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Original article

A growth model for *Pinus radiata* D. Don stands in north-western Spain

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Abstract – A dynamic whole-stand growth model for radiata pine (*Pinus radiata* D. Don) stands in north-western Spain is presented. In this model, the initial stand conditions at any point in time are defined by three state variables (number of trees per hectare, stand basal area and dominant height), and are used to estimate total or merchantable stand volume for a given projection age. The model uses three transition functions derived with the generalized algebraic difference approach (GADA) to project the corresponding stand state variables at any particular time. These equations were fitted using the base-age-invariant dummy variables method. In addition, the model incorporates a function for predicting initial stand basal area, which can be used to establish the starting point for the simulation. Once the state variables are known for a specific moment, a distribution function is used to estimate the number of trees in each diameter class by recovering the parameters of the Weibull function, using the moments of first and second order of the distribution. By using a generalized height-diameter function to estimate the height of the average tree in each diameter class, combined with a taper function that uses the above predicted diameter and height, it is then possible to estimate total or merchantable stand volume.

whole-stand growth model / radiata pine plantations / generalized algebraic difference approach / basal area disaggregation / Galicia

Résumé – Un modèle de croissance pour des peuplements de *Pinus radiata* D. Don du nord ouest de l'Espagne. Un modèle dynamique de croissance de peuplement est présenté pour *Pinus radiata* D. dans le nord ouest de l'Espagne. Dans ce modèle, les conditions initiales du peuplement en tout point et temps sont définies par trois variables d'état (nombre d'arbres à l'hectare, surface terrière et hauteur dominante) et sont utilisées pour estimer le volume total ou marchand du peuplement pour un âge donné. Le modèle utilise trois fonctions de transition dérivées avec une approche par différence algébrique généralisée (GADA) pour projeter les variables d'état correspondantes du peuplement à n'importe quel moment. Ces équations ont été ajustées en utilisant la méthode des variables indicatrices indépendantes de l'âge. En plus, le modèle incorpore une fonction de prédiction de la surface terrière initiale du peuplement qui peut être utilisée pour établir le point de départ de la simulation. Une fois que les variables d'état sont connues à un instant donné, une fonction de distribution est utilisée pour estimer le nombre d'arbres dans chaque classe de diamètre en récupérant les paramètres de la fonction de Weibull, en utilisant les moments de premier et de second ordre de la distribution. En utilisant une fonction généralisée hauteur-diamètre pour estimer la hauteur de l'arbre moyen de chaque classe de diamètre, combinée avec une fonction qui utilise la prédiction précédente du diamètre et de la hauteur, il est alors possible d'estimer le volume total ou marchand du peuplement.

modèle de croissance de peuplement / plantations de *Pinus radiata* / approche par différence algébrique généralisée / désagrégation de la surface terrière / Galice

1. INTRODUCTION

A managed forest is a dynamic biological system that is continuously changing as a result of natural processes and in response to specific silvicultural activities. Forest management decisions are based on information about current and likely future forest conditions. Consequently, it is often necessary to predict the changes in the system using growth and yield models, which estimate forest dynamics over time. Such models have been widely used in forest management because they allow updating of inventories, prediction of future yields, and exploration of management alternatives, thus providing information for decision-making in sustainable forest management [42, 98]. Forest growth models can be categorised according to their level of mechanistic detail in empirical growth and yield models and process-based models [9]. Although empirical growth models do little to elucidate the mechanisms of tree or stand growth, they are more widely used as practical tools in forest management, perhaps because of their simplicity.

According to Vanclay [99], Gadow and Hui [47] and Davis et al. [36], empirical growth and yield models can be grouped into three types of models that represent a broad continuum: whole-stand models, size-class models and individual-tree models. The most appropriate type of model depends on the intended use, the stand characteristics, the resources

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available and the projection length [17, 51, 98]. These factors also determine which data are required and the resolution of the estimates. Individual-tree growth models provide more detailed information than is available from other modelling approaches [50,51], and usually perform better than whole-stand models for short term projections [17]. For forest management planning, however, standard forest inventories do not usually provide sufficiently reliable estimates for initializing the tree-level starting conditions required by individual-tree models. Furthermore, over-parameterization of the functions may often limit accuracy and precision of quantitative predictions. Moreover, aggregated outputs from these types of models are required for decision-making, resulting in a projection of a simple state description through complicated functions.

At least for even-aged, single-species stands, whole-stand models are an attractive alternative, which directly project information that is easily obtained from inventory data [48, 51, 98]. In addition, model errors in inventory data may be magnified by individual-tree models but remain less altered by simpler models such as whole-stand models. In summary, whole-stand models may be preferable for plantation management planning applications because they represent a good compromise between generality and accuracy of the estimates [46, 51].

Whole-stand models require few details for growth simulation, but provide rather limited information about the future stand (in some cases only stand volume) [98, 99]. Considering that forest management decisions require more detailed information about stand structure and volume, as classified by merchantable products, whole-stand models can be disaggregated mathematically using a diameter distribution function, which may be combined with a generalized height-diameter equation and with a taper function to estimate commercial volumes that depend on certain specified log dimensions. Similar methodologies have been used by Cao et al. [20], Burk and Burkhart [14], Clutter et al. [32], Knoebel et al. [59], Zarnoch et al. [104], Uribe [97], Río [85], Mabvurira et al. [68], Kotze [60], Trincado et al. [96], and Diéguez-Aranda et al. [40] in the development of forest growth models, mainly for plantations.

Radiata pine (*Pinus radiata* D. Don) is well represented in the north of Spain, especially in the Basque Country and Galicia. According to the Third National Forest Inventory, radiata pine stands occupy a total surface area of approximately 90 000 ha in Galicia [102], with a current rate of planting of about 6 000 ha per year [1]. The wide distribution and the high growth rate of the species have also made it very important in the forestry industry in northern Spain, with an annual harvest volume of around 1 600 000 m^3 [70]. More than one third of this timber comes from Galicia. Nevertheless, to date, the only whole-stand growth model for the species in this region is a yield table developed by Sánchez et al. [88]. This model provides limited information about the forest stand and does not reflect accurately the evolution under different stand density conditions.

The objective of the present study was to develop a management-oriented dynamic whole-stand model for simulating the growth of radiata pine plantations in Galicia. The model is constituted by the following interconnected submodels: a site quality system, an equation for reduction in tree number, a stand basal area growth system, and a disaggregation system composed of a diameter distribution function, a generalized height-diameter relationship and a total and merchantable volume equation. All of the submodels were developed in the present study, except the site quality system and the height-diameter relationship, which have already been published [23, 39].

2. MATERIAL AND METHODS

2.1. Data

The data used to develop the model were obtained from three different sources. Initially, in the winter of 1995 the Sustainable Forest Management Unit of the University of Santiago de Compostela established a network of 223 plots in pure radiata pine plantations in Galicia. The plots were located throughout the area of distribution of this species in the study region, and were subjectively selected to represent the existing range of ages, stand densities and sites. The plot size ranged from 625 to 1200 m^2, depending on stand density, to achieve a minimum of 30 trees per plot. All the trees in each sample plot were labelled with a number. The diameter at breast height (1.3 m above ground level) of each tree was measured twice (measurements at right angles to each other), with callipers – to the nearest 0.1 cm – and the arithmetic mean of the two measurements was calculated. Total height was measured to the nearest 0.1 m with a digital hypsometer in a randomized sample of 30 trees, and in an additional sample including the dominant trees (the proportion of the 100 thickest trees per hectare, depending on plot size). Descriptive variables of each tree were also recorded, e.g., if they were alive or dead.

After examination of the data for evidence of plots installed in extremely poor site conditions, and taking into account that some plots had disappeared because of forest fires or clear-cutting, a subset of 155 of the initially established plots was re-measured in the winter of 1998. Following similar criteria, a subset of 46 of the twice-measured plots were measured again in the winter of 2004. Between each of the three inventories, 22 plots were lightly or moderately thinned once from below. These plots were also re-measured immediately before and after thinning operations. The first source of data comprises the inventories carried out in 1995, 1998, and 2004 and on the date of the thinning operations.

In addition, data from the first and second measurements of two thinning trials installed in a 12-year old stand of radiata pine were also used. Each thinning trial consisted of 12 plots of 900 m^2, in which four thinning regimes were evaluated on three different occasions. The four thinning treatments considered were: an unthinned control, a light thinning from below, a moderate thinning from below, and a selection thinning (selection of crop trees and extraction of their competitors). The plots were thinned immediately after plot establishment in 2003 and were re-measured three years later. The second source of data corresponds to the first and second inventories of these thinning trials.

For the fist two sources of data, the following stand variables were calculated for each plot and inventory: age (t), number of trees per hectare (N), stand basal area (G), and dominant height (H, defined as the mean height of the 100 thickest trees per hectare). Only live trees were included in the calculations for stand basal area and number of

Table I. Summarised data corresponding to the sample of plots and trees used for model development.

Variable	1st inventory (247 plots)				2nd inventory (179 plots)				3rd inventory (46 plots)			
	Mean	Max.	Min.	S.D.	Mean	Max.	Min.	S.D.	Mean	Max.	Min.	S.D.
t (years)	21.6	38	5	8.3	24.0	41	8	8.7	30.5	47	20	7.5
H(m)	19.0	32.5	5.9	5.4	21.2	34.0	11.0	4.9	26.6	35.2	17.8	4.2
G (m^{2}ha^{-1})	31.1	87.1	5.2	11.4	35.2	63.0	16.5	9.6	44.1	64.0	28.4	7.9
N(stems ha^{-1})	964.8	2048	200	459.2	895.8	1968	191.7	436.0	744.6	1488	280	311.7
	421 trees											
d (cm)	28.2	60.0	5.1	12.8								
h (m)	20.4	36.5	4.2	6.5								
v (m^3)	0.759	3.56	0.006	0.769								

t = stand age; H = dominant height; G = stand basal area; N = number of stems per hectare; d = diameter at breast height over bark; h = total tree height; v = total tree volume over bark above stump level.

trees per hectare. In addition, data on the number of trees per hectare and stand basal area removed in thinning operations were available.

Apart from these inventories, two dominant trees were destructively sampled at 82 locations in the winters of 1996 and 1997. These trees were selected as the first two dominant trees found outside the plots but in the same plantations within ± 5% of the mean diameter at 1.3 m above ground level and mean height of the dominant trees. Total bole length of felled trees was measured to the nearest 0.01 m. The logs were cut at 1 to 2.5 m intervals; the number of rings was counted at each cross-sectional point, and then converted to age above stump height. As cross-section lengths do not coincide with periodic height growth, we adjusted height-age data from stem analysis to account for this bias using Carmean's method [21] and the modification proposed by Newberry [75] for the topmost section of the tree. Additionally, 257 non-dominant trees were felled outside the 82 locations to ensure a representative distribution by diameter and height classes for taper function development. Log volumes were calculated by Smalian's formula. The top of the tree was considered as a cone. Tree volume above stump height was aggregated from the corresponding log volumes and the volume of the top of the tree. The third source of data corresponds to the 421 trees felled.

Summary statistics, including the mean, minimum, maximum, and standard deviation of the stand and tree variables used in model development are given in Table I.

2.2. Model structure

The model is based on the state-space approach [50], which assumes that the behaviour of any system evolving in time can be estimated by describing its current state, usually through a finite list of state variables (state vector), and a rate of change of state as a function of the current variables.

The state of a system at any given time may be roughly defined as the information needed to determine the behaviour of the system from that time on; i.e., given the current state, the future does not depend on the past [50]. Silvicultural treatments, such as thinning, cause an instantaneous change in the state variables of the stand, and therefore the system must estimate the trajectories starting from the new state after thinning. The requirements for an adequate state description are that the change in each of the state variables should be determined, to an appropriate degree of approximation, by the current state. In addition, it should be possible to estimate other variables of interest from the current values of the state variables through the so-called output functions [50, 51].

In selecting the state variables, the principle of parsimony must be taken into account [17, 46, 50, 99]: the model should be the simplest one that describes the biological phenomena and remains consistent with the structure and function of the actual biological system [73]. For unthinned stands, a two dimensional vector including dominant height and stand basal area as explanatory variables may be sufficient to describe the state of the stand at a given time [80]. Nevertheless, in situations covering a wide range of silvicultural regimes, the inclusion of an additional variable such as the number of trees per unit area is necessary [4, 50–52]. A fourth state variable representing relative site occupancy or canopy closure may improve predictions in some instances (especially when heavy thinning and pruning has been undertaken), at the cost of added complexity in model usage [49–51].

Transition functions are used to predict the growth by updating the state variables, and they must possess some obvious properties [50]: (i) consistency, which implies no change for zero elapsed time; (ii) path-invariance, where the result of projecting the state first from t_0 to t_1, and then from t_1 to t_2, must be the same as that of the one-step projection from t_0 to t_2; and (iii) causality, in that a change in the state can only be affected by inputs within the relevant time interval. Transition functions generated by integration of differential equations (or summation of difference equations when using discrete time) satisfy these conditions and allow computation of the future state trajectory.

Considering that we are dealing with single-species stands derived from plantations in which different management regimes have been carried out, three state variables (dominant height, number of trees per hectare and stand basal area) are needed to define the stand conditions at any point in time. These state variables are used to estimate stand volume, classified by commercial classes. The model uses three transition functions of the corresponding state variables, which are used to project the future stand state. Once the state variables are known for a given time, the model is disaggregated mathematically by use of a diameter distribution function, which is combined with a generalized height-diameter equation and with a taper function to estimate total and merchantable stand volumes.

The following sections describe how each of the three transition functions and the disaggregation system were developed.

2.3. Development and fitting of transition functions

2.3.1. Model development

Fulfilment of the above mentioned properties for the transition functions depends on both the construction method and the mathematical function used to develop the model. Most of these properties can be achieved by using techniques for dynamic equation derivation known in forestry as the Algebraic Difference Approach (ADA) [6] or its generalization (GADA) [28]. Dynamic equations have the general form (omitting the vector of model parameters) of $Y = f(t, t_0, Y_0)$, where Y is the value of the function at age t, and Y_0 is the reference variable defined as the value of the function at age t_0. The ADA essentially involves replacing a base-model site-specific parameter with its initial-condition solution. The GADA allows expansion of the base equations according to various theories about growth characteristics (e.g., asymptote, growth rate), thereby allowing more than one parameter to be site-specific and allowing the derivation of more flexible dynamic equations (see [24–26]).

The first step in the ADA or GADA is to select a base equation and identify in it any desired number of site-specific parameters (only one parameter in ADA). An explicit definition of how the site specific parameters change across different sites must be provided by replacing the parameters with explicit functions of X (one unobservable independent variable that describes site productivity as a summary of management regimes, soil conditions, and ecological and climatic factors) and new parameters. In this way, the initially selected two-dimensional base equation ($Y = f(t)$) expands into an explicit three dimensional site equation ($Y = f(t, X)$) describing both cross sectional and longitudinal changes with two independent variables t and X. Since X cannot be reliably measured or even functionally defined, the final step involves the substitution of X by equivalent initial conditions t_0 and Y_0 ($Y = f(t, t_0, Y_0)$) so that the model can be implicitly defined and practically useful [25, 28].

The ADA or GADA can be applied in modelling the growth of any site dependent variable involving the use of unobservable variables substituted by the self-referencing concept [77] of model definition [27], such as dominant height, number of trees per unit area or stand basal area.

2.3.2. Model fitting

The individual trends represented in dominant height, number of trees per hectare and stand basal area data of the plots can be modelled by considering that individuals' responses all follow a similar functional form with parameters that vary among individuals (local parameters) and parameters that are common for all individuals (global parameters). In practice both base-age specific (BAS) and base-age invariant (BAI) methods can be used. The assumption behind the BAS methods, which use selected data (e.g., heights at the given base age) as site-specific constants, is that the data measurements simultaneously do and do not contain measurement and environmental errors (on the left- and right-hand sides of the model, respectively) (e.g., [35, 74], which is clearly untenable [6]. The assumption behind the BAI methods, which estimate site-specific effects, is that the data measurements always contain measurement and environmental errors (both on the left- and right-hand sides of the model) that must be modelled [26]. From among the different BAI parameter estimation techniques available, we estimated the random site-specific effects simultaneously with the fixed effects by using the dummy variables method described by Cieszewski et al. [29]. In this method the initial conditions are specified as identical for all the measurements belonging to the same individual (tree or plot). The initial age can be, within limits, arbitrarily selected; however, age zero is not allowed. The variable corresponding to the initial age is then simultaneously estimated for each individual along with all of the global model parameters during the fitting process. The dummy variables method recognizes that each measurement is made with error and, therefore, it does not force the model through any given measurement. Instead, the curve is fitted to the observed individual trends in the data. With this method all the data can be used, and there is no need to make any arbitrary choice regarding measurement intervals. The dummy variables method was programmed using the SAS/ETS® MODEL procedure [91].

In the general formulation of the dynamic equations, the error terms e_{ij} are assumed to be independent and identically distributed with zero mean. Nevertheless, because of the longitudinal nature of the data sets used for model fitting, correlation between the residuals within the same individual may be expected, in which case an appropriate fitting technique should be used (see [105]). This problem may be especially important in the development of the dominant height dynamic model on the basis of data from stem analysis, because of the number of measurements corresponding to the same tree. Nevertheless, in the construction of the dynamic equations for reduction in tree number and for basal area growth, which involve the use of data from the first and second inventory of 179 plots and from the third inventory of 46 of these plots, respectively, the maximum number of possible time correlations among residuals is practically inexistent, and therefore the problem of autocorrelated errors can be ignored in the fitting process.

2.4. Transition function for dominant height growth

The site quality system, which combines compatible site index and dominant height growth models in one common equation, was developed by Diéguez-Aranda et al. [40]. The authors (op. cit.) took into consideration the following desirable attributes for dominant height growth equations: polymorphism, sigmoid growth pattern with an inflexion point, horizontal asymptote at old ages, logical behaviour (height should be zero at age zero and equal to site index at the reference age; the curve should never decrease), theoretical basis or interpretation of model parameters derived by analytically tractable algebraic operations, base-age invariance, and path invariance [6, 25, 26, 28]. Possession of multiple asymptotes was also considered a desirable attribute [25].

With these criteria in mind, Diéguez-Aranda et al. [39] examined different base models and tested several variants for each one, in which both one and two parameters were considered to be site-specific. The GADA formulation derived from the Bertalanffy–Richards model by considering the asymptote and the initial pattern parameters as related to site productivity (Eq. (9) in the original publication) resulted in the best compromise between graphical and statistical considerations and produced the most adequate site index curves.

2.5. Transition function for reduction in tree number

A dynamic equation was developed for predicting the reduction in tree number due to density-dependent mortality, which is mainly caused by competition for light, water and soil nutrients within a stand [79]. According to Clutter et al. [31], most mortality analyses are based on the values of age and number of trees per hectare at the beginning and at the end of the period involved. Therefore, the model was constructed using data from the plots measured more than one time.

Although many functions have been used to model empirical mortality equations, only biologically-based functions derived from differential equations include the set of properties that are essential in a mortality model [31, 101]: consistency, path invariance and asymptotic limit of stocking approaching zero as old ages are reached. Moreover, for even-aged stands it is usually assumed that in-growth is negligible [101].

In the present study, the equation for estimating reduction in tree number was developed on the basis of a differential function in which the relative rate of change in the number of stems is proportional to an exponential function of age:

$$\frac{\mathrm{d}N/\mathrm{d}t}{N} = \alpha N^{\beta}\delta^{t} \quad (1)$$

where N is the number of trees per hectare at age t, and α, β and δ are the model parameters.

This function was selected by Álvarez González et al. [3] to develop an equation in difference form for estimating reduction in stem number by using data from the first two inventories of the network of permanent plots described in the Data section. In the present study, a new dynamic equation developed by use of the ADA was fitted with the BAI dummy variables method to data from all the plot inventories available.

2.6. Transition function for stand basal area growth

The GADA was used to develop a function for projecting stand basal area. This requires having an initial value for stand basal area at a given age, which may generally be obtained from a common forest inventory where diameter at breast height is measured. If the initial stand basal area is not known, it must be estimated from other stand variables by use of an initialization equation. The stand basal area growth system is therefore composed of two sub-modules: one for stand basal area initialization and another for projection.

In the development of the stand basal area projection function, efforts were focused on six dynamic equations derived by applying the GADA to the base equations of Korf (cited in Lundqvist [67]), Hossfeld [54] and Bertalanffy-Richards [10, 11, 84]). For each base equation one (the scale parameter) and two parameters were considered to be site specific (see [8]).

The initialization function was developed on the basis of the corresponding base growth function from which the dynamic model that provided the best results on projection was derived. Because stand basal area at any specific point in time depends on stand age and other stand variables (theoretically the productive capacity of the site and any other measure of stand density), it was necessary to relate the site-specific parameters of the base function to these variables to achieve good estimates.

To ensure compatibility between the projection and initialization functions, the former must be developed on the basis of the same base growth function used for initialization. In addition, the site-specific parameters must be related to stand variables that do not vary over time (e.g., site index), whereas the remaining parameters must be shared by both functions. If any of these requirements is not reached, compatibility is not ensured.

The projection function was fitted with data from all the plots measured more than one time, whereas the initialization sub-module was only fitted with data from 98 inventories, corresponding to ages younger than 15 years, and assuming that if projections based on ages older than this threshold are required, the initial stand basal area should be obtained directly from inventory data.

2.7. Disaggregation system

2.7.1. Diameter distribution

Many parametric density functions have been used to describe the diameter distribution of a stand (e.g., Charlier, Normal, Beta, Gamma, Johnson SB, Weibull). Among these, the Weibull function has been the most frequently used for describing the diameter distribution of even-aged stands because of its flexibility and simplicity (e.g., [7, 18, 58, 68, 95]).

Expression of the Weibull density function is as follows:

$$f(x) = \left(\frac{c}{b}\right)\left(\frac{x-a}{b}\right)^{c-1} \mathrm{e}^{-\left(\frac{x-a}{b}\right)^{c}} \quad (2)$$

where x is the random variable, a the location parameter that defines the origin of the function, b the scale parameter, and c the shape parameter that controls the skewness.

The Weibull parameters can be obtained by different methodologies, which can be classified into two groups: parameter estimation and parameter recovery [56, 96, 98]. Several researchers have reported that the parameter recovery approach provides better results than parameter estimation, even in long-term projections [12, 20, 83, 95]. According to Parresol [78], the parameter recovery method is generally better than the parameter prediction method for projecting future distribution parameters, because diameter frequency distribution characteristics, such as mean diameter and diameter variance, can be projected with more confidence than the distribution parameters themselves.

The parameter recovery approach relates stand variables to percentiles [19] or moments [15, 76] of the diameter distribution, which are subsequently used to recover the Weibull parameters. The moments method is the only method that directly warrants that the sum of the disaggregated basal area obtained by the Weibull function equals the stand basal area provided by an explicit growth function of this variable, resulting in numeric compatibility [44, 56–58, 71, 95]. It was therefore the method selected for the present study.

In the moments method, the parameters of the Weibull function are recovered from the first three order moments of the diameter distribution (i.e., mean, variance and skewness coefficient, respectively). Alternatively, the location parameter (a) may be set to zero. The use of this condition restricts the parameters of the Weibull function to two, thus making it easier to model, and providing similar results to the three-parameter Weibull, at least for even-aged, single-species stands [2, 68, 69]. Thus, to recover parameters b and c the following expressions were used:

$$\mathrm{var} = \frac{\bar{d}^2}{\Gamma^2\left(1+\frac{1}{c}\right)}\left[\Gamma\left(1+\frac{2}{c}\right) - \Gamma^2\left(1+\frac{1}{c}\right)\right] \quad (3)$$

$$b = \frac{\bar{d}}{\Gamma\left(1+\frac{1}{c}\right)} \quad (4)$$

where $\bar{d}$ is the arithmetic mean diameter of the observed distribution, var is its variance, and Γ is the Gamma function.

Once the mean and the variance of the diameter distribution are known at any specific time, and taking into account that Equation (4) only depends on parameter c, the latter can be obtained using iterative procedures. Parameter b can then be calculated directly from Equation (5). Considering that the disaggregation system is developed for inclusion in a whole-stand growth model, only the arithmetic mean diameter requires to be modelled, because the variance can be directly obtained from the arithmetic and the quadratic mean diameters (d_g) by the relationship var $= d_g^2 - \bar{d}^2$.

The arithmetic mean diameter may be estimated at any point in time by the following expression [44], which ensures that predictions of $\bar{d}$ are lower than d_g for the ordinary range of stand conditions:

$$\bar{d} = d_g - e^{X\beta} \quad (5)$$

where **X** is a vector of explanatory variables (e.g., dominant height, number of trees per hectare, age…) that characterize the state of the stand at a specific time and must be obtained from any of the functions of the stand growth model, and β is a vector of parameters to be estimated. This procedure has been widely used in diameter distribution modelling in which the parameter recovery approach is used (e.g., [14, 20, 59]).

A diagram of the disaggregation system including all the components proposed in the present study is reported by Diéguez-Aranda et al. [40].

2.7.2. Height estimation for diameter classes

Once the diameter distribution is known, it is necessary to estimate the height of the average tree in each diameter class. A local height-diameter (*h-d*) relationship may be used for this purpose; nevertheless, the *h-d* relationship varies from stand to stand, and even within the same stand this relationship is not constant over time [34]. Therefore, a single curve cannot be used to estimate all the possible relationships that can be found within a forest. To minimise the level of variance, *h-d* relationships can be improved by taking into account stand variables that introduce the dynamics of each stand into the model (e.g., [34, 66, 93]).

The generalized *h-d* model used in the present study was developed by Castedo et al. [23] on the basis of the Schnute [92] function, which is one of the most flexible and versatile functions available for modelling this relationship [65]. Castedo et al. [23] modified the original Schnute function by forcing it (i) to pass through the point (0, 1.3) to prevent negative height estimates for small trees, and (ii) to predict the dominant height of the stand (H_0) when the diameter at breast height of the subject tree (d) equals the dominant diameter of the stand (D_0) (see Eq. (3) in the original publication).

2.7.3. Total and merchantable volume estimation

Once the diameter and height of the average tree in each diameter class are estimated, the total tree volume can be calculated directly by use of a volume equation. If volume prediction to any merchantable limit is required, two methods are commonly applied. One is to develop volume ratio equations that predict merchantable volume as a percentage of total tree volume (e.g., [16]). The other is to define an equation that describes stem taper (e.g., [62]); integration of the taper equation from the ground to any height will provide an estimate of the merchantable volume to that height. Merchantable volume equations obtained from taper functions are preferred nowadays, perhaps because they allow easy estimation of diameter at a given height.

Ideally, a volume estimation system should be compatible, i.e., the volume computed by integration of the taper equation from the ground to the top of the tree should be equal to that calculated by a total volume equation [30, 37]. The total volume equation is preferred when classification of the products by merchantable sizes is not required, thereby simplifying the calculations and making the method more suitable for practical purposes. An up-to-date review of compatible volume systems is provided by Diéguez-Aranda et al. [41].

Data on diameter at different heights and total stem volume from 421 destructively sampled trees were used for fitting a compatible system. To correct the inherent autocorrelation of the hierarchical data used, and taking into account that observations within a tree were not equally distributed, the error term was expanded by using an autoregressive continuous model, which can be applied to irregularly spaced, unbalanced data [105]. To account for k-order autocorrelation, the CAR(x) error structure expands the error terms in the following way:

$$e_{ij} = \sum_{k=1}^{k=x} I_k \rho_k^{h_{ij}-h_{ij-k}} e_{ij-k} + \varepsilon_{ij} \quad (6)$$

where e_{ij} is the jth ordinary residual on the ith tree, e_{ij-k} is the $j-k$th ordinary residual on the ith tree, $I_k = 1$ for $j > k$ and it is zero for $j \leq k$, ρ_k is the k-order autoregressive parameter to be estimated, and $h_{ij}-h_{ij-k}$ is the distance separating the jth from the $j-k$th observations within each tree, $h_{ij} > h_{ij-k}$. In such cases ε_{ij} now includes the error term under conditions of independence. To evaluate the presence of autocorrelation and the order of the CAR(x) to be used, graphs representing residuals plotted against lag-residuals from previous observations within each tree were examined visually.

The best compatible volume systems of the study by Diéguez-Aranda et al. [41] were tested. Analyses involved estimation of the parameters of the taper function and recovery of the implied total volume equation (see [33], for a detailed description of compatible volume systems fitting options), while addressing the error structure of the data and the multicollinearity among independent variables, which are the two main problems associated with stem taper analysis [61]. The fittings were carried out by use of the SAS/ETS® MODEL procedure [91], which allows for dynamic updating of the residuals.

Aggregation of total (v) or merchantable (v_i) tree volume times number of trees in each diameter class provides total or merchantable stand volume, respectively.

2.8. Selection of the best equation in each module

The comparison of the estimates of the different models fitted in each module was based on numerical and graphical analyses. Two statistical criteria obtained from the residuals were examined: the coefficient of determination for nonlinear regression (pseudo-R^2), which shows the proportion of the total variance of the dependent variable that is explained by the model, and the root mean square error (RMSE), which analyses the accuracy of the estimates.

Apart from these statistics, one of the most efficient ways of ascertaining the overall picture of model performance is by visual inspection. Graphical analyses, which involved examination of plots of observed against predicted values of the dependent variable and of plots of studentized residuals against the estimated values, were therefore carried out. Such graphs are useful for detection of possible systematic discrepancies. Specific graphs of the fitted curves overlaid on the trajectories of different variables were also examined. Visual inspection is essential for selecting the most appropriate model because curve profiles may differ drastically, even though statistical criteria and residuals are similar.

2.9. Overall evaluation of the model

Although the behaviour of individual sub-models within a model plays an important role in determining the overall outcome, the validity of each individual component does not guarantee the validity of the overall outcome, which is usually considered more important in practice. Therefore, the overall model outcome should also be evaluated.

Evaluation of forest growth models is not a single simple procedure, but consists of a number of interrelated steps that cannot be separated from each other or from model construction [100]. Some steps involve examination of the structure and properties of the model to confirm that it has no internal inconsistencies and is biologically realistic (model verification). Other steps require examination with additional data to quantify the performance of the model (model validation). Although the use of biological and theoretical criteria is important in model evaluation, the ability of a model to represent adequately the real world is normally addressed through model validation [90]. Ideally, such validation should involve the use of an independent data set [55, 63, 100, 103]. Moreover, variations in stand age and environmental factors must be included in the data set [13,81,94].

As new independent data for model validation were not available, observed state variables from the first and second inventories of the 179 and 46 plots measured two and three times, respectively, were used to estimate total stand volume at the age of the second and third inventories, including all the components of the whole-stand model. Total stand volume was selected as the objective variable because it is the critical output of the whole model, since its estimation involves all the functions included in it and is closely related to economical assessments.

Validation cannot prove a model to be correct, but may increase its credibility and the user's confidence in it [103]. According to Rykiel [87], validation is a demonstration that a model possesses a satisfactory range of accuracy consistent with its intended application. In the present study a chi-square test was used to assess whether the variance of the predictions is within some tolerance limits. The analysis was carried out for the time intervals for which real data were available (i.e., three, six and nine years), to determine the critical projection interval in terms of acceptable errors.

The χ^2 tests can be written in various forms. In this study the following formulation was used, which was computed re-arranging Freese's [45] χ^2_n statistic [82, 86]:

$$E_{crit.} = \frac{\sqrt{\tau^2 \sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / \chi^2_{crit.}}}{\bar{y}} \qquad (7)$$

where $E_{crit.}$ is the critical error, expressed as a percentage of the observed mean, n the total number of observations in the data set, y_i the observed value, $\hat{y}_i$ its prediction from the fitted model, $\bar{y}$ the average of the observed values, τ a standard normal deviate at the specified probability level ($\tau = 1.96$ for $\alpha = 0.05$), and $\chi^2_{crit.}$ is obtained for $\alpha = 0.05$ and n degrees of freedom. If the specified allowable error expressed as a percentage of the observed mean is within the limit of the critical error, the χ^2_n test will indicate that the model does not provide satisfactory predictions; otherwise, it will indicate that the predictions are acceptable.

In addition, plots of observed against predicted values of stand volume were inspected. If a model is good, the slope of the regression line between observed and predicted values should be 45° through the origin.

3. RESULTS

3.1. Transition function for dominant height growth[1]

The following model for height growth prediction and site classification was developed by Diéguez-Aranda et al. [39]:

$$\begin{aligned} H &= H_0 \left[\frac{1 - \exp(-0.06738t)}{1 - \exp(-0.06738t_0)} \right]^{-1.755+12.44/X_0}, \quad \text{with} \\ X_0 &= 0.5 \left[\ln H_0 + 1.755 L_0 \right. \\ &\quad \left. + \sqrt{(\ln H_0 + 1.755 L_0)^2 - 4 \times 12.44 L_0} \right], \quad \text{and} \qquad (8) \\ L_0 &= \ln\left[1 - \exp(-0.06738 t_0)\right] \end{aligned}$$

where H_0 and t_0 represent the predictor dominant height (metres) and age (years), and H is the predicted dominant height at age t.

To estimate the dominant height (H) of a stand for some desired age (t), given site index (SI) and its associated base age (t_{SI}), substitute SI for H_0 and t_{SI} for t_0 in Equation (8). Similarly, to estimate site index at some chosen base age, given stand height and age, substitute SI for H and t_{SI} for t in Equation (8).

Equation (8) explained 99.5% of the total variance of the data, and its RMSE was 0.552 m. In selecting the base age, it was found that 20 years was superior for predicting height at other ages. The curves for site indices of 11, 16, 21 and 25 m at a reference age of 20 years overlaid on the profile plots of the data set are shown in Figure 1.

3.2. Transition function for reduction in tree number

A dynamic equation considering only one parameter to be site-specific in the base model (Eq. (1)) described the data adequately:

$$N = \left(N_0^{-0.3161} + 1.053^{t-100} - 1.053^{t_0-100} \right)^{-1/0.3161} \qquad (9)$$

where N_0 and t_0 represent the predictor number of trees per hectare and age (years), and N is the predicted number of trees per hectare at age t.

[1] Although they were not developed in the present study, the site quality system developed by Diéguez-Aranda et al. (2005) and the generalized *h-d* equation developed by Castedo et al. (2006) are included in the Results section as part of a summary of all of the components of the dynamic whole-stand model.

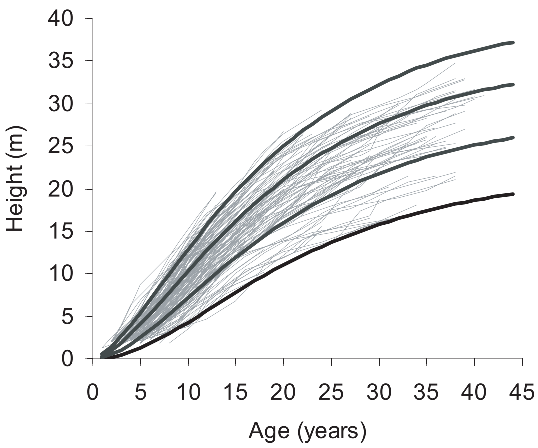

Figure 1. Curves for site indices of 11, 16, 21 and 25 m at a reference age of 20 years overlaid on the profile plots of the data set.

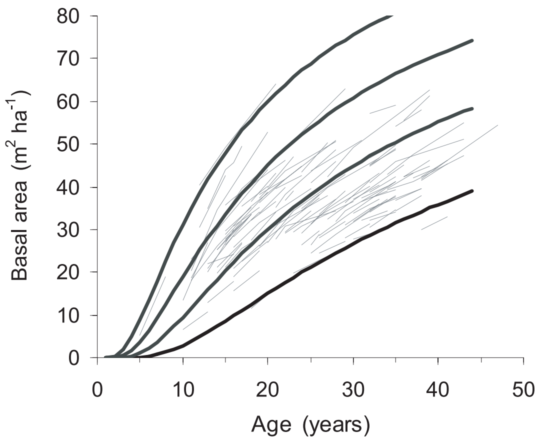

Figure 2. Trajectories of observed and predicted stem number over time. Model projections for initial spacing conditions of 400, 1100, 1800 and 2500 stems per hectare at 10 years.

Equation (9) explained approximately 99.3% of the total variance of the data and the RMSE was 54.8 trees/ha. The trajectories of observed and predicted number of trees over time for different initial spacing conditions are shown in Figure 2.

3.3. Transition function for stand basal area growth

Of the equations analysed, the models with two site-specific parameters provided similar results for projecting stand basal area over time. However, taking into account the adequate graphs (Fig. 3) and the high predictive ability of the model, as inferred from the goodness of fit statistics (R^2 = 0.994; RMSE = 1.29 m^2 ha^{-1}), a dynamic model derived from the

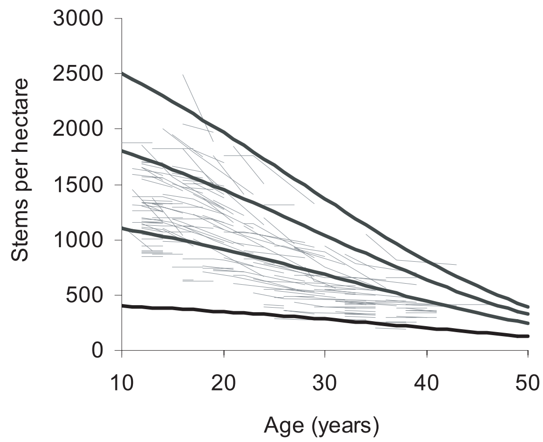

Figure 3. Stand basal area growth curves for stand basal areas of 15, 30, 45 and 60 m^2 ha^{-1} at 20 years overlaid on the trajectories of observed values over time.

Korf equation was selected. The model is expressed as follows:

$$G = \exp(X_0)\exp\left[-(-276.1 + 1391/X_0)\,t^{-0.9233}\right], \quad \text{with}$$
$$X_0 = 0.5t_0^{-0.9233}\left\{-276.1 + t_0^{0.9233}\ln(G_0) + \sqrt{4 \times 1391 t_0^{0.9233} + \left[276.1 - t_0^{0.9233}\ln(G_0)\right]^2}\right\} \quad (10)$$

where G_0 and t_0 represent the predictor stand basal area (m^2 ha^{-1}) and age (years), and G is the predicted stand basal area at age t.

The Korf base equation was also used to develop a stand basal area initialization function. The previously estimated parameters of the projection equation were substituted into the initialization equation, and the unknown site-dependent function X of the projection function was related to the inverse of the number of trees per hectare together with a power function of the site index:

$$G = \exp(X_0)\exp\left[-(-276.1 + 1391/X_0)\,t^{-0.9233}\right], \quad \text{with}$$
$$X_0 = 4.331SI^{0.03594} - \frac{114.3}{N} \quad (11)$$

where G is the predicted stand basal area (m^2 ha^{-1}) at age t, N the number of trees per hectare and SI the site index (m).

3.4. Disaggregation system

3.4.1. Diameter distribution

The equation selected for predicting arithmetic mean diameter and for use in the parameter recovery approach was:

$$\bar{d} = d_g - e^{0.1449 - 19.76\frac{1}{t} + 0.0001345N + 0.03264SI} \quad (12)$$

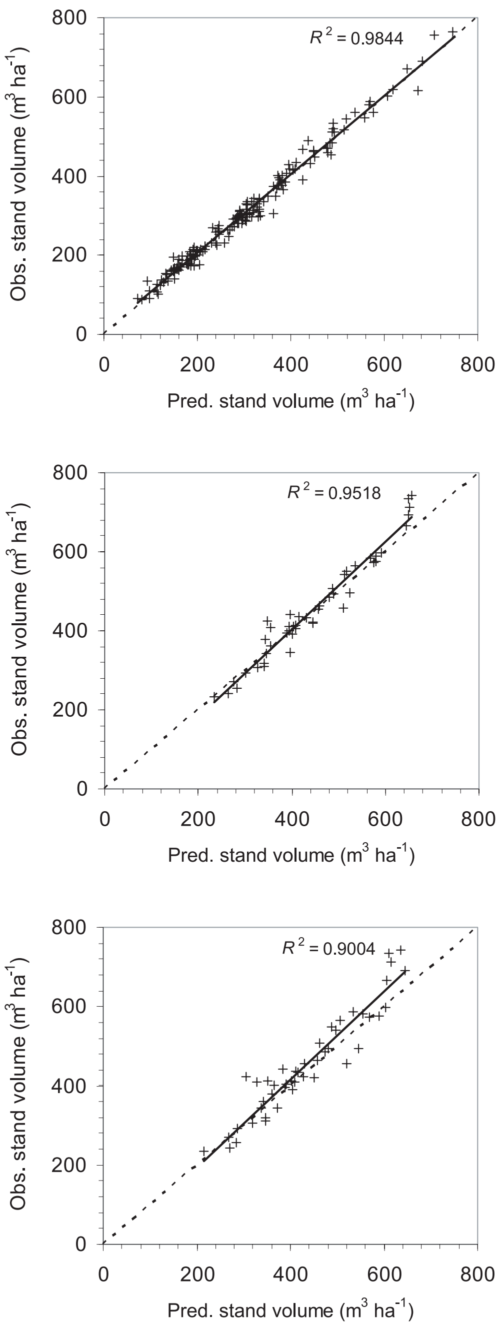

Figure 4. Plots of observed against predicted values of stand volume for the three time intervals evaluated. The solid line represents the linear model fitted to the scatter plot of data and the dashed line is the diagonal. R^2 is the coefficient of determination of the linear model.

where $\bar{d}$ is the predicted arithmetic mean diameter (cm), d_g the quadratic mean diameter (cm), t the stand age (years), N the number of trees per hectare, and SI the site index (m). The goodness of fit statistics were $R^2 = 0.999$ and RMSE = 0.34 cm.

3.4.2. Height estimation for diameter classes[1]

The following generalized *h*-*d* relationship was developed by Castedo et al. [23]:

$$h = \left[1.3^{0.9339} + \left(H^{0.9339} - 1.3^{0.9339}\right) \frac{1 - \exp^{-0.0661d}}{1 - \exp^{-0.0661D_0}}\right]^{1/0.9339} \quad (13)$$

where h is the predicted total height (m) of the subject tree, d its diameter at breast height (cm), and D_0 and H are dominant diameter and dominant height (the mean diameter and mean height of the 100 thickest trees per hectare, respectively) of the stand where the subject tree is included.

This modified expression of the Schnute function showed a high predictive ability ($R^2 = 0.945$; RMSE = 1.51 m), and is very parsimonious (it only depends on two stand variables).

3.4.3. Total and merchantable volume estimation

For total and merchantable volume estimation of the average tree in each diameter class, the compatible system proposed by Fang et al. [43] was selected. It is constituted by the following components:

Taper function:

$$d_i = c_1 \sqrt{h^{(k-b_1)/b_1} \left(1 - q_i\right)^{(k-\beta)/\beta} \alpha_1^{I_1+I_2} \alpha_2^{I_2}} \quad (14)$$

$$\text{where} \quad \begin{cases} I_1 = 1 \text{ if } p_1 \leq q_i \leq p_2;\ 0 \text{ otherwise} \\ I_2 = 1 \text{ if } p_2 < q_i \leq 1;\ 0 \text{ otherwise} \end{cases}$$

p_1 and p_2 are relative heights from ground level where the two inflection points assumed in the model occur

$$\beta = b_1^{1-(I_1+I_2)} b_2^{I_1} b_3^{I_2} \qquad \alpha_1 = (1 - p_1)^{\frac{(b_2-b_1)k}{b_1 b_2}}$$

$$\alpha_2 = (1 - p_2)^{\frac{(b_3-b_2)k}{b_2 b_3}} \qquad r_0 = (1 - h_{st}/h)^{k/b_1}$$

$$r_1 = (1 - p_1)^{k/b_1} \qquad r_2 = (1 - p_2)^{k/b_2}$$

$$c_1 = \sqrt{\frac{a_0 d^{a_1} h^{a_2 - k/b_1}}{b_1 (r_0 - r_1) + b_2 (r_1 - \alpha_1 r_2) + b_3 \alpha_1 r_2}}.$$

Merchantable volume equation:

$$v_i = c_1^2 h^{k/b_1} \Big(b_1 r_0 + (I_1 + I_2)(b_2 - b_1) r_1 + I_2 (b_3 - b_2) \alpha_1 r_2 - \beta (1 - q_i)^{k/\beta} \alpha_1^{I_1+I_2} \alpha_2^{I_2}\Big). \quad (15)$$

Volume equation:

$$v = a_0 d^{a_1} h^{a_2}. \quad (16)$$

A third-order continuous autoregressive error structure was necessary to correct the inherent serial autocorrelation of the experimental stem data. The model provided a very good data fit, explaining 98.9% of the total variance of d_i. Moreover, this model showed few problems associated with multicollinearity.

The resulting parameter estimates were:

a_0: $5.293 \cdot 10^{-5}$; a_1: 1.884; a_2: 0.9777; b_1: $9.193 \cdot 10^{-6}$;

b_2: $3.282 \cdot 10^{-5}$; b_3: $2.905 \cdot 10^{-5}$; p_1: 0.06832; p_2: 0.6566.

The following notation was used: d = diameter at breast height over bark (cm); d_i = top diameter at height h_i over bark (cm); h = total tree height (m); h_i = height above the ground to top diameter d_i (m); h_{st} = stump height (m); v = total tree volume over bark (m^3) above stump level; v_i = merchantable volume over bark (m^3), the volume from stump level to a specified top diameter d_i; a_0, a_1, a_2, b_1, b_2, b_3, p_1, p_2 = regression coefficients to be estimated; $k = \pi/40\ 000$, metric constant to convert from diameter squared in cm^2 to cross-section area in m^2; $q_i = h_i/h$.

3.5. Overall evaluation of the model

The growth model described above is comprehensive because it addresses all forest variables commonly incorporated in quantitative descriptions of forest growth. The method of construction adopted is robust because it is based on only three stand variables; any other variables are derived by auxiliary relationships.

As judged by the observed extrapolation properties, the behaviour of the different components is logical for ages close to the rotation length usually applied to radiata pine stands in Galicia (25–35 years) (see Figs. 1–3). Moreover, the model can efficiently project stand development starting from different spacing conditions and considering different thinning schedules.

To assess if the model satisfies specified accuracy requirements, observed dominant height, number of trees per hectare and stand basal area from the first and second inventory of the 179 and 46 plots measured two and three times, respectively, served as initial values for the corresponding transition functions (Eqs. (8), (9), and (10)). These equations were used to project the stand state at the ages of the second and third inventory. Equation (12) was then used to estimate the arithmetic mean diameter, which allowed calculation of the variance of the diameter distribution. Equations (3) and (4) were used to recover the Weibull parameters, which allowed estimation of the number of trees in each diameter class. Equations (13) and (16) were used to estimate the height and the total volume of the average tree in each diameter class, respectively. Aggregation of total tree volume multiplied by the number of trees in each diameter class provided total stand volume.

A plot of observed against predicted values of stand volume obtained following the above procedure for the three time intervals considered (3, 6 and 9 years) is shown in Figure 4. The linear model fitted for each scatter plot behaved well in all three cases (R^2 = 0.984, 0.952 and 0.901, respectively). The plot also showed that there were no systematic over- or underestimates of stand volume for prediction intervals of three and six years; however, there was a slight tendency towards underestimation for a time interval of nine years. Critical errors of 10.9%, 11.9% and 17.3% were obtained for projecting total stand volume for time intervals of 3, 6 and 9 years, respectively.

4. DISCUSSION

This study presents a whole-stand growth model for radiata pine plantations in north-western Spain, based on the state-space approach outlined by García [50]. The state of a stand was adequately described by the following state variables: dominant height, number of trees per hectare and stand basal area. The behaviour of the system is described by the rate of change of these state variables given by their corresponding transition functions. In addition, other stand variables of interest (quadratic mean diameter, total or merchantable volume, etc.) can be obtained from the current values of the state variables. According to this basic structure, the whole-stand model requires five stand-level inputs for simulation: the age of the stand at the beginning and the end of the projection interval, and the initial dominant height, number of trees per hectare and stand basal area.

All the transition functions used have a theoretical basis, and have been developed using a recently developed technique for dynamic equation derivation (GADA: [28]), which ensures that base-age and path invariance properties provide consistent predictions. Furthermore, the functions were fitted using a base-age invariant method that accounts for site-specific and global effects [29].

Dominant height growth transition function consistently provided accurate values of site indices from heights and ages, and accurate values of heights from age and site indices, regardless of the levels of site productivity. This is important as height growth transition function is one of the basic submodels in whole-stand and other type of growth models (e.g., [53,89]).

The accuracy of the stand survival function over a wide range of ages and other stand conditions ensures that the projections of the final output variables of the whole model (e.g., stand or merchantable volume) are realistic. This equation is especially important when light thinnings are carried out [5], as was the case in most of the studied stands. After heavy thinning operations it seems reasonable to assume that mortality is negligible.

As regards the stand basal area projection equation, initial basal area and initial age provided sufficient information about the future trajectory of the basal area of the stand, regardless its thinning history. Therefore, the thinning effect is built into the model, in accordance with the studies of other authors for several species and regions [8, 20, 71]. It must also be considered that the basal area initialization equation will work well in unthinned or lightly thinned stands younger than 15 years (similar to those where the experimental data were collected). Because the number of trees per hectare varies over time, the initialization and the projection functions are not compatible. However, this is not a major problem because the initialization function would only be used to provide an initial value of stand basal area when no inventory data are available [4].

Explanatory variables of the components of the disaggregation system can be easily obtained at any point in time from dominant height, number of trees and basal area transition functions. The only exception is dominant diameter of the generalized *h-d* relationship, which is a variable that is difficult to project [64] and must therefore be estimated from the diameter distribution.

Total stand volume was selected in the present study as the critical output variable for the whole-stand growth model, although other stand variables can be assessed on the basis of this model (e.g., biomass, carbon pools). The allometric equations for different biomass fractions developed for this species by Merino et al. [72], which use the diameter at breast height and the total height as independent variables, can, for example, be easily incorporated into the disaggregation system proposed.

The global whole-stand growth model presented was demonstrated to be robust for medium term projections of stand volume, even outside the domains of the database used in its construction. Considering the required accuracy in forest growth modelling, where a mean prediction error of the observed mean at 95% confidence intervals within ±10%−20% is generally realistic and reasonable as a limit for the actual choice of the acceptance and rejection levels [55], we can state that, on the basis of the critical error statistic obtained, the model provides satisfactory predictions even for the longest projection interval (nine years). Nevertheless, for long-term projections, direct volume estimations for six-year intervals are recommended. This alternative approach implies the availability of a new inventory of the stand every six years, but allows reduction, by almost a third, of the critical error of stand volume estimations.

The relatively simple structure of the growth model makes it suitable for embedding into landscape-level planning models and other decision support systems that enable forest managers to generate optimal management strategies. Nevertheless, because of the large number of calculations needed to obtain outputs (especially those involving use of the disaggregation system), the model was implemented into a forest growth simulator called GesMO [22, 38] to facilitate its use by forest managers.

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