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A state-space approach to stand growth modelling of European beech

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Abstract – Static models of forest growth, such as yield tables or cumulative growth functions, generally fail to recognize that forest stands are dynamic systems, subject to changes in growth dynamics due to silvicultural interventions or natural dynamics. Based on experimental data, covering a wide range of initial spacings and thinning practises, we developed a dynamic stand growth model of European beech in Denmark. The model entailed three equations for predicting dominant height growth, basal area growth, and mortality. The signs of the parameter estimates generally corroborated the anticipated growth paths of dominant height and basal area. Although statistical tests indicated significant systematic deviations between observed and predicted values, the deviations were small and of little practical importance. Cross validation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises without significant loss of precision.

difference equation / dominant height / basal area / stem number / *Fagus sylvatica* L.

Résumé – Une approche état-espace de la modélisation de la croissance des peuplements de hêtre. Les modèles statiques de croissance des peuplements forestiers, tels que les tables de production ou les fonctions cumulatives de croissance, ne reconnaissent pas que les peuplements forestiers sont des systèmes dynamiques, soumis à des changements de dynamiques de croissance dus aux interventions sylvicoles ou à des dynamiques naturelles. Sur la base de données expérimentales, couvrant un large éventail d'espacements initiaux et de pratiques d'éclaircie, nous avons développé un modèle dynamique de croissance de peuplement pour le hêtre au Danemark. Le modèle comporte trois équations pour prédire la croissance de la hauteur dominante, la croissance de la surface terrière et la mortalité. Les signes des paramètres estimés ont confirmé en général la trajectoire prévue de la croissance de la hauteur dominante et de la surface terrière. Bien que les tests statistiques aient indiqué des déviations systématiques significatives entre valeurs observées et valeurs prédites, les déviations ont été faibles et de peu d'importance pratique. Des procédures de validation croisées ont indiqué que le modèle peut être appliqué dans un large éventail de conditions de croissance et de pratiques sylvicoles sans perte significative de précision.

équation aux différences / hauteur dominante / surface terrière / nombre de troncs / *Fagus sylvatica* L.

1. INTRODUCTION

Fitting of simple growth curves for prediction of stand level variables such as average height, stand basal area or stem number is an old discipline in forest growth modelling [3,7,17,30]. Such models describe the course of stand variables over time and may yield reasonable estimates in many situations. However, these static models generally fail to recognize that forest stands are dynamic systems, subject to sudden changes caused by silvicultural interventions or natural dynamics. As the intensity of management increases, interventions may vary in timing and intensity and the stand variables may follow a potentially infinite number of paths [15].

Dynamic systems subject to environmental change may be modelled using the state-space approach. The state-space approach relies on the assumption that the state of a system at any given time contains the information needed to predict the behaviour of the system in the future [15]. Hence, the state of a system may be viewed as the cumulated information of the past, and only information on the present is needed to predict the future behaviour of the system. Change (increment or mortality) is modelled from the state of the system at any point in time and any future state is predicted from the current state and current and future actions through iteration. The state-space approach in this sense is closely related to the concept of control theory, and is adequate for modelling systems subject to control (i.e. environmental changes) with feed back because explicit modelling of the complex relation between interventions and responses of the system is avoided.

Covering 17% of the total forest area European beech is the most common deciduous species in Denmark [26] and also one of the most significant in economic terms. Current models for predicting stand level growth of beech in Denmark are standard yield tables based on graphical smoothing of permanent sample plot data [21,34]. Despite the practical importance of these tables, the methods applied in their construction have generally lacked statistical rigour and objectivity. The aim of this study was to develop a stand level model for predicting the growth of even-aged stands of European beech. The main focus was the development of dynamic models based on a state-space approach.

2. MATERIALS AND METHODS

The data potential for developing stand level models for beech comprised 60 permanent, even-aged and mono-specific spacing,

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species and thinning experiments in beech including a total of 149 individual plots. Plot sizes varied between 0.07 and 2.65 ha with an average of 0.40 ha. The experiments were located in most parts of Denmark and covered a wide range of different site types and growth conditions. The data was collected during the years 1872 to 2005 and the stands were observed for 10 to 120 years. The number of measurement occasions totalled 2065.

The data included a wide range of different treatments in terms of initial spacing and thinning practices from unthinned control plots to heavily thinned plots. In the thinning experiments, the treatments included A-, B-, C-, and D-grade thinnings, and in some cases even heavier thinnings. Usually, the D-grade is thinned to a basal area of 50% relative to the unthinned control (A-grade). The B- and C-grades are intermediate, dividing the interval between A-and D-grades equally. Some plots were managed according to other thinning strategies, such as group- or selection-thinning and others were managed according to the thinning strategy typical at the time.

In the majority of plots, all trees were numbered, marked permanently at breast height (1.3 m) and recorded individually. In 451 measurements carried out before 1930 and in some very young stands with high stem numbers, trees were recorded in tally lists to 1-cm diameter classes (before 1901 to 1-inch classes). Also in 13 very young stands with high stem numbers, only a subset of stems were measured, e.g. every fifth or tenth row. Breast height diameters were obtained by averaging two perpendicular calliper readings. Observations also included records on whether the tree was alive or dead at the time of measurement. Total height was typically measured for about 30 trees per plot on each measurement occasion. Finally, soil texture analyzes were carried out in 48 experiments, providing information on percentages of clay, silt, fine sand and coarse sand in the top one metre of the mineral soil.

2.1. Basic calculations

Based on paired observations of diameter and height, height-diameter equations were estimated for each plot and measurement occasion using a modified Näslund-equation [24, 36]:

$$h_{ij} = 1.3 + \left(\frac{d_{ij}}{\alpha + \beta \cdot d_{ij}}\right)^3 + \varepsilon_{ij} \tag{1}$$

where d_{ij} is diameter at breast height and h_{ij} is total tree height of the ith tree and jth plot and measurement occasion. α and β are parameters to be estimated and ε is the error term. The equations were used to estimate the height of trees not measured. Dominant height, H_{100} (m), defined as arithmetic mean height of the 100 thickest trees per hectare was subsequently calculated for each plot and measurement combination. In the few cases where stem numbers were less than 100 per hectare, H_{100} was estimated as the arithmetic mean height. Differences in plot size affect dominant height estimates, leading to underestimation on small plots. However, as there is no correlation between treatment and plot size (plots with many stems per hectare are not generally smaller than plots with few stems per hectare), there are no systematic effects of the choice of plot sizes. Further, although the span of plot sizes seem large, the majority of plots are approximately the same size (0.25–0.5 ha).

Stem numbers, N (100 ha^{-1}) were calculated as the number of individual trees per hectare taller than 1.3 m. When trees forked below 1.3 m, each stem was measured individually but multiple stems from the same root were counted as one tree. Within the research

Table I. Summary statistics of dominant height (H_{100}), basal area (G), stem number (N), quadratic mean diameter (D_g) and age (T).

Variable	Unit	N	Mean	Minimum	Maximum	Std. Dev.
H_{100}	m	1458	20.88	5.08	36.95	7.69
G	m^2 ha^{-1}	1458	20.04	0.21	73.58	8.92
N	ha^{-1}	1458	1372	0.49	24720	2317
D_g	cm	1458	26.72	2.70	82.85	17.56
T	years	1458	60.70	14	200	47.65

plots, trees were typically separated into over- and understorey and the understorey was measured less intensively than the overstorey. Understorey trees were excluded from this analysis.

Stand basal area, G (m^2 ha^{-1}), of each plot was estimated by summation of individual tree basal areas calculated from the diameter measurements. When trees were recorded in tally lists, the mid-diameter of each class was used as an estimate of the diameter of all trees in that class. Quadratic mean diameter, D_g (cm), was derived from the estimates of N and G. The data represent a wide range of stand ages and stand values such as H_{100}, G, N, and D_g (Tab. I, Fig. 1).

2.2. Model development

Any number of stand variables may be chosen to describe stand-level growth. The choice depends on the desired level of resolution and the practical application. Among the most commonly used variables in stand level models are H_{100}, G, N, D_g, and stand volume (V) and their derivatives. Since D_g and V may be derived from the first three variables, the models in this study included H_{100}, G, and N.

The model form used to describe the development of different variables essentially depends on the modelling subject and a great variety of model forms have been presented for various forestry applications. Forest growth dynamics are often characterized by an initial expansion followed by a dampening effect and may adequately be described with a sigmoid model form. Among the most well known sigmoid models are the mono-molecular [33], logistic [45,46], Gompertz [16], Bertalanffy [2] and Richards [39] equations. Despite the apparent diversity of growth models, [48] found that most of the mentioned equations can be transformed into a single equation in which the two opposing factors, initial multiplicative expansion followed by exponential dampening are expressed as:

$$\frac{dy}{dt} = \alpha y^\beta e^{\gamma y} \tag{2}$$

where y represents the size of the modelling subject and α, β, and γ are parameters. This equation is very similar to that of Bertalanffy [2], and was initially developed for predicting individual tree growth and has in a number of studies been expanded to include a number of additional elements such as basal area and basal area in larger trees [18, 19, 23]. Different forms of Equation (2) have also been used in stand growth modelling [23]. Greatly inspired by the latter work and based on the proposition that density measured as stand basal area affects both basal area growth and dominant height growth, we used the following equations to describe height and basal area growth:

$$\frac{dH_{100,ij}}{dt} = \alpha_0 H_{100,ij}^{\alpha_1} e^{\alpha_2 H_{100,ij} + \alpha_3 G_{ij}} + \varepsilon_{H,ij} \tag{3}$$
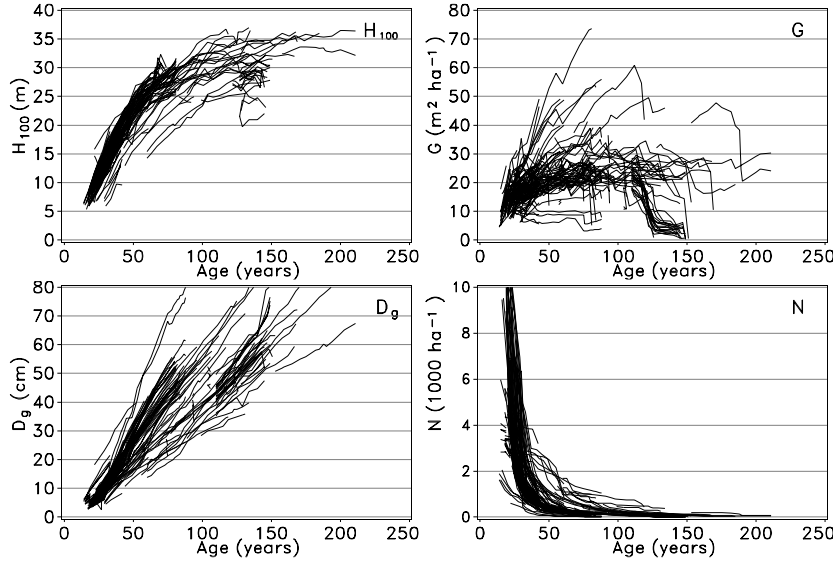
Figure 1. Stand-level values of H_{100}, G, N, and D_g.

$$\frac{dG_{ij}}{dt} = \beta_0 G_{ij}^{\beta_1} e^{\beta_2 G_{ij} + \beta_3 H_{100,ij}^{\beta_4}} + \varepsilon_{G,ij}, \tag{4}$$

where $\alpha_0 - \alpha_3$ and $\beta_0 - \beta_4$ are parameters to be estimated and $\varepsilon_{H,ij} \sim N\left(0, \sigma_H^2\right)$ and $\varepsilon_{G,ij} \sim N\left(0, \sigma_G^2\right)$ are the error terms of the ith measurement occasion on the jth plot.

The reduction in stem number in even-aged stands is caused by thinning operations and mortality. When using the state-space approach, thinnings are simulated explicitly and need not be modelled. Mortality may be perceived to consist of two factors: (i) simple chance of death and (ii) a density-dependent mortality that increases with density. We modelled the simple chance of death as a fraction of the stem number and the density dependent reduction in stemnumbers by the exponential of the inverse relative spacing ($RS = \sqrt{10000/N}/H$):

$$\frac{dN_{ij}}{dt} = -\gamma_1 N_{ij}^{\gamma_2} e^{\gamma_3 \sqrt{N_{ij}} H_{100,ij}} + \varepsilon_{N,ij} \tag{5}$$

where ε is the error term and $\gamma_1 - \gamma_3$ are parameters to be estimated. Preliminary estimation of the model revealed that a simpler model and similar fit statistics were obtained for $\gamma_2 = 1$, while ensuring a reasonable model behaviour. Thus in the final estimation of the system of equations, γ_2 was fixed at 1.

In Equations (3), (4) and (5) the state-space problem is formulated as a continuous-time model. However, since the equations above have no analytical solution they must be estimated numerically which is rather cumbersome. To reduce the computational load we used a discrete-time model in which $\Delta y / \Delta t$ is substituted for dy/dt:

$$\frac{\Delta H_{100,ij}}{\Delta t} = \alpha_0 H_{100,ij}^{\alpha_1} e^{\alpha_2 H_{100,ij} + \alpha_3 G_{ij}} + \varepsilon_{H,ij} \tag{6.1}$$

$$\frac{\Delta G_{ij}}{\Delta t} = \beta_0 G_{ij}^{\beta_1} e^{\beta_2 G_{ij} + \beta_3 H_{100,ij}^{\beta_4}} + FV[G]_{i+1,j} + \varepsilon_{G,ij} \tag{6.2}$$

$$\frac{\Delta N_{ij}}{\Delta t} = -\gamma_1 N_{ij}^{\gamma_2} e^{\gamma_3 \sqrt{N_{ij}} H_{100,ij}} + FV[N]_{i+1,j} + \varepsilon_{N,ij} \tag{6.3}$$

In the discrete model, shifts in G and N caused by thinnings or environmental hazards are formulated explicitly by "Forcing Values", *FV[G]* and *FV[N]* respectively.

2.3. Site-specific effects

Modelling growth and yield requires some measure of site quality to make reasonable forecasts. In a number of studies the site-specific effects have been included by allowing some parameters to be local or plot-specific and others to be general or global [1, 6, 14]. Subsequently the local parameters may be related to site index or environmental properties such as climate, elevation or soil properties, or the parameter estimate may be perceived as an indicator of site quality itself [23, 27, 31].

Which parameter to make local and which to make global depends on the modelling subject. The simplest formulation of Equations (6.1) and (6.2) emerges from leaving α_0 and β_0 to be local and the remaining parameters to be global since the site-specific parameter is then a simple factor. Preliminary studies showed similar fit statistics and extrapolation properties of making α_0 and α_1 local whereas making α_2 local resulted in poorer model performance. Although the fit statistics showed no differences between the two first formulations, making α_0 and β_0 local resulted in greater ease of fit and a simpler model as the site specific effect is then merely a factor.

When fitting a similar system of equations, Johannsen [23] hypothesized that it is possible to find an allometric relation between the site-specific parameters of the height and basal area equations. Hence the site-specific effect of both equations may be captured in one rate constant (a). Preliminary studies showed that α_0 and β_0 were highly correlated and their relation was adequately modelled by a linear model. Hence, the following system of equations was obtained:

$$\frac{\Delta H_{100,ij}}{\Delta t} = a_j H_{100,ij}^{\alpha_1} e^{\alpha_2 H_{100,ij} + \alpha_3 G_{ij}} + \varepsilon_{H,ij} \tag{7.1}$$

$$\frac{\Delta G_{ij}}{\Delta t} = \left(\beta_{01} + \beta_{02} \cdot a_j\right) G_{ij}^{\beta_1} e^{\beta_2 G_{ij} + \beta_3 H_{100,ij}^{\beta_4}} + FV[G]_{i+1,j} + \varepsilon_{G,ij} \tag{7.2}$$

$$\frac{\Delta N_{ij}}{\Delta t} = -\gamma_1 N_{ij}^{\gamma_2} e^{\gamma_3 \sqrt{N_{ij}} H_{100,ij}} + FV[N]_{i+1,j} + \varepsilon_{N,ij} \tag{7.3}$$

where α_0 in Equation (6.1) is substituted by the local parameter a and β_0 in Equation (6.2) is substituted by a linear function of a and the two global parameters β_{01} and β_{02}. The remaining parameters were

estimated globally. Note that *a* represents a site-specific effect that may be considered a random effect in a mixed, hierarchical model (for an example see [20]). However, this requires that the random effect is normally or otherwise distributed. Rather than making such assumptions we estimated *a* specifically for each experiment using an index variable method.

For practical application of the stand model, *a* must be estimated from a series of observations of height and basal area. When the model is applied where beech has not been grown before or when there are no sequential observations of stand variables the estimation cannot be carried out. In a preliminary study we therefore related *a* to the proportion of different soil fractions (clay, silt, fine sand, and coarse sand) in the uppermost 1 m of the soil to see if *a* could be estimated from soil properties alone, but found no statistically significant correlations. However, *a* was highly correlated with the more traditional measure of site quality, site index, defined as the dominant height at age 50. To allow flexible use of the model, depending on the available data, we also estimated the stand level model where site specific effects were substituted by a linear function of site index (S):

$$\frac{\Delta H_{100,ij}}{\Delta t} = \left(\alpha_{01} + \alpha_{02} \cdot S_j\right) H_{100,ij}^{\alpha_1} e^{\alpha_2 H_{100,ij} + \alpha_3 G_{ij}} + \varepsilon_{H,ij} \quad (8.1)$$

$$\frac{\Delta G_{ij}}{\Delta t} = \left(\beta_{01} + \beta_{02} \cdot S_j\right) G_{ij}^{\beta_1} e^{\beta_2 G_{ij} + \beta_3 H_{100,ij}^{\beta_4}} + FV[G]_{i+1,j} + \varepsilon_{G,ij} \quad (8.2)$$

$$\frac{\Delta N_{ij}}{\Delta t} = -\gamma_1 N_{ij}^{\gamma_2} e^{\gamma_3 \sqrt{N_{ij}} H_{100,ij}} + FV[N]_{i+1,j} + \varepsilon_{N,ij} \quad (8.3)$$

Site index was estimated for each experiment prior to fitting of the dynamic stand model using a site equation developed for beech in Denmark [37].

2.4. Model estimation

Different forms of the state-space approach have been used by various authors to model individual tree or stand-level growth. García [14] modelled height growth of even-aged stands by a stochastic differential equation. The parameters were estimated simultaneously by a maximum-likelihood procedure that included an explicit expression of the error term.

Instead of using continuous-time models, a number of authors have fitted discrete-time models of individual tree and stand level growth. Lynch and Moser [28] as well as Hein and Dhôte [20] related average rates of change to the current state of the system ("averaging method" or "difference quotient method"). Clutter [7] recognized that the average growth rate is more likely to be closest to the actual growth rate at the midpoint of the measurement interval and related average changes to the interpolated state variables at the midpoint of the observed growth interval ("midpoint method").

Rather than assuming the growth rate to be constant and equal to average growth throughout the growth period McDill and Amateis [32] suggested that discrete time models should be fitted from observations with any time interval using the hypothesized functional form of the difference equation as basis for interpolation. This approach was later generalized for predicting annual growth rates for a number of individual tree and stand level variables [4,5,23].

Following the approach of McDill and Amateis [32] the estimation problem may be written as a series of annual difference equations that increment stand height, stand basal area or stem numbers from some initial state to the state at some later point in time, using the years

between the two observations as the number of iterations. Considering height, the state at the end of the growth period may be predicted from the state at the beginning of the growth period by a series of predicted annual increments:

$$\hat{H}_{i+1,j} = H_{ij} + f\left(H_{ij}, G_{ij}\right) \quad (9.1)$$

$$\hat{H}_{i+2,j} = \hat{H}_{i+1,j} + f\left(\hat{H}_{i+1,j}, \hat{G}_{i+1,j}\right) \quad (9.2)$$

$$\vdots$$

$$\hat{H}_{i+t,j} = \hat{H}_{i+t-1,j} + f\left(\hat{H}_{i+t-1,j}, \hat{G}_{i+t-1,j}\right), \quad (9.3)$$

where $f\left(H_{ij}, G_{ij}\right)$ is expressed in Equation (7.1) and models annual height increment at the *j*th plot at the time $i + t$ $(t = 0, 1, 2,\dots,n)$. The parameters of the annual difference equation may then be estimated using a nonlinear least squares procedure that minimizes the squared deviations of $\hat{H}_{i+t,j}$ from $H_{i+t,j}$.

As indicated in Equation (9.1), the procedure requires some initial observation to initiate the iterations. The initial state may be either [23]:

1. Fixed initial values;
2. The first measurement at each plot;
3. The previous measurement of each state-variable ;
4. Estimated initial values, (i) common to all observations, (ii) common to each plot or (iii) unique for each observation.

Using fixed initial values for the estimation procedure as in (1) and (4) requires that all thinnings throughout the stands life have been recorded to account for shifts in G and N (see Eqs. (6.2) and (6.3)). Since unrecorded thinnings oftentimes occurred before the establishment of the experiments, this option was precluded. Options (2) and (3) both use measured values as initial conditions and avoid the problem of silvicultural activities before the initiation of the experiments. Using the previous measurement as initial state prevents error accumulation due to errors in the shift vectors and this method to a greater extent reflects the practical application. Consequently, the estimation procedure was carried out using option (3).

The system of equations presented in (7.1)–(7.3) is referred to as a seemingly unrelated regression (SUR) system since only one dependent variable occurs in each equation. If no error correlation exists between the individual regressions they may be treated as independent problems. However, if error correlations are present OLS estimates are inefficient. In this study cross-equation error correlations were included in a generalized least squares procedure using iterated seemingly unrelated estimation (ITSUR) [41].

The data used for this study represents a structure of repeated measurements on individual plots. Failure to recognize that within-plot measurements are correlated may result in inefficient estimates and underestimated standard errors when correlations are strong. When growth is viewed as an incremental process where only current conditions influence current growth, the problems of serial correlation are usually avoided [14, 42]. However, we explicitly modelled the serial correlation by including a generalized formulation of the first-order autoregressive model that accommodates the irregular spacing of measurements:

$$\varepsilon_i = \rho_m^{t_i - t_{i-1}} \varepsilon_{i-1} + u_i \ (i = 1, 2, ..., n) \quad (10)$$

where ε_i is the error at the *i*th measurement, *t* is the time, ρ_m is the coefficient of correlation of the *m*th equation and the u_i's are normally and independently distributed random errors.

2.5. Statistical fit of the model

Characterization and assessment of errors cannot be performed directly on the model subject since the model predicts annual increment, which is not observed directly. Instead model evaluation may be carried out on the predicted state of the model subject at the end of the period. However, this leads to highly inflated estimates of fit statistics since much of the variation is explained by the initial state of the model subject. Instead the errors may be characterized by the deviations between predicted and observed periodic annual increment (*PAI*). The two measures were both applied in the analyzes.

Model error were first characterised in terms of magnitude and distribution by plotting residuals against predicted values of the model subject. Furthermore, residuals were plotted against observed values of other stand variables to expose any obvious trends. Temporal and regional trends were evaluated by plots of residuals against measurement years and natural-geographical regions of Denmark according to Jakobsen [22].

In addition to the visual appraisal of the errors a number of summary statistics were calculated for the entire data set as well as for different strata and initial values of the model subject. The summary statistics include average bias (AB), average absolute bias (AAB), root mean squared error (RMSE), R^2-statistics and critical error confidence bounds (CEB) [12, 38]. The latter provides an estimate of the magnitude of the error that can be expected when using the model.

Statistical tests of model bias, model stability, and for the model assumptions on patterns and distribution of the residuals, were carried out. The statistical tests of model bias included simultaneous F-tests for unit slope and zero intercept of the linear regression of observed versus predicted data [9]. Predictive performance and stability of the parameter estimates were evaluated by leave-one-out cross validation in which entire experiments were left out of the estimation data one at a time and subsequently the estimated model was applied to the left-out experiment. This procedure was extended to evaluate the stability of parameter estimates across site index, thinning practises, regions and time of birth by iteratively leaving out different strata of data.

3. RESULTS

Parameter estimates of equations (7.1)–(7.3) and (8.1)–(8.3) were all significant ($P < 0.05$) except for α_{01} and β_{01}, which were both eliminated from the models. After reduction of the models all parameters were significant. The correlation coefficient of the height model (ρ_H) was non-significant, indicating no correlation of height growth in subsequent growth periods. The correlation coefficient of basal area growth (ρ_G) was highly significant, which may indicate that basal area growth in subsequent periods was positively correlated or may originate from model misspecification.

The reduced model system, using the site specific parameter a (Eqs. (7.1)–(7.3)) accounted for more than 98% of the observed variation of H_{100}, G, and N at the end of the growth period (Tab. II). Based on *PAI* the height and basal area models explained 33% and 72% of the total variation in annual growth, respectively, whereas the mortality model explained 44% of the observed annual changes in stem numbers. Also based on *PAI*, average bias (AB) was very close to 0 for all models. Average absolute bias (AAB) was 0.14 m for the height growth model, 0.18 m^2 ha^{-1} for the basal area

growth model, and 24 ha^{-1} for the mortality model. Root mean squared error (RMSE) was 0.22 m for the height growth model (based on PAI), 0.27 m^2 ha^{-1} for the basal area growth model and 80 ha^{-1} for the mortality model. Critical error confidence bounds (CEB) was 0.42–0.44 m for the height growth model, 0.51–0.55 m^2 ha^{-1} for the basal area growth model and 153–164 ha^{-1} for the mortality model. Precision and bias of system of equations using site index (Eqs. (8.1)–(8.3)) was almost identical to that of Equations (7.1)–(7.3).

Plots of residual *PAI* of H_{100}, G, N and D_g against their corresponding predicted values revealed no obvious trends (Fig. 2). Neither did plots of residual *PAI* for the three models against other stand variables (not shown). Simultaneous F-tests did not reveal any model bias of the height and mortality models but showed a significant bias of the basal area model. However, the systematic deviations were small and of little practical importance.

Residuals were approximately homogeneous with zero mean for H_{100} and G, but residual variance for N increased with increasing stem numbers. As variance heterogeneity only affects parameter estimates when it expresses some model misspecification, the latter may only be important in relation to model inference. Distributions of the residuals of the three models all deviated significantly from normality, although a graphical analysis indicated that deviations were small. Residuals of individual experiments after correction for first-order serial correlation had no significant correlations.

The cross-validation procedure of leaving out entire experiments in the estimation resulted in only a small increase in RMSE of the H_{100} and G models (0.6% and 5.4% respectively) but a rather large increase for the N model (61%). Further cross-validation procedures in which different classes of data were left out based on different characteristics (i.e. site index, growth region, year of birth and thinning intensity) resulted in only a small increase in RMSE, indicating a remarkable stability of the parameter estimates.

4. DISCUSSION
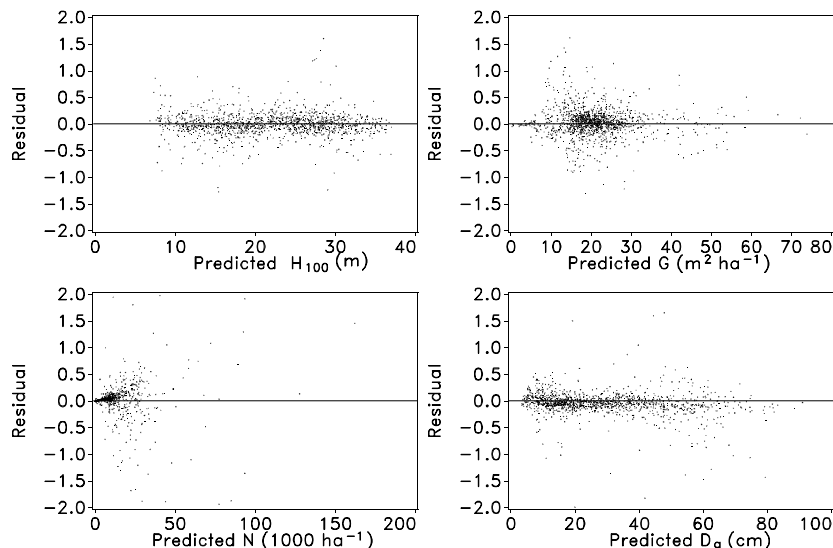
4.1. Parameter estimates

The signs of the parameter estimates generally corroborated the anticipated growth paths of both H_{100} and G (Tab. II). The positive α_2 and β_2 indicates an initial multiplicative expansion of growth followed by an exponential dampening as a result of the negative estimates of α_3 and β_3, the resulting growth curve being sigmoid.

The estimate of α_4 indicates a positive response of dominant height growth to increasing levels of stand density (Fig. 3). This finding contradicts the generally accepted notion that height growth is essentially unaffected by stand density. A similar pattern is also observed for a number of other species including Scots pine [13], oak [23], ash [25], jack pine and aspen [11]. Conversely, MacFarlane et al. [29] and DeBell and Harrington [8] found the opposite effect of density on height growth in loblolly pine and red alder, respectively. The specific effect is probably dependent on species, site, and stand

Table II. Parameter estimates of the system of equations presented in equations (7.1)–(7.3) and (8.1)–(8.3) along with their standard errors. R was calculated from the deviations between predicted and observed values at the end of the growth periods.

Site parameter		a			Site index		
Model	Parameter	Estimate	Std. err.	R^2	Estimate	Std. err.	R^2
H_{100}	a	0.0281[a]	0.0100[a]	0.9909	–	–	0.9909
	α_{02}	–	–		1.842×10^{-3}	6.06×10^{-4}	
	α_1	2.1092	0.1913		1.8290	0.1844	
	α_2	–0.1907	0.0117		–0.1791	0.0113	
	α_3	0.0138	0.0023		0.0145	2.18×10^{-3}	
	ρ_H	0.0128	0.2357		0.0143	0.2386	
G	β_{02}	31.3437	11.1644	0.9904	0.0406	5.66×10^{-3}	0.9882
	β_1	0.5087	0.0744		0.5736	0.0690	
	β_2	–0.0125	0.0033		–0.0151	3.18×10^{-3}	
	β_3	–0.0175	0.0071		–0.0756	0.0240	
	β_4	1.3125	0.1089		0.9466	0.0797	
	ρ_G	0.7173	0.0178		0.7299	0.0177	
N	γ_1	0.0008	0.0001	0.9883	6.93×10^{-4}	1.30×10^{-4}	0.9885
	γ_2	1	–		1	–	
	γ_3	0.0342	0.0016		0.0349	0.0177	

[a] Estimated individually for each experiment. Number represents a simple average.

Figure 2. Residual plots of H_{100}, G, N, and D_g. Residuals were calculated as the difference between predicted and observed periodic annual increments. Residuals of D_g were derived from the estimates of G and N.

age [10]. Increased height growth at increasing densities is probably mediated through the phytocrome system as an allometric response in crowded populations towards allocating more resources to height growth, reducing the possibility of being overtopped by future competitors [40].

The negative parameter estimate of β_4 and positive estimate of β_5 causes basal area growth to decrease as height increases (Fig. 3). As height may be viewed as an expression of physiological age, this may be an anticipated effect of aging, but may also reflect a tendency towards allocating more resources to the upper part of the stem and the crown as tree size increases

in closed stands. Again, this may be related to phytocrome response patterns. The parameters of the mortality model show a low probability chance of death that is increasing with increasing density.

4.2. Comparison with Danish yield tables

The model was compared to the two most commonly used yield tables for beech in Danish forestry [21, 34] by simulating height development of each of the height classes (Fig. 4).
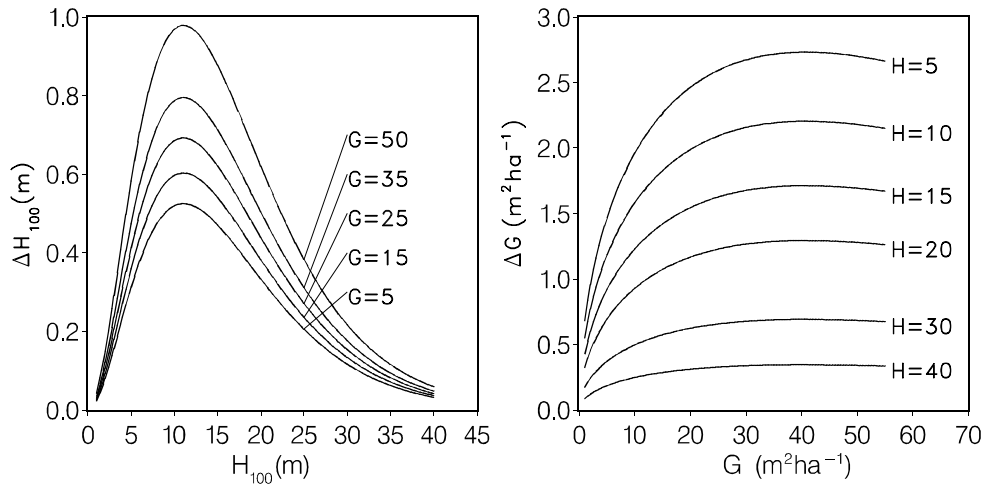
Figure 3. Simulated annual height (H_{100}) and basal area (G) growth at different levels of basal area and height, respectively.
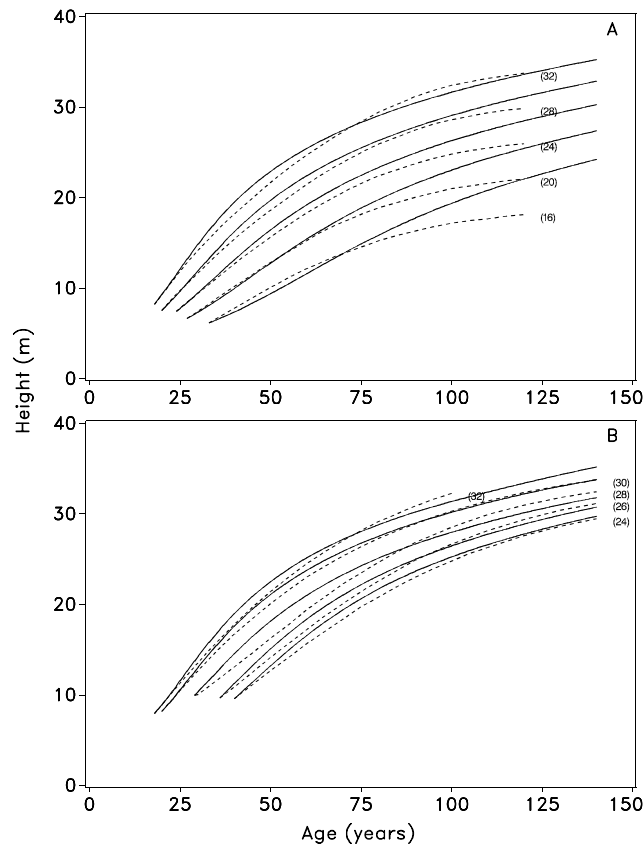

Figure 4. Plot of H_{100} derived from (A) the yield tables by Møller [34] and (B) Henriksen and Bryndum [21] (dotted lines) and the corresponding values simulated by the dynamic model (full lines). Simulations were started at the first observation of the yield table, using the prescribed reductions in stem numbers and basal area derived from the yield table. Site index (height at age 100) are provided in parenthesis.

Simulations were carried out by first estimating the local parameter corresponding to each site class using all growth intervals. Subsequently, height growth was simulated from the first observation using the timing and size of thinnings prescribed in the yield table. The height growth predicted by the dynamic model is greater than that of the yield table by Møller [34]. This is due to a well-known bias in this yield table [35]. When comparing simulated growth with that of the yield table by Henriksen and Bryndum [21] the results are much more consistent, although there is a tendency for the dynamic model to predict a more rapid height growth at young ages. The latter could, in part be due to inclusion of a greater number of recently established young stands in our study.

4.3. Other modelling efforts

Height and basal area growth peak at 10.7 m and 38.9 m^2 ha^{-1}, respectively, regardless of site quality, basal area, or height. This property of the selected models may be dubious from a biological point of view as we might expect the location of the peak to depend on e.g. site quality. We tested this proposition by modelling α_3 and β_3 as linear functions of the site-specific parameter, basal area (height model) and height (basal area model). In all cases the slope parameter was non-significant; hence the hypothesis of the location of peak growth varying with site quality, stand density, or height was not supported.

The effects of thinnings were modelled solely through the effect of the reduction in stem numbers and basal area. Release effects were not modelled explicitly, although such effects have been observed for beech [47]. We attempted to model release effects by an exponentially decreasing multiplier function of the proportion of basal area removed in the thinning and the time since thinning. Although parameter estimates were significant, the predicted release effect on basal area growth was only present the first year after thinning and was very small. As the inclusion of release effects added to model complexity with little improvement to the model we did not include this in the final model.

4.4. Cross validation

The stability of the parameter estimates and fit statistics shown by the cross validation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises without loss of precision of practical importance. As suggested by a number of authors, growth of European forests may have changed significantly over the past century [43, 44]. This may have serious implications for the practical application of the estimated models to predict future tree growth since parameters are estimated from data which dates back more than a century. Therefore, in a cross validation procedure parameters of the growth models were estimated on data from stands germinated before 1870 and applied to stands germinated after 1950 and vice versa. The results did not reveal any significant biases to suggest that future applications are affected by the change in forest growth.

Table III. Statistics for predicted stand values based on different numbers of available observations (p). Average absolute bias (AAB), average bias (AB), and root mean square error (RMSE) were calculated from the deviations between predicted and observed values at the end of the growth periods. For comparison statistics were calculated for predictions based on site index (dominant height at age 50), using the linear relation between SI and the site-specific parameter.

p	H_{100}			G		
	AB	AAB	RMSE	AB	AAB	RMSE
1	–0.514	0.799	1.054	–1.397	1.740	2.466
2	0.141	0.631	0.850	0.404	1.307	1.805
3	0.091	0.556	0.768	0.267	0.906	1.276
4	0.111	0.568	0.780	0.324	0.812	1.118
5	0.104	0.576	0.781	0.295	0.783	1.050
6	0.075	0.577	0.783	0.190	0.712	0.931
SI	–0.019	0.495	0.692	0.033	0.626	0.864

There is often a limited amount of data available for estimating the site-specific parameter. We employed a sensitivity analysis to assess the importance of the available amount of data for estimating a. First, plots having six or more measurements were selected. From this data set the first 1, 2, … 6 observations were used for estimating a of the height function only using the global parameters in Table B. For the situation where only one observation was available, the initial values were arbitrarily set at $H_{100} = 1.3$ m and $G = 2$ m^2 ha^{-1} at age 4. Based on these estimates, we predicted subsequent stand values and calculated lack of fit statistics (Tab. III).

As expected, increasing numbers of observations available for predicting a resulted in smaller prediction errors. The errors of the height function converged quickly and no additional gain was achieved when more than three observations were available. The errors of the basal error function converged more slowly and the gain of having six observations instead of five was 11% improvement in RMSE. When information on basal area was available, additional improvements were observed when a was estimated from the simultaneous height and basal area equations. The superior performance of the model when the site-specific parameter was estimated from site index is probably due to the fact that site index was estimated from all available observations.

5. CONCLUSIONS

The signs of the parameter estimates generally corroborated the anticipated growth paths of dominant height and basal area. Although statistical tests indicated significant systematic deviations between observed and predicted basal areas, the deviations were small and of little practical importance. Cross validation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises without significant loss of precision. In practical application, the site-specific parameter may be estimated locally from

site index or from height and basal area observations of that particular site.

The dynamic model provides a flexible tool for predicting stand level growth for a wide range of silvicultural treatments. Hence, stand growth modelling based on the state-space approach represents a significant leap forward from the static yield tables. The model concept further allows for continuous update of the site-specific parameter as more data is obtained for the particular stand and thus allows for changes in growth potential e.g. due to climate change.

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