Quantifying size-asymmetric growth among individual beech trees

Thomas Nord-Larsen, Christian Damgaard, and Jacob Weiner

Abstract: We modelled the growth of individual trees in populations of European beech (*Fagus sylvatica* L.) grown under different thinning regimes using a modified Richards equation. The effect of competition on growth was modelled by coupling the n individual equations simultaneously with a saturation term. By assuming that the growth of an individual within the population is a function of its size to a power a, a measure of the growth advantage of larger individuals (size-asymmetric growth) is provided. If $a > 1$, larger trees have a disproportionate advantage in growth and by inference, in competition. The degree of size-asymmetric growth, a, exceeded one in stands with large size variability and increased significantly at increasing density. This suggests that the predominant mode of competition is size asymmetric and that this size asymmetry increases with density. A measure of growth asymmetry is more informative than static measures of size inequality in understanding the growth dynamics of managed forest stands. Since a provides a measure of the relative importance of above- versus below-ground competition, it may be useful in interpreting the growth dynamics of forest stands and may provide an additional level of information for modellers of forest growth.

Résumé : Les auteurs ont modélisé la croissance de tiges individuelles dans des populations de hêtre commun (*Fagus sylvatica* L.) soumises à différents régimes d'éclaircie à l'aide d'une équation de Richards modifiée. L'effet de la compétition sur la croissance a été modélisé en couplant simultanément les n équations individuelles à un terme de saturation. Cet article fournit une mesure de l'avantage de croissance des individus les plus grands (croissance asymétrique) en assumant que la croissance d'un individu dans une population est une fonction de sa taille à une puissance a. Lorsque $a > 1$, les arbres les plus grands ont un avantage disproportionné en termes de croissance et, par déduction, de compétition. Le degré d'asymétrie de la croissance due à la taille, a, dépassait l'unité dans les peuplements où la taille des tiges varie fortement et augmentait de façon significative avec la densité. Cela indique que le mode prédominant de compétition est asymétrique et que cette asymétrie due à la taille augmente avec la densité. Une mesure de l'asymétrie de la croissance fournit plus d'information, comparativement à des mesures statiques d'inégalité de taille, pour comprendre la dynamique de croissance des peuplements forestiers sous aménagement. Puisque a fournit une mesure de l'importance relative de la compétition aérienne par rapport à la compétition souterraine, cette valeur peut être utile pour l'interprétation de la dynamique de croissance des peuplements forestiers et peut fournir un niveau additionnel d'information aux modélisateurs de la croissance de la forêt.

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Introduction

Growth of forest trees depends on their ability to compete for potentially limiting resources such as moisture, nutrients, and light. The partitioning of a resource for which neighbouring individuals compete depends on the type of resource and whether the competition is mediated by depletion or by preemption of the resource. Completely symmetric competition occurs when contested resources are divided equally between competitors irrespective of their size, whereas size-symmetric competition occurs when uptake of contested resources is proportional to size. Similarly, completely asymmetric competition is a one-sided interaction in which the few largest individuals receive all contested resources leaving nothing for their smaller competitors (Schwinning and Weiner 1998). In forest stands, competition among individual trees involves competition for several resources, where competition for the individual resource is more or less prominent. The resulting interaction is somewhere on a continuum in which completely symmetric and completely asymmetric competition are the extremes.

Light is the primary example of a preemptable resource that generates size-asymmetric competition (i.e., larger individuals obtain a disproportionate share of contested resources; Schwinning and Weiner 1998). In crowded populations, large individuals intercept most of the light, causing a steep vertical gradient of resource availability (Schwinning 1996). The suppression of smaller individuals caused by size-asymmetric competition for light is considered to be the driving force in mortality and size inequality in crowded populations (Schwinning and Fox 1995). Competition for belowground resources, on the other

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T. Nord-Larsen.[1] Royal Veterinary and Agricultural University, Forest & Landscape, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark.
C. Damgaard. Department of Terrestrial Ecology, National Environmental Research Institute, Vejlesøvej 25, DK-8600 Silkeborg, Denmark.
J. Weiner. Royal Veterinary and Agricultural University, Department of Ecology, Rolighedsvej 21, DK-1958 Frederiksberg, Denmark.

[1] Corresponding author (e-mail: tnl@kvl.dk).

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hand, appears to be size symmetric (i.e., contested resources are divided in proportion to competitor size; Casper and Jackson 1997, Weiner et al. 1997).

Although the underlying mechanisms of competitive interference between individual plants are difficult to investigate directly, we can observe the resultant growth patterns of individuals. If competition is intense and size-asymmetric, larger individuals receive more resources relative to their sizes, suppressing the growth of smaller individuals, such that larger individuals have higher relative growth rates than smaller individuals (size-asymmetric growth). This results in increasing size inequality (in the absence of significant density-dependent mortality; Weiner 1990). Thus, if competition is size asymmetric, plants grown in dense populations should exhibit greater size inequality than plants growing at lower densities. If competition in dense populations is size symmetric, size variability should be unchanged or lower at higher densities.

Models of individual tree growth that include the effects of competition have a long tradition in forest growth and yield modelling (for numerous references, see Vanclay 1994). Most of these efforts have aimed to describe individual-tree growth over a time interval as a function of plant size across the population (Mcdill and Amateis 1993). This approach has been criticized because each plant and time interval is treated separately and because the dynamic interactions among individuals are not modelled explicitly (Weiner et al. 1998). Coupling growth equations of individual plants allows for explicit modelling of these interactions and may help us to build more biologically meaningful equations, because we can observe the effects of factors or treatments on parameters that can have clear biological interpretations (Damgaard 1999). Coupled differential equations have been used to estimate the degree of size-asymmetric growth in monocultures of herbaceous plants at varying densities (Damgaard 1999, Damgaard et al. 2002).

In this study we model individual tree growth with coupled differential equations to describe the dynamic nature of competition among trees. We use this approach to address the following questions:

(1) Can coupled equations provide reasonable models for describing forest stand and individual tree growth?

(2) What is the degree of size-asymmetric growth in beech stands grown at various densities?

(3) How do thinning practices affect the degree of size-asymmetric growth?

Materials and methods

Data collection

The data originate from the permanent experiment DQ at Bregentved forest district in southeastern Denmark, located in zone 32 at UTM coordinates E695747 m, N6136389 m (European datum 1950), 18 m a.s.l. The parent material is moranic till from the Weichel glaciation, with high clay content and a good nutrient supply. This site represents excellent growing conditions for European beech (*Fagus sylvatica* L.) in Denmark. The experiment was located in a beech stand established by strip sowing in 1916, and the sample plot structure was established in 1941. At the initiation of the experiment in 1941 the stand appeared quite uniform and the initial spacing of the individual plots was similar, although not identical (Holmsgaard 1985).

The experiment comprises 11 individual sample plots with an area of 0.08–0.35 ha. Two of the sample plots are unthinned controls, and the remaining plots were thinned according to two different thinning strategies named after their proponents: Jagd and Bavngaard (Holmsgaard 1985). Jagd advocated early, heavy thinnings to achieve a rapid diameter growth and early financial returns, whereas Bavngaard advocated moderate thinnings at young ages and retention of understorey trees to achieve longer bole lengths and higher wood quality. The two thinning strategies lead to quite different stand structures, where the plots thinned according to the ideas of Jagd is more homogeneous in size than those thinned according to the ideas of Bavngaard. To reduce the computational load, 4 of the 11 plots were used in the estimation (A1, Bavngaard; B2, Jagd; C1, Jagd; and E2, unthinned control). The four plots were chosen to represent the entire range of stand densities.

The plots were measured at every thinning, 11–13 times from 1941 to 1998. The total data set comprised 136 individual measurement occasions. From 1941 to 1950 diameters were recorded in tally lists to 1 cm diameter classes. From 1953 all trees were numbered, marked permanently at breast height (1.3 m), and recorded individually, although understorey trees were still recorded in tally lists. Hence, from 1953 most of the individual trees are positively identifiable in subsequent years and these data were used for the analysis of individual tree growth in this study.

Observations of diameter are obtained by two sets of perpendicular calliper readings at breast height for each tree. The average of the two measurements is used as a measure of DBH. Whether the tree is alive or dead at the time of measurement was also recorded. The total data set comprises 24 843 diameter measurements of 3530 individual trees. Individual tree height of living trees was obtained by a hypsometer, and felled trees were measured on the ground using a tape measure. The database comprises 3949 height measurements on 1538 individual trees.

Based on the paired observations of diameter and height, height–diameter equations were developed for each plot and measurement combination using a modified Näslund equation (Näslund 1936, Johannsen 2002):

$$[1] \qquad h = \left(\frac{d}{\alpha + \beta d}\right)^3 + 1.3$$

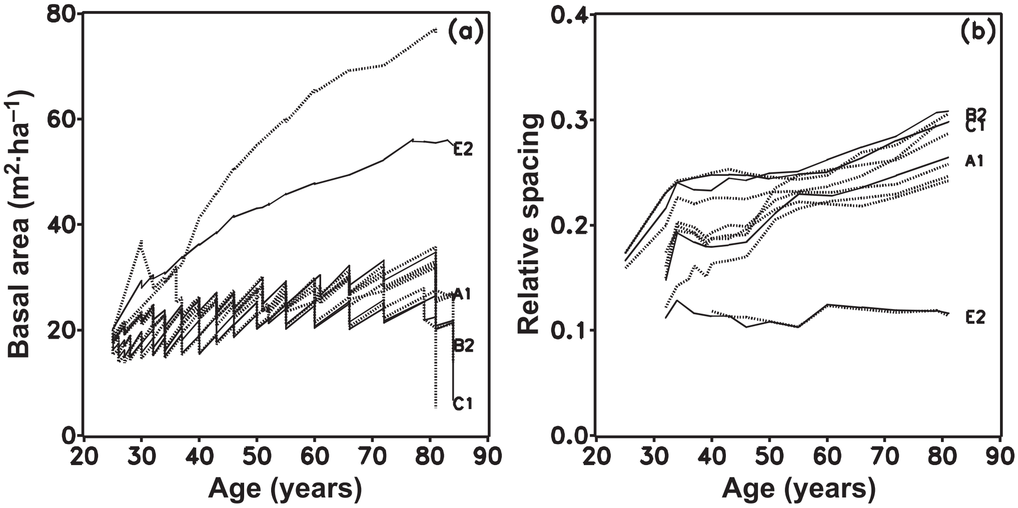
where d is DBH, h is the total tree height, and α and β are the parameters to be estimated. The equations were then used to estimate the height of trees not measured. Individual tree volume was subsequently calculated for each individual tree based on a volume equation for beech (Madsen 1987).

The four plots used in the analysis represent a wide range of stand densities expressed by stand basal area (G), obtained by summation of the cross-sectional areas of the individual stems per hectare, and relative spacing ($\text{RS} = \left(\sqrt{10\,000/N}\right)/H$, where N is the number of stems per hectare and H is dominant height measured as the average height of the 100 thickest trees per hectare) (Fig. 1).

Model description

The choice of scalar measure of growth is not a trivial one, as tree size represents a multidimensional vector and exhibits

Fig. 1. (*a*) Basal area and (*b*) relative spacing for the 11 sample plots at experiment DQ. The four plots used in the analysis, A1 (Bavngaard), B2 (Jagd), C1 (Jagd), and E2 (unthinned control), are represented by the solid black lines, whereas the other plots are presented by dotted lines. The vertical drops in basal area represent the basal area removed in individual thinnings.



a high degree of plasticity under different conditions. For each of the four plots we modelled both individual tree volume and basal area growth. This choice of scalar measures of size was dictated by available data that did not entail other measures of tree size, such as crown dimensions, and we thus assumed that the amount of physiologically active tissue is correlated with volume and basal area.

We modelled individual tree growth by a modified Chapman–Richards growth model (Richards 1959, Damgaard et al. 2002). The model has well-known properties, is mathematically flexible, and is among the most commonly used for modelling forest growth. The growth of n competitively interacting plants is modelled by n coupled differential equations, where the absolute growth rate is a function of tree size and a parameter accounting for the degree of asymmetric growth (a). The effect of competition between plants within the population is modelled by the cumulative size of the n individual trees relative to the fitted maximum cumulative size of the n trees ($n(\alpha)$):

$$[2] \qquad \frac{dv_i(t)}{dt} = \begin{cases} \frac{\kappa}{1-\delta} f[v_i(t), a] \left\{ \left[\frac{1}{n\alpha} \sum_{j=1}^{n} v_j(t) \right]^{\delta-1} - 1 \right\} & \delta \neq 1 \\ \kappa f[v_i(t), a] \left\{ \log(n\alpha) - \log\left[\sum_{j=1}^{n} v_j(t) \right] \right\} & \delta = 1 \end{cases}$$

for $t \geq 0$, $\kappa > 0$, and $\alpha > 0$. $v_i(t)$ is the size (volume or basal area) of tree i at time t, and κ, δ, and $f(v_i(t), a)$ determine the absolute growth rate of the tree. If $\delta > 0$, the growth curve is sigmoidal and the slope of the tangent at the point of inflexion decreases with δ (Richards 1959, Seber and Wild 1989). α is the fitted maximum average tree size, and $n\alpha$ is the maximum cumulative size of the n competing trees. Thus, when the cumulative size reaches its maximum, reflecting maximum total biomass of the stand, growth stops.

The growth of individual trees is assumed to be proportional to a power function of their size (Schwinning and Fox 1995, Damgaard 1999, Wyszomirski et al. 1999):

$$[3] \qquad f\left(v_i\left(t\right), a\right) = \begin{cases} 1 & a = 0 \\ v_i\left(t\right)^a & a > 0 \\ 1 \text{ (large plants) or } 0 \text{ (small plants)} & a = \infty \end{cases}$$

where the effect of plant size on growth is quantified by the size asymmetry parameter, a. If $a = 0$, all trees have the same growth rate irrespective of their size (i.e., growth is completely symmetric). If $0 < a < 1$, the growth rate is less than proportional to the size of the tree. If $a = 1$, the growth rate is proportional to the size of the tree (i.e., growth is perfectly size symmetric). If $a > 1$, the growth rate is more than proportional to the size of the tree and growth is size -asymmetric. If $a = \infty$, only the largest trees grow and growth is completely asymmetric.

Model estimation

To adequately describe the growth of a plant with a dimensionless size less than one, the power function in eq. 3 was modified to $f\,[v_i(t), a] = [v_i\,(t) + 1]^a - 1$, since this is a monotonically increasing function of both size and the parameter a, for all $v_i(t) > 0$, while still passing through the origin (Damgaard 1999). All parameters except for δ were exponentially reparameterized to ensure that they were strictly positive (all results are reported after parameter values have been transformed back). Both model and increment data were log transformed to ensure homogeneity of variance. Trees that died or were thinned were only modelled until the time of death and thereafter assumed to no longer to contribute to the population biomass (i.e., they no longer compete with living trees).

The coupled differential equations (eq. 2) cannot be solved analytically, and the equations were solved numerically using the NDSolve routine of Mathematica (Wolfram 2003). This routine simultaneously made incremental changes to the size of all trees at each measurement to the subsequent measurement for a specific parameter combination using sufficiently small steps. The likelihood of each parameter combination was then calculated from the transformed predicted increments and transformed observed increments for all n plants. The maximum likelihood estimates of the parameter values were found using the NMaximize routine of Mathematica (Wolfram 2003).

The hypothesis of $a = 1$ was tested using a likelihood ratio test. The Bayesian posterior probability distributions of the parameters were calculated using the Metropolis–Hastings algorithm assuming an uninformative uniform prior distribution (100 000 samples with a burn-in period of 1000 iterations for stabilizing parameter values) (Carlin and Louis 1996). Since the computational load increases rapidly with increasing number of trees, 100 randomly selected trees from each plot were used for calculating the posterior distributions. Statistical inferences were based on the 95% credibility intervals (2.5th to 97.5th percentile of the posterior distribution) of the parameters. Parameters were concluded to be significantly different if the 2.5th percentile of the high parameter was higher than the 97.5th percentile of the low parameter.

The data used for this study represent a nested structure of repeated measurements on individual trees within different plots. Failure to recognize this correlation structure could result in inefficient estimates and underestimated standard errors when correlations are strong. However, both within-plot correlations and the correlation of individual tree increments are generally not strong (Gertner 1985, Reed and Burkhart 1985). Further, when growth, as in the present study, is viewed as an incremental process where only current conditions affect current growth, the problems of serial correlation are generally avoided (García 1983, Seber and Wild 1989). Hence, in present study we assumed that errors were uncorrelated but tested this assumption in the post hoc analysis.

Statistical fit of the model

Model assumptions were tested by visual inspection of residual plots and by statistical tests of homogeneity (Bartlett–Box test) and normality (Kolmogorov–Smirnov and Andersson–Darling tests) of residuals. Further, the hypothesis of no autoregression was tested using a Durbin–Watson test (Durbin and Watson 1950):

$$[4]\qquad d = \frac{\sum_{t=2}^{n} (e_t - e_{t-1})^2}{\sum_{t=1}^{n} e_t^2}$$

where e_t is the residual at time t and d is the test statistic.

Statistical tests of model bias included simultaneous F tests for unit slope and zero intercept on the linear regression of observed versus predicted data (Dent and Blackie 1979):

$$[5]\qquad F = \frac{(n_j - 2)\left\{n_j a_j^2 + 2n_j \overline{X} a_j\,(b_j - 1) + \sum_{i=1}^{n_j}\left[X_i^2\,(b_j - 1)^2\right]\right\}}{2n_j\mathrm{MSE}}$$

where a_j and b_j are the intercept and slope of the regression of observed versus predicted values at the jth plot, respectively, X_i is the predicted values of the ith tree, and MSE is the mean square error of the linear regression.

Precision of the model was evaluated using R^2 statistics, the root mean square error, and the absolute average bias of the back-transformed values.

Results

The Richards model accounted for more than 99% of the variation in the observed diameter and volume of the individual trees at the end of the measurement intervals (Table 1). The model accounted for 81.2%–92.2% of the observed diameter increment and 68.2%–93.9% of the observed volume increment (data not shown). Residuals were approximately normally distributed with zero mean for all the plots, and variances were approximately homogeneous (Fig. 2). According to the simultaneous F tests, the model was unbiased for both measures of size for plots B2 and C1. While the model was significantly biased for plots A1 and E2 for both measures of size, the bias was very small (Table 1). Residuals were significantly correlated among individual trees, but correlations were small and did not affect model inferences adversely.

In heterogeneous stands, such as the control plots and the plots subjected to the Bavngaard regime, $a > 1$, whereas $a < 1$

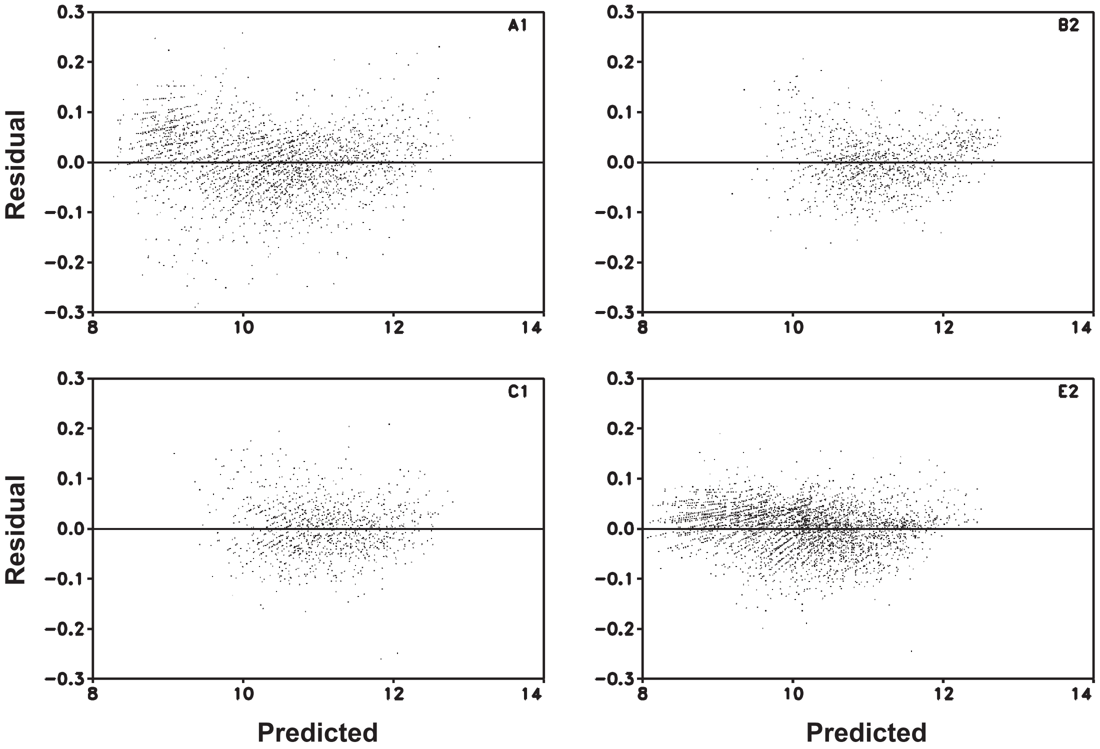
Table 1. Maximum likelihood estimates of the parameter a in the growth model (eq. 2).

Measure	Regime	Plot	a	2.5%	50%	97.5%	R^2[a]	RMSE[a]	AAB[a]
Diameter^2	Bavngaard	A1	1.4290	1.3699	1.4251	1.4919	0.994	7.621	4.772
	Jagd	B2	0.8333	0.6315	0.6776	0.7154	0.994	7.256	5.590
	Jagd	C1	0.9068	0.7707	0.8420	0.9018	0.993	7.377	5.257
	Control	E2	1.8900	1.8103	1.8645	1.9382	0.997	3.968	2.747
Volume	Bavngaard	A1	1.1979	0.0426	0.3497	0.6853	0.991	0.069	0.029
	Jagd	B2	0.6174	0.4459	0.7050	0.9113	0.995	0.064	0.040
	Jagd	C1	0.4609	0.2014	0.4076	0.5707	0.992	0.071	0.040
	Control	E2	2.4201	1.8904	2.1581	2.4018	0.985	0.043	0.023

Note: All estimates of a were significantly different from one ($P < 0.0001$). The Bayesian posterior probability distributions of a based on a subsample of 100 trees are reported by the 2.5th percentile, 50th percentile, and 97.5th percentile.

[a] The R^2 statistic, root mean square error (RMSE), and absolute average bias (AAB) are based upon back-transformed residuals of diameter and volume.

Fig. 2. Residual plot of untransformed residuals of diameter^2 versus the natural logarithm of predicted values (in mm) for the four plots.



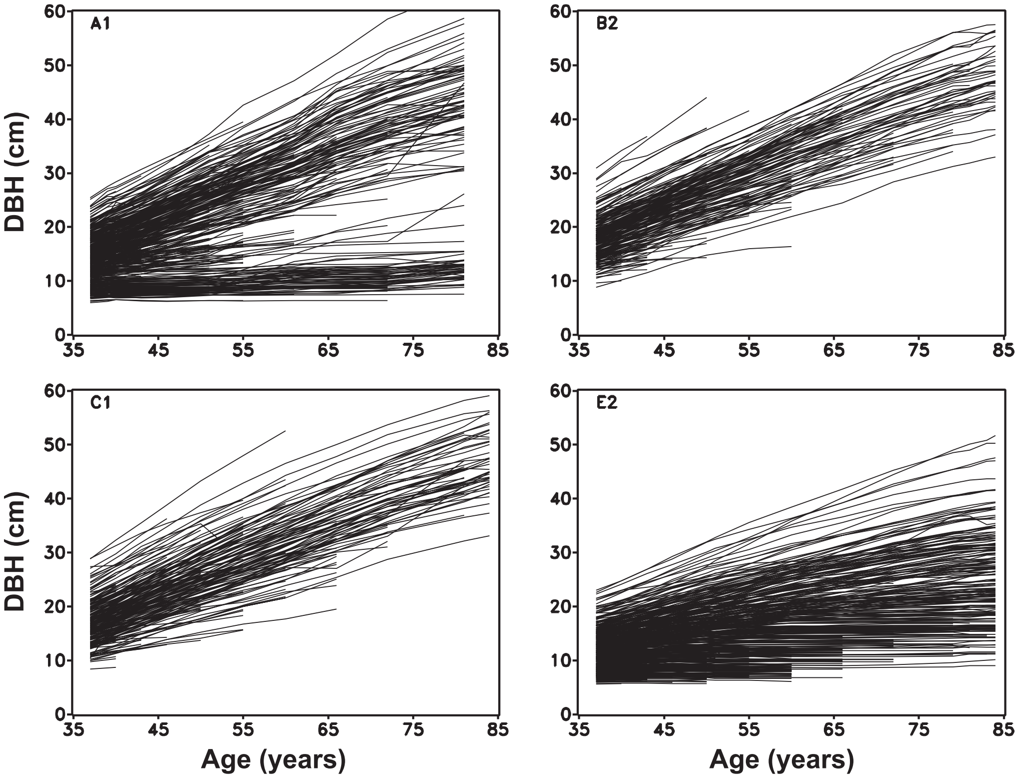
in the homogeneous stands of the Jagd thinning regime (Table 1). For both measures of tree size (basal area or estimated volume), a was significantly higher in the plots with higher densities (control and Bavngaard) than in those with lower density (Jagd).

The 50th percentile of the posterior distributions of a were similar to the maximum likelihood estimate for most of the plots. However, in some cases the maximum likelihood estimate deviated significantly from the posterior distribution, which indicated that the estimation of the posterior distribution was somewhat sensitive to the selection of individual trees analyzed.

The posterior distributions of the other parameters of the sigmoidal curve were also sampled. However, since diameter and volume growth are close to linear in the observed interval (Fig. 3), these parameters have a rather large credibility interval and are not very informative about the shape of the growth curves.

It may be argued that since the growth curves are almost linear, a simpler growth model may be used to fit the parameter of interest, a, instead of a sigmoidal growth model. We also fitted a simple saturation model, the monomolecular model ($\delta = 0$), to the data. In the cases where δ differed significantly from zero, the Richards model fit better than the simpler model. In the other cases where δ of the Richards model was not significantly different from zero, the maximum likelihood estimates of a were almost identical (results not shown). As the choice of model in those cases apparently did not affect the estimates of

Fig. 3. Individual tree growth at plots A1 (Bavngaard), B2 (Jagd), C1 (Jagd), and E2 (unthinned control).



the parameter of interest, a, the more flexible Richards growth model was used in the reported fitting procedures.

Discussion

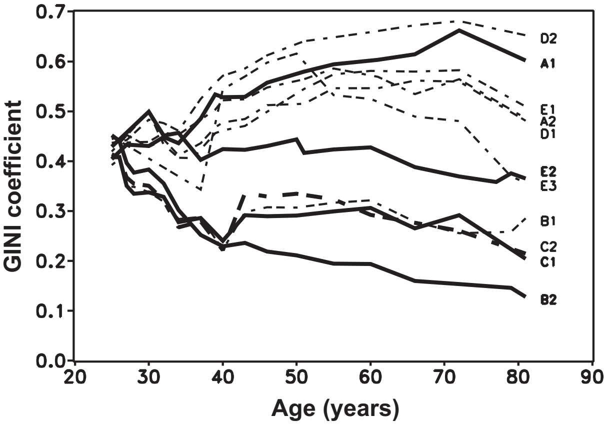
Consistent with the previous studies showing that growth is size asymmetric in crowded plant populations, $a > 1$ in the control plots and in the plots subjected to the Bavngaard regime. For both measures of tree size (basal area and estimated volume), a increased significantly with increasing stand density. Thus, our findings provide further evidence that the overall mode of competition between individual trees is size asymmetric and that size asymmetry of growth increases with population density, that is, the advantage of being larger is greater in more crowded populations.

In the more size-homogeneous stands of the Jagd thinning regimes, $a < 1$. This may simply reflect a general inability to observe size-asymmetric growth in homogeneous stands (i.e., if all trees have the same size, size-asymmetric growth will not be observed, even if the underlying competitive process is size asymmetric). Another possible explanation is that the Jagd thinning regime has an overall lower density and hence competition is expected to be more size symmetric, although the differences in density between the two regimes are not very pronounced. Thinning will reduce the intensity of competition and therefore the degree of competitive asymmetry, but if the thinning regime increases size variation within the population it will increase the potential for size-asymmetric competition to result in size-asymmetric growth.

Our findings are consistent with those from a study on interspecies competition in cedar–hemlock forests in British Columbia. Using measures of relative height and distance-dependent competition indexes, competition was found to be asymmetric and depended on neighbour identity (Simard and Sachs 2004). Asymmetric competition has also been reported in numerous nonwoody species including *Helianthus annuus* (Watkinson et al. 1983), *Impatiens pallida* (Weiner and Thomas 1992), *Pennisetum americanum* (Schwinning 1996), *Kochia scoparia* (Weiner and Fishman 1994), *Brassica napus* (Damgaard 1999), and *Chenopodium album* (Damgaard et al. 2002). In monospecific, even-aged, and spatially heterogeneous stands of black spruce (*Picea mariana*), both resource depletion and resource preemption processes were identified (Newton and Jollife 1998). Our results suggest that the strength of preemption processes increases more sharply with density than does the strength of depletion processes. This leads to an increasing overall asymmetry of competition and therefore growth at higher densities.

The degree of growth asymmetry observed at different thinning intensities in this study is an expression of the average growth pattern during the time the plots were measured as trees grew (i.e., a probably varies across time). As a stand ages, the effect of competitive processes may vary because of changes in stand characteristics, size, limiting resources, and age-dependent physiological changes within the trees. Competitive processes were similar among 25- to 50-year-old stands of cedar–hemlock forests, but these contrasted sharply with 11-year-old stands (Simard and Sachs 2004). There is also evidence that the expression of the resulting competitive processes may vary as a result of variation in resource availability (Weiner 1985, Knox et al. 1989, Cescatti and Piutti 1998). Medium and large trees of Sitka spruce (*Picea sitchensis*) in an even-aged

Fig. 4. Gini coefficients as a function of stand age for the individual plots. The four plots used in the analysis, A1 (Bavngaard), B2 (Jagd), C1 (Jagd), and E2 (unthinned control), are represented by the solid black lines, whereas the other plots are presented by dotted lines.



stand were found to respond more vigorously to increasing water availability, thereby expressing increasing asymmetry of competition (Wichmann 2001, 2002). Similarly, differentiation in unthinned stands of Sitka spruce was more pronounced in fertile stands, indicating that ample belowground resources lead to a more pronounced asymmetric growth (Skovsgaard 1997). Thus, increased availability of belowground resources results in an increase in competition for light and therefore increased asymmetric growth. Since *a* varies with the relative importance of above- versus below-ground competition, it may be useful in interpreting the growth dynamics of forest stands and the relative roles of competition for light and soil resources.

The degree of asymmetric growth has been assessed by measuring the size inequality of the plant population (Weiner and Solbrig 1984, Weiner and Thomas 1986, Knox et al. 1989, Weiner 1990). One approach to describe inequality of plant size is with the Lorenz curve and the Gini coefficient. The Lorenz curve depicts the cumulative plant size when individuals are ranked according to their size (Lorenz 1905, Damgaard and Weiner 2000). Based on the Lorenz curve of a theoretical population in which all individuals are equal to the mean (line of equality), the Gini coefficient expresses the ratio of the area between the line of equality and the Lorenz curve to the area under the line of equality. The depiction of Gini coefficients (based on diameter^2) across stand ages of the individual plots (Fig. 4) shows a clear distinction between the thinning regime by Jagd on one side (plots B1–C2) and unthinned controls (E1–E2) and the thinning regime by Bavngaard (plots A1, A2, D1, and D2) on the other. Although we found the asymmetric growth to be largest in the dense, unthinned plots, size inequality is apparently largest in the plots subjected to the Bavngaard thinning regime. This is not surprising, since the Bavngaard regime aims at actively maintaining a vigorous understorey and hence a large diversity of sizes compared to that of the Jagd regime and the unthinned controls. The size inequality of these stands is not primarily a result of the competitive processes but rather a direct result of the thinning practices. This emphasizes the need for dynamic measures of size-asymmetric growth in managed forest stands.

Recent developments in computational statistics afford us the opportunity to break down the distinction between theoretical and statistical modelling in ecology. We can now build and fit biologically based (and biologically motivated) models, that is, models in which the parameters have clear biological interpretations that, until a few years ago, one would not even think of fitting to real data. In this study, competition among individuals was modelled by simultaneously coupling differential equations for the individual trees. Thus, each plant's growth rate is affected not only by its own size and growth parameters but also by the cumulative size of all the other individuals in the population. The relationship between individual plant size and growth rate across the population contains important information about the size symmetry of competition among individuals. Explicit modelling of this relationship represents another level of information that offers the possibility of bridging the gap between predictive and descriptive models of forest growth.

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