of ingrowth trees (cm) at the end of a 10-year growth period. Another version of the models using species dummies as predictors for the number and mean dbh of ingrowth was also evaluated.

2.5. Survival modelling

When analysing the data, two types of mortality were identified: density-independent mortality and density-dependent. The density-independent tree-level survival rate for a 10-year period was estimated at 0.962 overall. All mortality of plots having basal area values at the second measurement lower than 1 m^2 ha^{-1} or lower than 90% of the stand basal area at the first measurement were considered as density-independent (usually caused by fire).

A model for the density-dependent probability of a tree to survive for the next 10-year growth period was estimated from the remaining sample plots. The following survival models for *P. sylvestris*

$$P(survive)_{lkt} = \frac{1}{1 + \exp\left(-\left(\beta_0 + \beta_1 \times \frac{BAL_{lkt}}{\ln(dbh_{lkt}+1)} + \beta_2 \times h_{lkt} + \beta_3 \times ELE_{lk} + \beta_4 \times CON_{lk}\right)\right)} + e_{lkt} \quad (12)$$

$$P(survive)_{lkt} = \frac{1}{1 + \exp\left(-\left(\beta_0 + \beta_1 \times \frac{BAL_{lkt}}{\ln(dbh_{lkt}+1)} + \beta_2 \times G_{lk} + \beta_3 \times ELE_{lk}\right)\right)} + e_{lkt} \quad (13)$$

(Eq. (12)) and *P. nigra* (Eq. (13)) were estimated using the Binary Logistic procedure in SPSS [35].

See equations (12) and (13) above

where *P*(*survive*) is the probability of a tree surviving for the next 10-year growth period. Another version of the models was developed using the presence of particular plant species as a site fertility indicator.

2.6. Model evaluation

2.6.1. Fitting statistics

The models were evaluated quantitatively by examining the magnitude and distribution of residuals for all possible combinations of variables included in the model. The aim was to detect any obvious dependencies or patterns that indicate systematic discrepancies. To determine the accuracy of model predictions, the bias and precision of the models were calculated [10, 21, 25, 38]. The absolute and relative biases and the root mean square error (RMSE) were calculated as follows:

$$bias = \frac{\sum (y_i - \hat{y}_i)}{n} \quad (14)$$

$$bias\% = 100 \times \frac{\sum (y_i - \hat{y}_i) / n}{\sum \hat{y}_i / n} \quad (15)$$

$$RMSE = \sqrt{\frac{\sum (y_i - \hat{y}_i)^2}{n-1}} \quad (16)$$

$$RMSE\% = 100 \times \sqrt{\frac{\sum (y_i - \hat{y}_i)^2 / (n-1)}{\sum \hat{y}_i / n}} \quad (17)$$

$$R^2 = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2} \quad (18)$$

where n is the number of observations; and y_i and $\hat{y}_i$ are observed and predicted values, respectively. In the models that included a random plot factor, the predicted value ($\hat{y}_i$) was calculated using a model prediction of the plot factor.

2.6.2. Simulations

In addition, the models were further evaluated by graphical comparisons between measured and simulated stand development. The simulated 10-year change in stand basal area of the inventory plots was compared to the measured change. The dynamics of accompanying species, present in several plots, was simulated using equations shown in the Appendix. The simulation of a 10-year time step consisted of the following steps:

1. For each tree, add the 10-year diameter increment (Eqs. (1) and (2)) using the predicted plot factor (Eqs. (3) and (4)) to the diameter.

2. Multiply the frequency of each tree (number of trees per hectare that a tree represents) by the density-dependent 10-year survival probability. The density-dependent probability is provided by equations (12) and (13).

3. Calculate the number of trees per hectare (Eqs. (8) or (9)) that enter the first dbh-class and the mean dbh of ingrowth (Eqs. (10) or (11)) at the end of a 10-year growth period.

4. Calculate tree heights using equation (5), and the predicted plot factor provided by equations (6) or (7).

In addition, the development of two plots – one representing a mixed *P. sylvestris* and *P. nigra* stand and another representing a pure stand of *P. sylvestris* – was simulated at different elevations to evaluate the model set in long-term simulation.

3. RESULTS

3.1. Diameter growth models

Parameter estimates of the diameter growth models (Eqs. (1) and (2)) were logical and significant at the 0.001 level (Tab. IV). Parameter estimates of the plot factor models were significant at the 0.05 level. The R^2 values were 0.13 and 0.14 for the *P. sylvestris* and *P. nigra* diameter growth models, respectively. The R^2 value of the random plot factor model was 0.06 for *P. sylvestris* and 0.10 for *P. nigra*, showing that only a small part of the variation in plot factor was explained by site characteristics. The explained variation was higher when species dummies were used, resulting in R^2 values of 0.11 for *P. sylvestris* and 0.18 for *P. nigra*.

The R^2 values of predictions using both the diameter growth and plot factor models (Eq. (18)) were 0.16 for *P. sylvestris* and 0.18 for *P. nigra*. When using species dummies in the plot factor models, these values were 0.18 for *P. sylvestris* and 0.21 for *P. nigra*.

The shape of the relationship between dbh and diameter growth is typical of tree growth processes ([39], Fig. 2). Diameter increment of dominant trees ($BAL_x = 0$) increases to a maximum at dbh of 17 cm and then slowly decreases, approaching zero asymptotically as the tree matures (Eqs. (1) and (2)). Increasing competition (*G*, *BALsyl* and *BALnig* + *acc* in Eq. (1)*; BALnig* and *BALsyl* + *acc* in Eq. (2)) decreases the diameter growth. The models indicate that *P. nigra* causes more competition because the coefficients of competition calculated from *P. nigra* trees (β_4 in Eq. (1) and β_3 in Eq. (2)) always had higher absolute values than BAL computed from *P. sylvestris* (β_3 in Eq. (1) and β_4 in Eq. (2)).

The thinned competition (*BALthin*) had a positive effect on diameter growth (Eqs. (1) and (2)) (Fig. 3). This variable improved the fit and logical behavior of the other predictors in the models, although the variable is seldom used when the models are applied in simulation (i.e. this variable is given a zero value). Increasing slope decreased the plot factor and consequently the diameter growth of all trees on a plot (Eqs. (3) and (4)). According to the models, elevation affects differently the two studied species: higher growth rates of *P. sylvestris* are observed at extreme elevations (Fig. 4)*,* while

Table IV. Estimates of the parameters and variance components of the *P. sylvestris* and *P. nigra* diameter growth models (Eqs. (1) and (2)) and the corresponding plot factor models (Eqs. (3) and (4))[a,b].

Parameter	*P. sylvestris*			*P. nigra*		
	Diameter growth model (Eq. (1))	Plot factor model without sp. dummies (Eq. (3))	Plot factor model with sp. dummies (Eq. (3))	Diameter growth model (Eq. (2))	Plot factor model without sp. dummies (Eq. (4))	Plot factor model with sp. dummies (Eq. (4))
β_0	5.5117	0.5180	0.5005	5.0363	–16.3119	–14.7547
	(0.3304)	(0.1065)	(0.1059)	(0.3324)	(2.5990)	(2.5225)
β_1	–15.1681	–0.0936	–0.1005	–15.4677	0.1602	0.1218
	(1.3670)	(0.0198)	(0.0195)	(1.3352)	(0.0470)	(0.0487)
β_2	–1.0376	0.0048	0.0051	–1.0055	–0.0036	–0.0050
	(0.0877)	(0.0009)	(0.0009)	(0.0881)	(0.0013)	(0.0012)
β_3	–0.0649	–0.0033	–0.0030	–0.0962	–0.0061	–0.0057
	(0.0045)	(0.0013)	(0.0013)	(0.0051)	(0.0009)	(0.0009)
β_4	–0.1081	–	–	–0.0673	0.3576	0.3283
	(0.0102)			(0.0083)	(0.0561)	(0.0546)
β_5	0.0749	–	–	0.0621	–	–
	(0.0144)			(0.0143)		
β_6	–0.2031	–	–	–	–	–
	(0.0323)					
ROS	–	–	0.1317	–	–	–
			(0.0252)			
JPH	–	–	–0.1328	–	–	–
			(0.0516)			
ROM	–	–	–	–	–	–0.1244
						(0.0302)
CRA	–	–	–	–	–	0.0996
						(0.0311)
JUN	–	–	–	–	–	–0.0989
						(0.0331)
σ^2_{pl}	0.1449	0.0987	0.0937	0.1263	0.0840	0.0776
σ^2_{tr}	0.3747	–	–	0.2671	–	–
RMSE	0.7208	0.3141	0.3061	0.6272	0.2898	0.2786
R^2	0.13	0.06	0.11	0.14	0.10	0.18

[a] S.E. of estimates are given in parenthesis. [b] ROS is *Rosa* spp., JPH is *Juniperus phoenicea*, ROM is *Rosmarinus officinalis*, CRA is *Crataegus* sp., JUN is *Juniperus communis*.

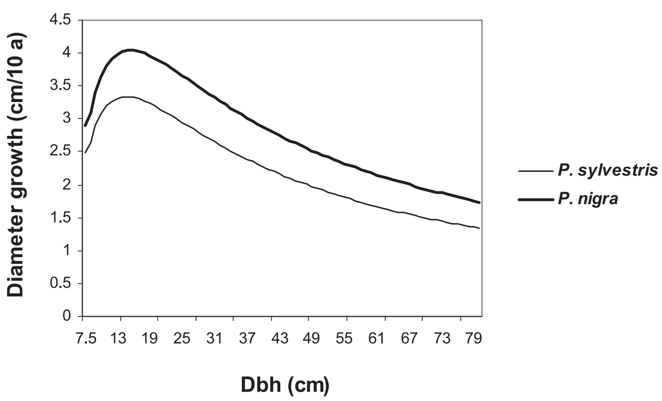

Figure 2. Diameter increment of *P. sylvestris* (Eqs. (1) and (3)) and *P. nigra* (Eqs. (2) and (4)) as a function of *dbh*. Used predictor values: *BALsyl* = 0, *BALnig* = 0, *BALnig+acc* = 0, *BALsyl + acc* = 0, *BALthin* = 0, G = 25 m^2 ha^{-1}, *SLO* = 35%, *ELE* = 800 m, *LAT* = 46.42 × 10^2 km, *CON* = 80 km.

increasing elevation increases the growth of a *P. nigra* tree. The signs of coefficients of the plot factor model of *P. nigra* were logical, bearing in mind the climatic models (predicting mean extreme temperatures and precipitation) developed by Ninyerola et al. [23] for the Catalan region: increasing continentality decreases the growth of a tree, and the more northern the latitude the higher is the stand growth (Fig. 5).

The ratio estimators for bias correction in the fixed part of the *P. sylvestris* and *P. nigra* diameter growth models (Eqs. (1) and (2)) were 2.6324/2.1288 = 1.2365 and 2.7981/2.5352 = 1.1037, respectively. The ratio estimators for bias correction using both the fixed part and the predicted plot factors (Eqs. (1), (2), (3) and (4)) were 2.6324/2.1389 = 1.2307 for *P. sylvestris* and 2.7981/2.5639 = 1.0914 for *P. nigra*. When using species dummies in the plot factor models, the ratio estimators were 2.6324/2.1453 = 1.2270 for *P. sylvestris* and 2.7981/2.4847 = 1.1261 for *P. nigra*.

The bias of the growth models, when the fixed model part and the plot factor models without species dummies were used, showed no trends when displayed as a function of predictors or predicted growth in Figures 6 and 7. The residuals

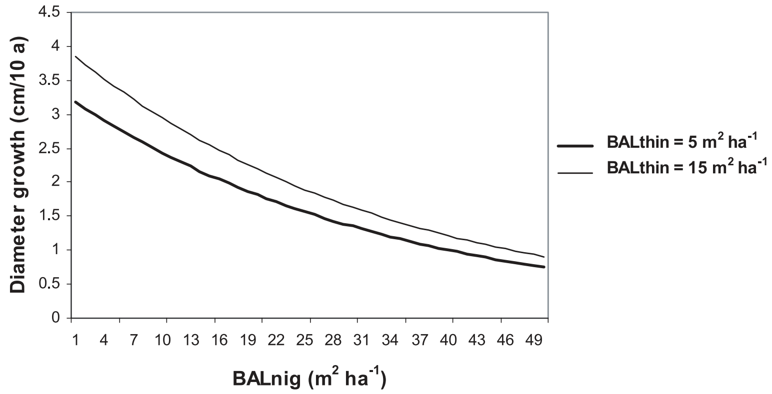

Figure 3. Diameter increment of *P. nigra* (Eqs. (2) and (4)) as a function of remaining and removed competition (*BALnig*, by *BALthin*). Used predictor values: *dbh* = 25 cm, *BALsyl + acc* = 10 m^2 ha^{-1}, *SLO* = 35%, *ELE* = 800 m, *LAT* = 46.42 × 10^2 km, *CON* = 80 km.

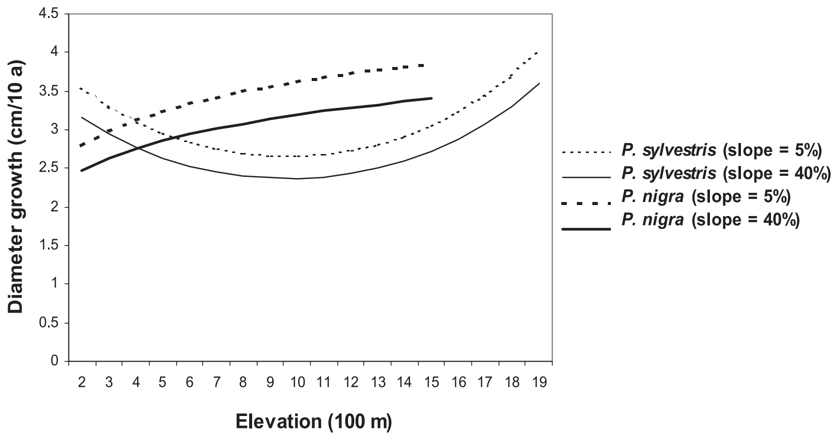

Figure 4. Diameter increment of *P. sylvestris* (Eqs. (1) and (3)) and *P. nigra* (Eqs. (2) and (4)) as a function of elevation and slope. Used predictor values: *dbh* = 25 cm, *BALsyl* = 5 m^2 ha^{-1}, *BALnig* = 5 m^2 ha^{-1}, *BALsyl + acc* = 5 m^2 ha^{-1}, *BALnig + acc* = 5 m^2 ha^{-1}, *BALthin* = 8 m^2 ha^{-1}, *G* = 30 m^2 ha^{-1}, *LAT* = 46.42 × 10^2 km, *CON* = 80 km.

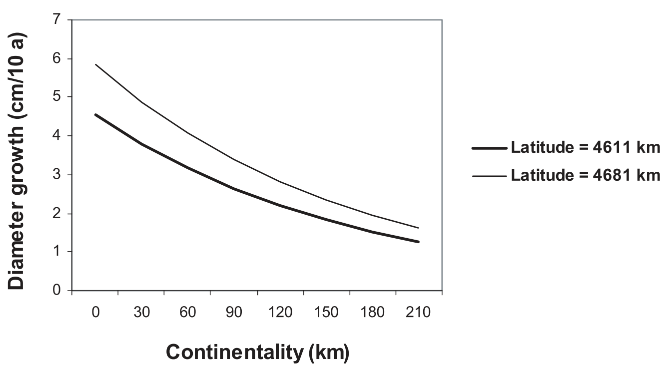

Figure 5. Diameter increment of *P. nigra* (Eqs. (2) and (4)) as a function of continentality and latitude. Used predictor values: *BALthin* = 5 m^2 ha^{-1}, *dbh* = 25 cm, *BALnig* = 5 m^2 ha^{-1}, *BALsyl + acc* = 5 m^2 ha^{-1}, *SLO* = 35%, *ELE* = 800 m.

of the diameter growth and height models are correlated within each plot – part of the residual variation is explained by random between-plot factor, but only a small part of the between-plot variation is explained by plot factor model. This should be taken into account when analyzing Figures 6 and 7.

The absolute and relative biases for *P. sylvestris* and *P. nigra* diameter growth models were zero due to the ratio estimator used for bias correction. The relative RMSE values were 56.4% and 48.6% for the *P. sylvestris* and *P. nigra* models, respectively (Tab. V and VI).

3.2. Height models

The estimated height models describe tree height as a function of diameter at breast height (Eq. (5)). According to the models for the random plot factor (Eqs. (6) and (7)), the effect of site characteristics on tree height of both pine species is very similar: increasing elevation decreases the height of a tree; continentality first increases the height (up to around 80 km) and then decreases the height; and latitude increases the height. The use of species dummies resulted in a clear improvement of the plot factor models. Parameter estimates of the height models and plot factor models were logical and significant at the 0.05 level (Tab. VII). The R^2 values were 0.30 for the *P. sylvestris* height model, 0.41 for the *P. nigra* height model, 0.15 for the *P. sylvestris* plot factor model without species dummies, 0.18 for the *P. nigra* plot factor model without species dummies, 0.32 for the *P. sylvestris* plot factor model with species dummies, and 0.35 for the *P. nigra* plot factor model with species dummies. The R^2 values, when adding the predicted plot factor to the fixed part of the height model, were 0.33 (0.43 using species dummies) for *P. sylvestris* and 0.47 (0.55 using species dummies) for *P. nigra*. The relative biases were 6.7% and 3.3% and the relative RMSE were 24.0% and 21.7% for the *P. sylvestris* and *P. nigra* height models, respectively (Tabs. V and VI). There were no obvious trends in bias for the height models, but the residuals had a slightly heterogeneous variance as a function of predicted height.

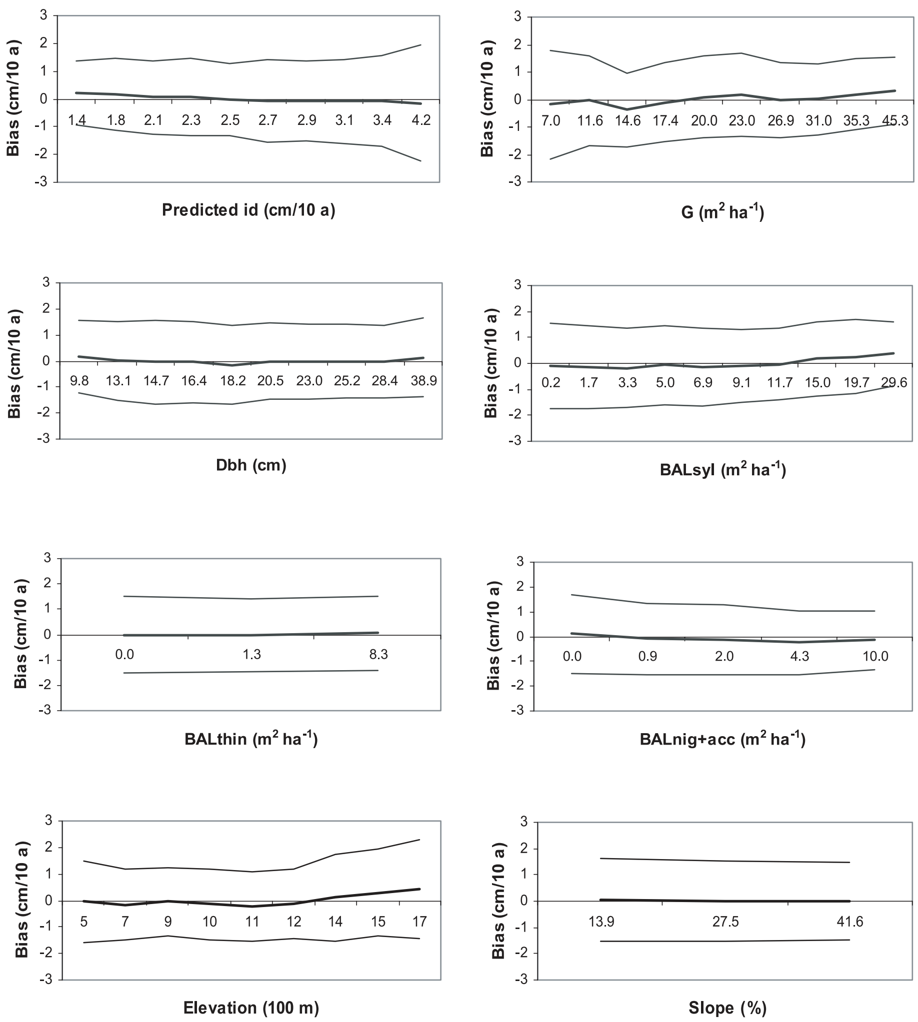

Figure 6. Estimated mean bias (in anti-log scale) of the diameter growth model for *P. sylvestris* as a function of predicted diameter growth, basal area, dbh, total basal area of *P. sylvestris* larger trees, total basal area of larger trees thinned during the next 10-year period, total basal area of larger trees of *P. nigra* and accompanying species, elevation, and slope (thin lines indicate the standard error of the mean).

Table V. Absolute and relative biases and RMSEs of the *P. sylvestris* diameter growth model (Eqs. (1) and (3)), height model (Eqs. (5) and (6)), ingrowth model (Eq. (8)) and mean dbh of ingrowth model (Eq. (10)).

Criteria	Diameter growth model (Eqs. (1) and (3))	Height model (Eqs. (5) and (6))	Ingrowth model (Eq. (8))	Mean dbh of ingrowth model (Eq. (10))
Bias	–	0.77 m	–	–
Bias %	–	6.7	–	–
RMSE	1.48 cm/10 a	2.76 m	115.43 trees/ha	0.92
RMSE %	56.4	24.0	224.3	10.1

Table VI. Absolute and relative biases and RMSEs of the *P. nigra* diameter growth model (Eqs. (2) and (4)), height model (Eqs. (5) and (7)), ingrowth model (Eq. (9)) and mean dbh of ingrowth model (Eq. (11)).

Criteria	Diameter growth model (Eqs. (2) and (4))	Height model(Eqs. (5) and (7))	Ingrowth model (Eq. (9))	Mean dbh of ingrowth model (Eq. (11))
Bias	–	0.37 m	–	–
Bias %	–	3.3%	–	–
RMSE	1.36 cm/10 a	2.44 m	125.54 trees/ha	0.92 cm
RMSE %	48.6	21.7	257.3	10.2

Table VII. Estimates of the parameters and variance components of the *P. sylvestris* and *P. nigra* height models (Eq. (5)) and the corresponding plot factor models (Eqs. (6) and (7))[a,b].

Parameter	*P. sylvestris*			*P. nigra*		
	Height model (Eq. (5))	Plot factor model without sp. dummies (Eq. (6))	Plot factor model with sp. dummies (Eq. (6))	Height model (Eq. (5))	Plot factor model without sp. dummies (Eq. (7))	Plot factor model with sp. dummies (Eq. (7))
β_0	–	–75.3769	–24.8350	–	–47.9430	6.3610
		(16.2566)	(5.5437)		(17.9836)	(0.5574)
β_1	22.0554	–0.1198	–0.1504	26.2556	–0.0818	–0.1157
	(0.4878)	(0.0323)	(0.0297)	(0.7565)	(0.0421)	(0.0348)
β_2	21.5227	0.9691	–	29.2372	1.1267	–
	(1.3816)	(0.3689)		(2.0075)	(0.3830)	
β_3	–37.2536	–0.3306	–0.2323	–22.1194	–0.0003	–0.0003
	(9.7673)	(0.0617)	(0.0564)	12.0301)	(0.0001)	(0.0000)
β_4	–	11.9904	9.4383		–99.2999	–142.7067
		(2.2890)	(2.0423)	–	(22.0784)	(17.5221)
β_5	–	0.0009	0.0006		–	–
		(0.0002)	(0.0002)	–		
CRA	–	–	0.8921		–	0.9853
			(0.1816)	–		(0.1944)
ACR	–	–	0.7929		–	–
			(0.1737)	–		
FAG	–	–	1.4019		–	–
			(0.3990)	–		
THI	–	–	–1.6133		–	–1.3741
			(0.1635)	–		(0.1609)
JUN	–	–	–		–	–1.0055
						(0.2121)
σ^2_{pl}	5.5952	4.4089	3.5158	5.2091	3.9956	3.1565
σ^2_{tr}	2.6564	–	–	2.0623	–	–
RMSE	2.8726	2.0997	1.8751	2.6966	1.9989	1.7767
R^2	0.30	0.15	0.32	0.41	0.18	0.35

[a] S.E. of estimates are given in parenthesis. [b] CRA is *Crataegus* sp., ACR is *Acer* sp., FAG is *Fagus sylvatica*, THI is *Thimus* ssp., JUN is *Juniperus communis*.

Table VIII. Estimates of the parameters and variance components of the *P. sylvestris* ingrowth model (Eq. (8)), *P. sylvestris* mean dbh of ingrowth model (Eq. (10)), *P. nigra* ingrowth model (Eq. (9)) and *P. nigra* mean dbh of ingrowth model (Eq. (11))[a].

Parameter	*P. sylvestris*		*P. nigra*	
	Ingrowth model (Eq. (8))	Mean dbh of ingrowth model (Eq. (10))	Ingrowth model (Eq. (9))	Mean dbh of ingrowth model (Eq. (11))
β_0	41.7165	8.5625	–14.9174	9.4537
	(13.4778)	(0.2225)	(14.4563)	(0.1523)
β_1	–1.7840	–0.0250	–1.0679	–0.0270
	(0.5109)	(0.0076)	(0.4261)	(0.0094)
β_2	–102.3057	0.0868	79.4949	–
	(53.9212)	(0.0196)	(11.6668)	
β_3	98.2668	–	4.5272	–
	(9.5461)		(1.2399)	
σ^2_{pl}	13369.0371	0.8513	15812.3576	0.8578
R^2	0.11	0.12	0.11	0.05

[a] S.E. of estimates are given in parenthesis.

3.3. Ingrowth models

Parameter estimates of the models for the number and mean dbh of ingrowth were logical and significant at the 0.05 level (Tab. VIII). The R^2 values were 0.11 for the *P. sylvestris* ingrowth model, 0.11 for the *P. nigra* ingrowth model, 0.12 for the *P. sylvestris* mean dbh of ingrowth model, and 0.05 for the *P. nigra* mean dbh of ingrowth model. The developed models

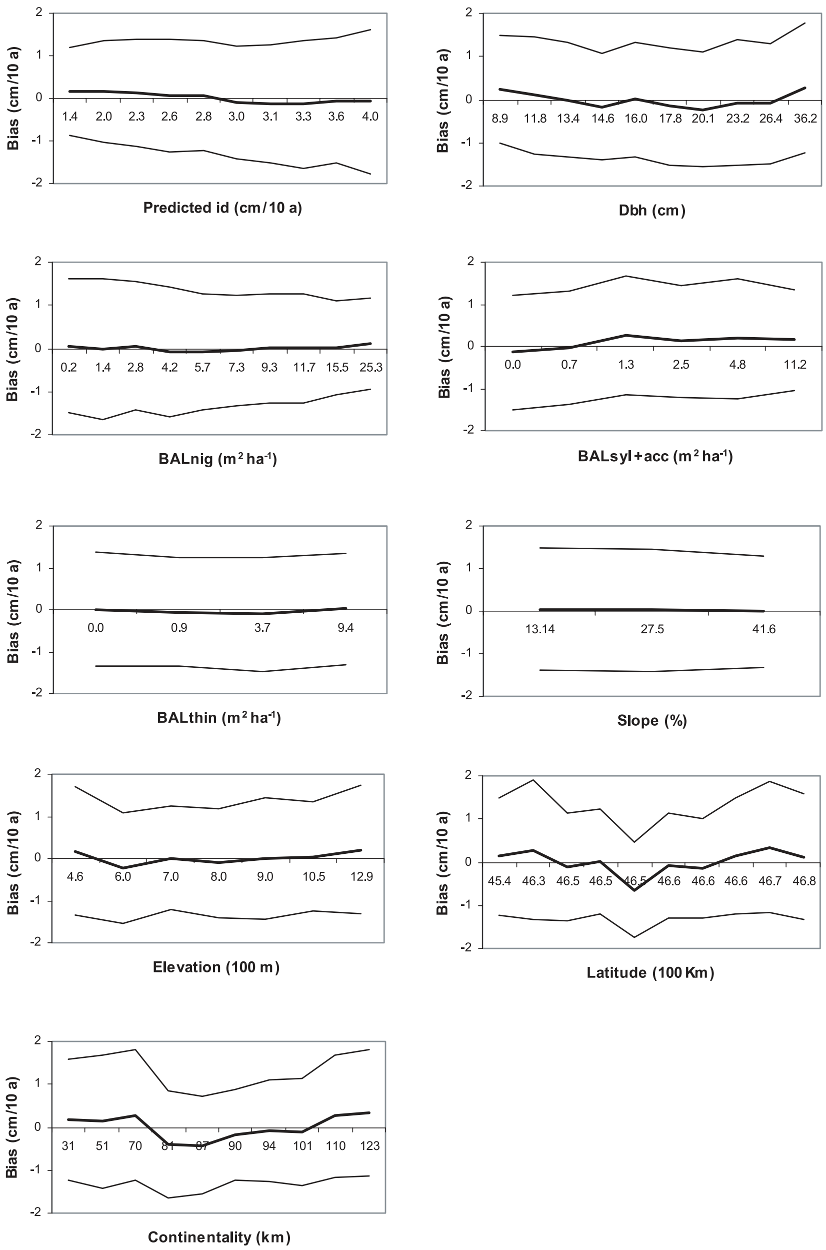

Figure 7. Estimated mean bias (in anti-log scale) of the diameter growth model for *P. nigra* as a function of predicted diameter growth, dbh, total basal area of larger *P. nigra* trees, total basal area of larger *P. sylvestris* and accompanying species trees, total basal area of larger trees thinned during the next 10-year period, slope, elevation, latitude, and continentality (thin lines indicate the standard error of the mean).

for the number and mean dbh of ingrowth use stand basal area and site characteristics as independent variables: increasing stand basal area increases the amount of ingrowth for *P. sylvestris* (Eq. (8)) up to 8 m^2 ha^{-1}, and then decreases the amount of ingrowth; increasing stand basal area decreases the amount of ingrowth for *P. nigra* (Eq. (9)) and the mean dbh of ingrowth for both pine species (Eqs. (10) and (11)); increasing values of the ratio of the subject species' basal area to the total stand basal area increases ingrowth (Eqs. (8) and (9)); increasing ratio between continentality and elevation increases *P. nigra* ingrowth; and increasing stand elevation increases the mean dbh of *P. sylvestris* ingrowth (Eq. (10)). The main difference between both species relies on higher ingrowth for *P. nigra*, at low and continental sites (β_3 in Eq. (9)). The use of species dummies did not bring about a significant improvement in the models. The absolute and relative bias for the *P. sylvestris* and *P. nigra* ingrowth and mean dbh of ingrowth models were zero. The relative RMSE value was 224.3% for *P. sylvestris* ingrowth, 257.3% for *P. nigra* ingrowth, 10.1% for *P. sylvestris* mean dbh of ingrowth, and 10.2% for *P. nigra* mean dbh of ingrowth. There were no obvious trends in the bias for the ingrowth models, but the residuals had a slightly heterogeneous variance as a function of predicted ingrowth, *P. sylvestris* basal area, *P. nigra* basal area and elevation. The graphs of bias as a function of predicted ingrowth showed that the models may predict negative ingrowth (e.g. with very high stand basal area). In simulations, negative ingrowth predictions should be replaced by zero.

Table IX. Estimated parameters, their standard errors (S.E.), statistical significance and odds ratios for the logistic density-dependent *P. sylvestris* and *P. nigra* survival models (Eqs. (12) and (13))[a].

Parameter	Estimate	S.E	Wald statistics	Significance	Odds ratio ($\exp(\beta)$)
P. sylvestris survival model without sp. dummies (Eq. (12))					
β_0	2.728	0.294	85.916	0.000	15.309
β_1	–0.148	0.013	124.650	0.000	0.862
β_2	0.107	0.019	31.719	0.000	1.113
β_3	0.067	0.023	8.901	0.003	1.070
β_4	–0.006	0.002	7.476	0.006	0.994
χ^2-value	167.250				
P. sylvestris survival model with sp. dummies (Eq. (12))					
β_0	5.700	0.893	40.768	0.000	298.750
β_1	–0.169	0.013	159.706	0.000	0.845
β_2	0.105	0.019	30.273	0.000	1.111
β_3	–	–	–	–	–
β_4	–	–	–	–	–
CIT	–1.910	0.721	7.018	0.008	0.148
CAV	0.955	0.301	10.079	0.001	2.599
JUN	–0.931	0.148	39.379	0.000	0.394
COA	–0.886	0.367	5.822	0.016	0.412
ACR	–0.797	0.153	27.229	0.000	0.451
BUX	–0.306	0.128	5.750	0.016	0.737
χ^2-value	244.768				
P. nigra survival model without sp. dummies (Eq. (13))					
β_0	5.189	0.519	100.030	0.000	179.258
β_1	–0.288	0.057	25.971	0.000	0.750
β_2	0.094	0.024	14.915	0.000	1.099
β_3	–0.146	0.056	6.854	0.009	0.864
χ^2-value	33.430				
P. nigra survival model with sp. dummies (Eq. (13))					
β_0	2.336	0.504	21.495	0.000	10.337
β_1	–0.286	0.057	25.103	0.000	0.751
β_2	0.087	0.024	12.739	0.000	1.091
β_3	–	–	–	–	–
PRU	1.089	0.345	9.988	0.002	2.971
AUU	1.002	0.324	9.591	0.002	2.724
χ^2-value	42.969				

[a] CIT is *Cistus* spp., CAV is *Calluna vulgaris*, JUN is *Juniperus communis*, COA is *Corylus avellana*, ACR is *Acer* sp., BUX is *Buxus sempervirens*, PRU is *Prunus* sp., AUU is *Arctostaphylos uva-ursi*.

3.4. Survival models

The probability of a tree surviving for the next 10 years was best explained by the ratio of the basal area of trees larger than the subject tree to the subject tree's dbh (*BAL*/ln(*dbh*+1)) (Eqs. (12) and (13)), tree height (Eq. (12)), continentality (Eq. (12)), stand basal area (Eq. (13)), and elevation (Eqs. (12) and (13)). The Wald tests showed that the parameter estimates of equations (12) and (13) are significant ($P < 0.05$) (Tab. IX). By analysing equations (12) and (13) it can be deduced that: (1) the greater the ratio of basal area of trees larger than the subject tree (competition index) to tree dbh, the smaller the survival probability; (2) the taller the tree and the higher the elevation, the greater the probability of a *P. sylvestris* tree to survive; (3) the higher the elevation, the smaller the survival probability of a *P. nigra* tree; (4) the denser the stand, the greater the survival probability of a *P. nigra* tree; and (5) the greater the continentality, the smaller the probability of a *P. sylvestris* tree surviving. The main differences between the two species rely on survival rate for short trees (β_2 in Eq. (12)) and dense stands (β_2 in Eq. (13)). The odds ratios of the covariates showed that *BAL*/ln(*dbh*+1) (Eqs. (12) and (13)) has the strongest relative effect on the probability of a tree surviving. The use of species dummies gave a significant improvement of the survival models [7].

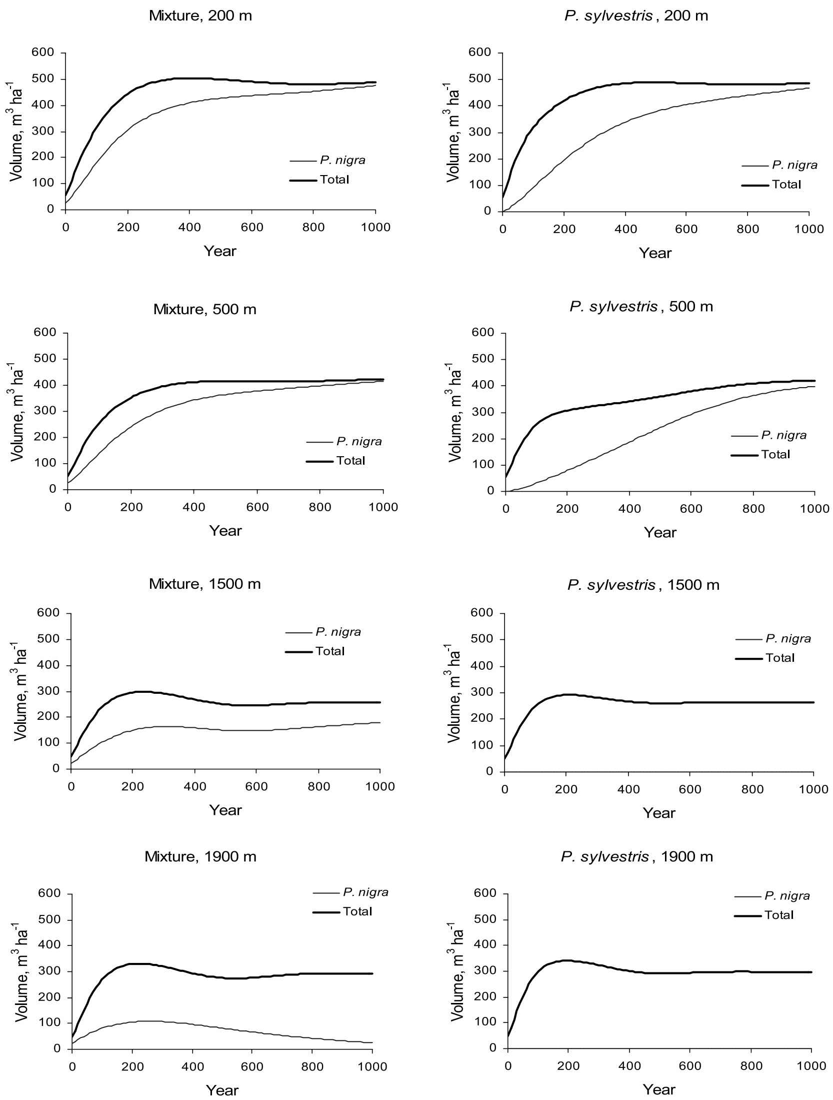

Figure 8. Long-term simulations of total stand volume and *P. nigra* stand volume in mixed *P. sylvestris* and *P. nigra* stands and pure stands of *P. sylvestris*, at different elevations (values used for other site characteristics: *SLO* = 30%, *LAT* = 46.00×10^2 km, *CON* = 80 km). The density-independent survival of 0.962 per 10 years is included, the predicted plot factors have been added to the predictions, and the diameter increment models are corrected for logarithmic transformation.

3.5. Simulation results

Figure 8 shows long-term simulations without any treatments of two plots, one representing a mixed *P. sylvestris* and *P. nigra* stand, and the other representing a pure stand of *P. sylvestris*. The simulations were carried out for four different elevations (200, 500, 1500, 1900 m a.s.l.). Site characteristics were the same for both plots. The long-term simulations include the density-independent survival of 0.962 per 10 years. The predicted plot factors (without using species dummies) have been added to the predictions and the diameter increment models have been corrected for logarithmic transformation. In simulations, *P. nigra* occupies the site at lower elevations in both plots, and even tends to dominate at 1500 a.s.l. in the mixed plot. At higher elevations (from 1500 m a.s.l. upwards in *P. sylvestris,* and at 1900 m a.s.l. in the mixed plot) *P. sylvestris* occupies the stands. The simulation results correspond to the observed species distribution. Maximum volume is higher at low elevations. However, the volume stops decreasing at higher elevations (1500 m a.s.l.) and even increases to some extent at the highest elevation (1900 m a.s.l.).

Figure 9 shows the measured and predicted 10-year changes of stand basal area for those non-thinned plots that were used to develop the density-dependent survival models. In the simulations the density-independent 0.962 survival per 10 years was not applied, but the diameter increment models were corrected for logarithmic transformation. In Figure 9A just the fixed part of the diameter increment model was used; in Figure 9B the random plot factors predicted without species dummies were added to the fixed part of the models; in Figure 9C the random plot factors predicted using species dummies were added to the fixed part of the models; and in Figure 9D the fixed part of the models and the true random plot factors were used. There was a small improvement in the predictions when the predicted plot factors were used. The predictions were slightly better when the predictions were based on models that use species dummies. The improvement

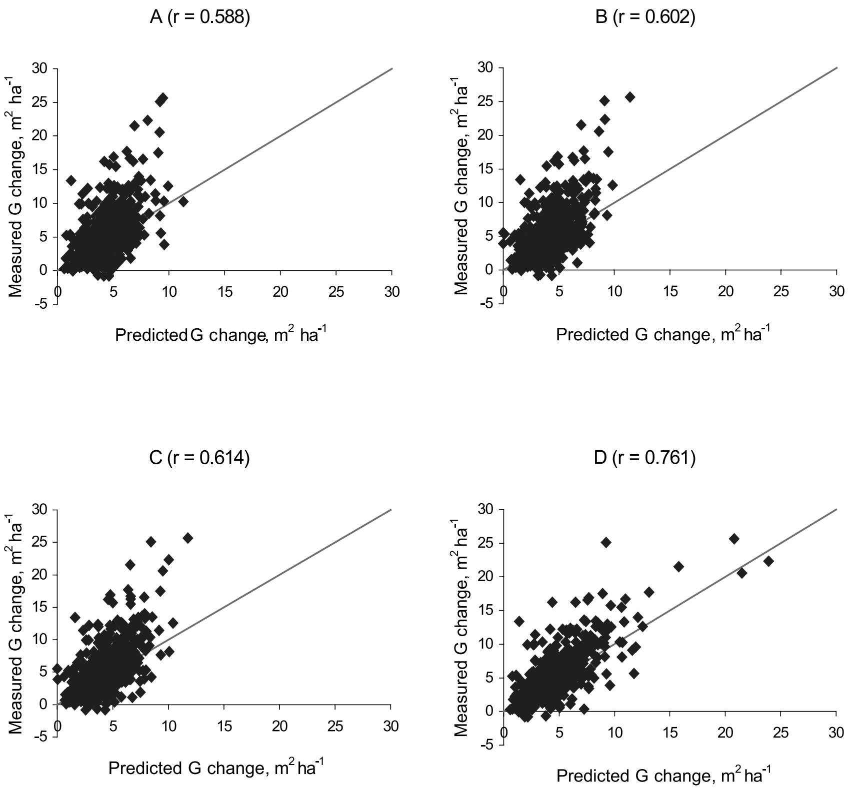

Figure 9. Measured and predicted 10-year changes in the stand basal area (G) of density-dependent survival plots (no drastic events) using the fixed part of the models (A); the fixed part of the models and the predicted plot factors (B); the fixed part of the models and the predicted plot factors using species dummies (C); the fixed part of the models and the true plot factors (D). The different correction factors for bias correction in diameter increment logarithmic regression were applied in each case.

was more significant when the true plot factors were added to the fixed part of the model. The model set underpredicted the 10-year change in stand basal area of plots having exceptionally high growth. A careful inspection of the plot data showed that plots with the highest underprediction were young fast-growing, rather even-aged stands. The residuals of the simulated 10-year change in stand basal area were also plotted against site characteristics (results not shown). No systematic trends were found, showing that there were no model failures related to these variables in the models. Nonetheless, the residuals were positively biased due to the inability of the model set to predict high enough growth in young fast-growing stands.

4. DISCUSSION

This study presents individual-tree models for uneven-aged mixtures of *P. sylvestris* and *P. nigra* in Catalonia, based on permanent sample plots measured two times in all sites represented by the Spanish National Forest Inventory. This sample provides an outstanding database in terms of size (14 470 diameter growth observations) and forest conditions. However, it should be taken into account that the sampling methodology was not specifically designed to develop growth and yield models. A disadvantage of this data is that diameter growth is determined as a difference of two diameters. 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 on different measurement occasions. This results in greater errors than measuring radial increment directly from increment borings. This is reflected in the value of the coefficients of determination, 0.18 for *P. sylvestris* and 0.21 for *P. nigra*, when the species dummies are used in the plot factor models. The low R^2 of this study agrees with the results obtained by Monserud and Sterba [22], using similar data from the Austrian National Forest Inventory. Nevertheless, assuming that the measurement errors were random, the large sample should compensate for this disadvantage.

The variable-radius circular plot sampling method, used to collect the modelling data, selected trees with unequal probability (Tab. I). This method results in ingrowth to dbh classes larger than the smallest class, 7.5–12.4 cm. The ingrowth models prepared in this study predict only the number of trees that enter the smallest dbh class during a 10-year period. However, despite its specific features, the variable radius circular plot is often the only feasible method to sample irregular stand structures efficiently. This sampling method gives a good representation of large trees, which is usually a benefit from both inventory and modelling stand points.

Sampling methods often have limitations to represent spatial variability in stands [37]. Hence, competition predictors used in the models might have sampling error associated with them, which will create bias when using the models in simulations.

The site effects were modelled from site characteristics (e.g. elevation), avoiding the use of site index and stand age. More accurate description of site fertility was obtained when species dummies were used, although it should be remembered that the presence of species in stands can be affected by management, forest fires or grazing. The between-plot factors in the diameter growth and height models correlated logically with site variables. Nevertheless, site characteristics adopted illogical signs when included directly in the fixed part of the models. For that reason, site characteristics were used to develop models that predict the plot factors of the diameter increment and height models.

Because it was not known whether a tree removed in thinning was living or dead, the thinned trees were not used as observations. If dead thinned trees had been recorded differently from live trees, the survival and growth models might have been better for trees facing much competition. Height growth models were not developed because there were obvious and large errors in the height measurement of the first measurement occasion. The developed height prediction models provide typical values for a given dbh-class and can be used for growth simulation. The number and mean dbh of ingrowth can be predicted using stand level models.

A density-independent 10-year tree survival rate of 0.962 was estimated from the study material. However, this rate should not be automatically used in simulation because the rate may depend on location, fire management, etc. In most cases it might be better to use only the density-dependent survival models. Models for the occurrence of fire may improve the prediction of density-independent mortality.

Long-term simulations with the model set suggest that *P. nigra* occupies the site at lower elevations if no treatments are applied, which is reasonable if we take into account that this species shows higher shade tolerance than *P. sylvestris*. Furthermore, succession in temperate forests appears to be driven by differences in light availability and shade tolerance; however, water limitation is also important for the distribution of forest species in Mediterranean plant communities [40].

The ingrowth and survival models do not have a strong impact on short-term simulations, but in long-term simulations they are very important. The system of models shows some weaknesses with very large trees (over 50 cm of dbh), because the data included very few large trees. The growth of very large trees may be overpredicted and the tree survival models may underpredict the mortality of very large trees. Other authors [15, 21, 33, 39] used squared dbh when modelling the effect of tree size, in order to get the growth predictions to approach zero for large dbh values. However, dbh^2 was not a significant predictor in our data. Hence, long-term simulations may produce trees older than 200–300 years, which is the observed range of maximum tree age (244 years for *P. sylvestris* and 215 years for *P. nigra*), provided by the Ecological and Forest Inventory of Catalonia [12, 13]. An age-dependent survival model could be considered in future studies. However, the weaknesses of the models with very large trees do not have any practical importance in short- and medium-term simulations because very large trees are rarely found in these types of stands.

The models provide correct average predictions (Fig. 9), but they account for only a small part of the site specific growth variation among stands. The highest underpredictions are related to young fast-growing, rather even-aged stands. The lack of age and site index reduces the ability of the models to accurately predict growth in even-aged stands. Nevertheless, the unexplained site-specific variation could be accounted for by using model calibration [15, 20, 22, 39]. Figure 9D, where the true plot factors have been used, gives an idea about the performance of a calibrated model.

The potential for application of the models is wide. They can be applied using the data normally available from stand inventories in the region, and they can be adapted to all age structures and degrees of mixture, including pure stands. However, as mentioned above, for even-aged stands, models that use site index as a predictor should be considered as the first option.

This study being the first, known by the authors, on individual-tree growth models for uneven-aged mixed stands in Spain is a starting point for further research on the topic. Future studies could evaluate the effect of using other potential predictors in the models, such as tree age, crown width or length (characterising the variation in the vigour of trees of similar size) [22, 33, 39], or additional locally measured site variables, such as soil depth [22, 33]. Future studies should also focus on evaluating the use of past increment as a model predictor or for calibrating the models for a specific stand. The models presented in this study can be used to optimise the stand management and to evaluate alternative management regimes for uneven-aged stands of *P. sylvestris* and *P. nigra.*

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APPENDIX

In addition to *P. sylvestris* and *P. nigra*, other tree species where also present in several stands. The accompanying species were divided into two major groups: conifers and hardwoods. A set of models was developed for each group of accompanying species using the ordinary least squares (OLS) method in SPSS (SPSS Inc., 1999), in order to include them in simulations.

Conifers:

$$\ln(id10_{lkt}) = 7.680 - 32.177/dbh_{lkt} - 1.495 \times \ln(dbh_{lkt}) - 0.020 \times BALacc_{lk} - 0.052 \times ELE_{lk} + e_{lkt}$$

$$h_{lkt} = \frac{36.755 - 2.407 \times (\cos(ASP_{lk}) \times \ln(ELE_{lk}))}{1 + (43.405 / dbh_{lkt})} + \frac{-0.046 \times CON_{lk} + 2.852 \times \sin(ASP_{lk})}{1 + (43.405 / dbh_{lkt})} + e_{lkt}$$

$$SV_{lk} = 0.9939$$

$$ING_{lk} = 5.28$$

$$DIN_{lk} = 5.06;$$

Hardwoods:

$$\ln(id10_{lkt}) = 1.650 - 3.514 / dbh_{lkt} - 0.229 \times \ln(G_{lk}) - 0.004 \times CON_{lk} - 0.177 \times \sin(ASP_{lk}) + e_{lkt}$$

$$h_{lkt} = \frac{13.644 - 0.231 \times ELE_{lk} + 0.023 \times CON_{lk}}{1 + \left(130.795 / dbh_{lkt}^2\right)} + e_{lkt}$$

$$SV_{lk} = 0.9739$$

$$ING_{lk} = 32.77$$

$$DIN_{lk} = 6.27$$

where *id10* is future diameter growth (cm per 10 years); *dbh* is diameter at breast height (cm); *G* is stand basal area (m^2 ha^{-1}); *BALacc* is the total basal area of accompanying tree species larger than the subject tree (m^2 ha^{-1}); *ELE* is elevation (100 m); *CON* is continentality (linear distance to the Mediterranean sea, km); *ASP* is aspect (rad); *SV* is survival rate for a 10-year time step; *ING* is ingrowth (number of trees ha^{-1}) at the end of a 10-year time step; *DIN* is the mean dhh of ingrowth trees (cm) at the end of a 10-year step.

The ratio estimators for bias correction in logarithmic diameter growth models were 1.3220 and 1.2386 for conifers and hardwoods, respectively.

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