Application of volume growth and survival graphs in the evaluation of four process-based forest growth models

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Summary Volume growth and survival (VGS) graphs, which show volume growth rate and risk of mortality for individual trees (or tree size classes), have been proposed as a tool for assessing the validity of models that describe the development over time of tree size distributions within forest stands. We examined the utility of the VGS method in evaluating four process-based models. The performance of the models FORSKA, 4C, MORG, and PipeQual is analyzed against long-term data from a Scots pine stand in Evo, Finland, and the models FORSKA and 4C are also assessed with respect to data from a beech stand in Fabrikschleichach, Germany. Comparison of the measurement-based VGS graphs with those produced from the model-based data shows that although the models yield similar stand-level predictions, they can differ widely in their projections of individual tree growth and size distributions. Examination of the discrepancies between models and data in the context of the VGS graphs reveals several areas in which the models could be improved. We conclude that the method is useful in model evaluation, especially if used in combination with indicators of stand structure, such as the height/diameter ratio.

Keywords: model evaluation, size distribution, Pinus sylvestris, Fagus sylvatica, stand structure, permanent sample plot.

Introduction

Evaluation of process-based stand growth models is difficult because of the complexity of the models, and in many cases, the absence of appropriate data. Few comprehensive tests are available, although some models have been tested for a few variables at a time. Several models have been evaluated in comparison with short-term stand-level fluxes of water, carbon, and nitrogen measured at intensively studied sites (e.g., Grinsven et al. 1995, Ryan et al. 1996). Other tests have been conducted with stand-level forestry data, such as basal area, volume, or dominant height (Mäkelä 1988, Sievänen 1993, Landsberg and Waring 1997, Valentine et al. 1997, Bartelink 1998). However, although the models are based on individual trees, model predictions concerning the growth of individual trees at different positions in the stand have seldom been tested.

In one of the few tests focusing on individual trees, Korol et al. (1996) evaluated the performance of the model TREE-BGC against field measurements. They compared size distributions and growth of individual trees after 20 simulation years, and also performed a qualitative analysis of long-term stand dynamics over a 100-year period. Lindner et al. (1997) compared simulated forest structures of the forest gap model FORSKA with long-term observations from a beech forest. Strong deviations from measured height:diameter ratios and size distributions were observed, although stand-level characteristics were simulated realistically. The graphical analysis of simulated and measured stand structures proved useful in model evaluation and improvement.

One of the main obstacles in conducting tests on individual-tree growth has been the lack of data. But there are usually ample conventional forest mensuration data available, including tree number versus diameter, height or volume. A method for testing process-based models on the basis of such data would be of great value.

Sievänen et al. (2000) introduced volume growth and survival (VGS) graphs for evaluating models with respect to the development of size distributions. In VGS graphs, the growth rates of trees in different size classes are plotted relative to each other, and the relative mortality rates are plotted as a function of relative tree size. The VGS graphs show stem volume growth and mortality of trees in size classes on a relative scale. As shown by Sievänen et al. (2000), for the realistic prediction of size distributions forest growth models must yield VGS graphs that agree with field measurement data, although additional tests are required to validate model predictions of absolute growth and mortality rates. Because VGS graphs can be generated by most process-oriented individual-tree-based models, such graphs offer a potentially useful tool for testing one aspect of model accuracy.

We have evaluated four process-based models by comparing VGS graphs generated by the models with VGS graphs based on measurement data from two stands. The behavior of the models is discussed in the context of the VGS graphs.

The models

We tested the performance of four models of stand growth. Models FORSKA and 4C are gap-type models developed for areas of mixed stands, whereas models MORG and PipeQual have been developed and parameterized for even-aged stands of Scots pine (*Pinus sylvestris* L.) in Fenno-Scandia. All of the models are based on the carbon balance of individual trees, including submodels for photosynthesis, respiration, and carbon allocation. They represent stand structure in terms of size classes of trees; i.e., they are distance-independent. Natural mortality is represented by functions that depend on tree size or carbon balance or both. All four models simulate a full stand rotation. Earlier comprehensive references are available for FORSKA (Prentice et al. 1993, Lindner et al. 1997) and MORG (Sievänen 1993). Models 4C and PipeQual are currently under development and will be more thoroughly described below. Table 1 summarizes some characteristics of the models.

FORSKA   The FORSKA model is a gap-type model that was originally developed to simulate forest dynamics in Scandinavia (Prentice and Leemans 1990, Prentice et al. 1993). It simulates growth, regeneration and mortality of individual trees on small forest patches, based on more mechanistic formulations of tree growth than most earlier gap models (cf. Bugmann et al. 1997). Net growth of a tree is calculated by integrating the balance of net assimilation and respiration of leaves in different crown layers over the canopy. Growth is converted to height and diameter growth by empirical constants and relationships. Mortality is a combination of an intrinsic mortality rate depending on maximum age for the species (Botkin et al. 1972) and a stress-induced mortality based on the relative growth efficiency of the individual tree.

In this study, we employed a version of FORSKA that was adapted for applications to northeast Germany and includes a modified height growth function as described in Lindner et al. (1997). Height growth of individual trees in this model version depends on the competitive status of the tree as evaluated from the relative radiation flux density in the centre of the tree crown.

FORESEE (4C)   The model 4C ('FORESEE'—Forest ecosystems in a changing environment) was developed to describe long-term forest behavior under changing environmental conditions (Bugmann et al. 1997). The model includes descriptions of tree species composition, forest structure, and total ecosystem carbon content as well as leaf area index. Establishment, growth and mortality of tree cohorts are modeled on a 200-m^2 patch on which horizontal homogeneity is assumed.

The model simulates explicitly the availability of water and nutrients for individual trees, based on the assumption of scramble competition (Krebs 1994). It also incorporates comparatively detailed submodels of heat flux, water, carbon and nitrogen dynamics in the soil. The annual course of net photo-

Table 1. Comparison of some model characteristics significant for the present study.

Characteristic	FORSKA	4C	MORG	PipeQual
Purpose	Growth and succession in natural and managed forests subject to climate change	Growth and succession in natural and managed forests subject to climate change	Growth of pure Scots pine stands in different regions	Growth and wood quality in Scots pine; management through stocking and thinning
Species	Multiple; pine and beech	Multiple; pine and beech	Monoculture; pine	Monoculture; pine
Time step	1 year	Multiple (1 year, 1 week, 1 day)	1 year	1 year
Productivity	Maximum productivity per species reduced by response functions for temperature, drought, N-availability	Dependent on the temporal patterns of radiation, temperature, water and N availability and CO_2	Maximum productivity per unit area, regional parameterization	Maximum productivity per unit area, calibrated for each site
Tree interactions	Shading, through photosynthesis	Shading, through photosynthesis; competition for water	Shading, through photosynthesis and crown rise	Shading, through photosynthesis; physical space, through crown rise and mortality
Diameter growth	Pipe model	Pipe model	Pipe model	Pipe model
Height growth	Allocation between height and diameter based on relative radiant flux density	Proportional to foliage growth and relative radiant flux density	Allocation between height and diameter based on radiant flux density	Allometric relationship between foliage and crown length; crown rise
Mortality	Maximum age; relative growth efficiency	Carbon balance; shade tolerance	Diameter and diameter growth	Diameter and diameter growth; crown coverage

synthesis is formulated mechanistically as a function of environmental factors (temperature, water and nitrogen availability, radiation, and CO_2) (Haxeltine and Prentice 1996). The share of any tree cohort in total stand gross photosynthetic CO_2 assimilation is proportional to the fraction of photosynthetic active radiation absorbed by the cohort. The description of allocation patterns is derived from the model of Mäkelä (1986), with an extension that responds dynamically to water and nutrient limitations. The model also includes a simplified phenology scheme based on the work by Kramer (1995).

The mortality model is a development of models by Keane et al. (1996) and Mäkelä and Hari (1986), where the mortality rate of a tree cohort is based on the growth behavior of the cohort. It is calculated as a function of the number of years with a negative foliage increment and parameterized depending on the shade tolerance of the species. Thus, differences in growth rates of the tree cohorts result from their different share in stand gross assimilation, which defines the total amount of carbon to be partitioned. Additionally, height growth of trees depends on the relative radiation in the center of the tree crown (Lindner et al. 1997).

Different integration steps are used for the various submodels, ranging from a daily time step for soil water dynamics, more than one week for soil carbon and nitrogen dynamics and the simulation of net primary production, to an annual time step for tree demography and carbon allocation. Hence the model requires weather data (i.e., temperature, precipitation and solar radiation) with a daily resolution that can be provided by a weather generator (Bürger 1997). Currently the model is parameterized for three tree species, beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), and spruce (*Picea abies* (L.) Karst.).

MORG The model MORG (Sievänen 1993, Sievänen and Burk 1993) is a process-based, stand growth model that predicts tree dimensions. The MORG model uses simple expressions for photosynthesis, other aspects of physiology, and tree structure, to derive growth of diameter and height. The basic unit in MORG is a tree responding to its light climate. Tree growth is based on the standard carbon balance method (e.g., Landsberg 1986). The stand is described as a collection of trees in size classes, the members of which are randomly distributed over the area of interest. Stand growth can be aggregated from the growth of individual trees and the number of members in each size class. Because distance to neighboring trees is not used in evaluating the environmental conditions, MORG can be termed a distance-independent, individual-tree growth model.

MORG assumes (referring to an even-aged stand) that the height of the crown base is the same for all trees (except for those in which relative height of the crown base would exceed a maximum; their crown base is at a lower height). The recession of the crown base is treated as a stand process controlled by the crowding of trees; when crowding, measured as the stand cross-sectional area at the crown base, increases, the crown base recedes. The height of the crown base affects the amount of foliage and height growth of the trees. Tree survival

is dealt with by an empirical model that depends on diameter and its growth rate. The MORG model has been parameterized for Scots pine in southern Finland growing on soils ranging from poor to fertile. Thus, MORG did not require tuning or parameter estimation for the present study.

PipeQual PipeQual was developed to simulate the branchiness and other timber quality characteristics of trees of different sizes in a Scots pine stand (Mäkelä et al. 1997). It consists of a whole-tree growth model, CROBAS (Mäkelä 1997), and modules that describe the whorl and branch structure of the tree. The whole-tree model is based on carbon balance, and allocates carbon to maintain some structural relationships, such as the pipe model. A special characteristic of the model is the derivation of crown rise and consequently height growth from a carbon allocation strategy dependent on crowding (Mäkelä 1997).

The whole-tree model can be run in different stand configurations and under different assumptions about tree interactions. In the version of PipeQual used here, a stand consists of size classes of individual trees, characterized by a mean tree of the class, trees of each class being randomly distributed in space. Interactions between trees are described through a simple presentation of crown and stand geometry that not only affects shading, but also has a direct effect on crown rise and mortality. The formulations used here are extensions of an earlier study where the stand consisted of one size class only (Mäkelä 1997).

Crown geometry is described through the shape of the crown envelope, which was assumed to be conical, tree height and height of the crown base in each tree class. Stand-level photosynthesis is calculated using an analog of the Beer-Lambert law (Mäkelä 1997), and is distributed between the size classes based on a modification of the scheme suggested by Sievänen (1993). The crown coverage affecting tree class i, C_i, is defined as the sum of the crown coverage at the crown base of the tree class, including itself (C_{ic}), and that at the top of the tree class (C_{it}):

$$C_i = C_{ic} + C_{it}. \tag{1}$$

In the case of one tree class only, this definition reduces to the same as that used by Mäkelä (1997). The crown rise strategy, *s* (Mäkelä 1997) depends on C_i as follows:

$$s = \min\{1, C_i^q\}, \tag{2}$$

where *q* is a parameter. If $s = 0$, there is no crown rise, and if $s = 1$, crown rise is so heavy that no net foliage growth can be maintained.

The mortality function is a combination of two major effects, crowding and random causes. In addition, the crowding effect has been combined with an empirical function where mortality depends on the growth rate and tree size (Belcher et al. 1982, Sievänen 1993), a function also used in MORG. The mortality equation is hence:

$$M = [m_0 + m_1(dD_{1.3}, D_{1.3})C_i^p]N, \tag{3}$$

where m_0 and p are parameters and $m_1(\mathrm{d}D_{1.3}, D_{1.3})$ is a function dependent on the growth and value of the breast height diameter.

The whorl and branch modules of PipeQual allow for the inclusion of parameters dependent on distance from the tree top to the whorl. Some of these parameters were made dependent on tree interactions in an earlier version of PipeQual (Mäkelä et al. 1997), but to make the analysis easier to interpret, such relationships have been excluded. Furthermore, the assumption underlying the original CROBAS model (Mäkelä 1997) that increasing crown size reduces photosynthesis, presumably through an effect on water relations, has been relaxed. Differences in growth between trees in this version of PipeQual are hence simply caused by (1) shading, (2) the ratio of respiration to gross photosynthesis, which is a function of size and form, and (3) allocation, which also depends on the local environment through the crown rise strategy. Differences in mortality are caused by (1) direct differences in the local environment through crown coverage, (2) differences in growth rate, and (3) differences in size.

Data

Model outputs were compared with two sets of forest mensuration data from long-term permanent plot experiments with Scots pine in Evo, Finland and beech in Fabrikschleichach, Germany. The MORG and PipeQual models were tested against only the Evo data, because parameter values were not available for beech, whereas FORSKA and 4C were run for both the Evo and Fabrikschleichach sites.

The Evo data are for a Scots pine stand on medium to poor soil (site index 22 m at base age 100 years). Mean annual temperature is 3.3 °C. The stand was established from seed in 1880 and was 46 years (growing periods) old when the experiment was established in 1925. There are two plots, thinned (2500 m^2) and unthinned (1429 m^2), and the natural stand was included in the test. The plots have been measured nine times between 1925 and 1989. The measurements include diameter and height for each tree in the plot, and in the two most recent measurements, the height of the crown base also. Volume growth rate was derived from the differences in height and diameter between two consecutive measurements, together with standard functions for stem form. Mortality in each diameter class could also be derived from individual tree measurements. In addition to Scots pine, the plots contain some larch (*Larix decidua* Mill.), comprising about 15% of the total stem number and basal area. For this test, the trees were pooled, because no large differences could be detected between the species.

The Fabrikschleichach data were from a beech thinning trial in Bavaria, Germany (Franz et al. 1993). The trial consists of three plots of 0.369 ha with light, moderate and heavy thinning from below, respectively. The trial was established in 1870 when the stand was 48 years old, and subsequent stand measurements were taken every 5 to 15 years until 1990. The measurements include individual-tree heights and diameters, and were processed in the same way as the Evo data to obtain volume growth and mortality. The site is located in the submontane vegetation zone, 460 m above sea level, on a fer-

tile well-watered soil. The mean annual temperature is 6.4 °C. The site index (base age 100 years) at Fabrikschleichach was estimated at 28 m in 1870, but has increased to 30 m at the end of the observation period. The enhanced stand productivity reflects a trend seen in many European forests (Spiecker et al. 1996); however, it is not certain which factors (e.g., nitrogen deposition, or increases in either CO_2 concentration or temperature) are responsible, or to what extent, for this trend at the Fabrikschleichach site.

Simulation experiment

We report a simulation experiment with the four models. Specifically, we compared model results for stand-level variables, tree structure, and the VGS graphs with the respective field data from the two sites.

Initialization   The data sets include information about tree height and stem number in diameter classes at particular time intervals. Because the models are based on the carbon balance, they also need initial information about biomass components, most importantly, the foliage mass of the trees. All the models make use of some conservative structural relationships that reduce the requirements for initialization data. The height of the crown base, for example, proved sufficient to estimate the foliage mass by means of regression equations based on various inventory data sets. The initial size distributions generated by each model based on these three input variables are shown in Table 2. For example, MORG and 4C utilized the height of the crown base to estimate the basal area at crown base from a standard taper curve, then used this as a basis for the foliage estimate. PipeQual estimated the amount of foliage directly from crown length with an allometric equation, and FORSKA used the diameter at breast height in combination with an empirical parameter and the assumption that sapwood pipes are alive for a certain period of time.

Stand-level results of the models   The models were first adjusted for standard stand-level measurements: stocking, mean diameter, and stem volume. For this, the models were initialized based on the oldest field measurements for both sites (Table 2) and run over the measurement period. The model results at the end of the measurement period were then compared with the corresponding field measurements. Some of the parameter values, mainly related to overall site productivity, were changed to provide the right order of magnitude of growth for the test sites. The results for pine in Evo are shown in Figure 1 and those for beech in Fabrikschleichach are shown in Figure 2. Note that stem volume for beech includes branches in FORSKA (2c). The model 4C underestimates the absolute stem volume for beech (2c), although its projection of the quadratic mean diameter is realistic (2a) and there is only slight deviation from data in stem number (2b). This suggests that 4C underestimates height growth (see Figure 4c below).

Stand structure   Stand structure is conventionally described in terms of diameter distributions and height:diameter relationships. Model predictions of size distributions were compared with data after 56 (pine, Figure 3a) and 80 (beech, Figure 4a) simulation years, respectively. The relative diameter distribu-

Table 2. Initial size distributions used for the pine and beech stands at Evo and Fabrikschleichach. Abbreviations: D_{13} is breast height diameter, H is tree height, H_c is height of the crown base, and N is stocking density.

Diameter class	1	2	3	4	5	6	7	8	9	10
Evo, Pinus sylvestris Age 46										
$D_{1.3}$ (cm)	3.5	5.5	7.5	9.5	11	12	13.5	15.5	17.5	
H (m)	4	5.4	7.2	9	10.2	10.9	11.7	13.5	14.4	
H_c (m)	3	3.8	4.7	5.3	5.6	5.7	5.8	5.8	5.8	
N (ha^{-1})	609	962	860	384	211	99	167	71	41	
Evo, Pinus sylvestris Age 78										
$D_{1.3}$ (cm)	7.5	9.5	11.5	13.5	15.5	17.5	19.5	21.5	23.5	25.5
H (m)	10.5	11.9	13.7	15.1	15.9	17.2	17.6	18.4	19	19.3
H_c (m)	7.4	8.1	8.9	9.5	9.7	10.1	10.2	10.4	10.6	10.6
N (ha^{-1})	98	259	280	189	197	167	119	77	42	28
Fabrikschleichach, Fagus sylvatica Age 82										
$D_{1.3}$ (cm)	7.4	10.1	12.9	15.9	19.1	22	25	27.9	30.8	34
H (m)	10.9	14.1	16.7	19	20.8	22.2	23.4	24.4	25.2	26
H_c (m)	7.4	9.4	10.9	12.2	13.1	13.7	14.2	14.6	14.9	15.2
N (ha^{-1})	144	339	263	225	209	155	119	68	46	16
Fabrikschleichach, Fagus sylvatica Age 128										
$D_{1.3}$ (cm)	18.9	22.5	25.8	30.4	34.2	37.8	41.9	45.8	49.6	55.4
H (m)	25.5	27.3	28.7	30.2	31.2	31.9	32.7	33.3	33.8	34.4
H_c (m)	16.9	17.6	18.1	18.6	18.8	19	19.1	19.3	19.3	19.4
N (ha^{-1})	8	68	106	87	73	89	46	11	8	2

tion was also plotted to compare the relationships between the different size classes (Figures 3b and 4b). Lindner et al. (1997) found that graphs of tree height versus diameter were useful in
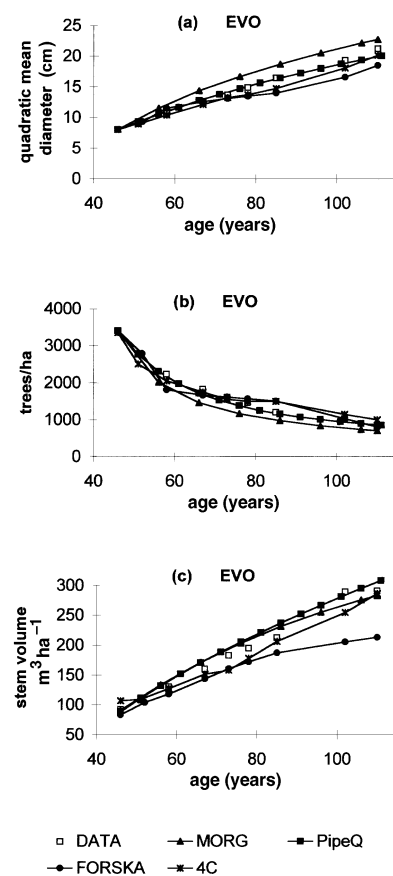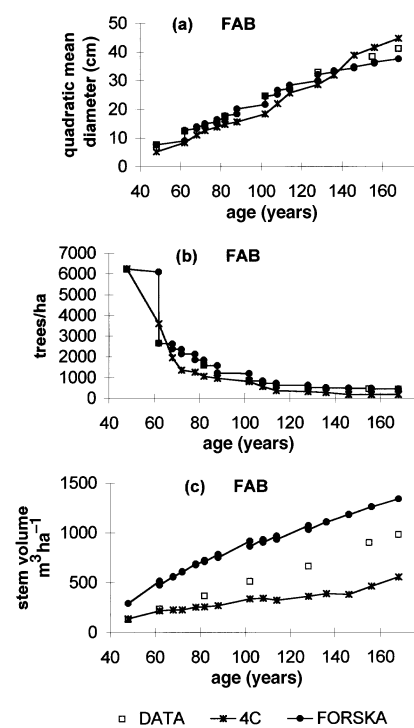

Figure 1. Stand-level predictions of the models for the Evo site. (a) Quadratic mean diameter (cm), (b) stand density, and (c) stem volume (m^3 ha^{-1}). PipeQual has been abbreviated as PipeQ in the figures.

Figure 2. Stand-level predictions of the models for the Fabrik-schleichach site. (a) Quadratic mean diameter (cm), (b) stand density, and (c) stem volume (m^3 ha^{-1}).
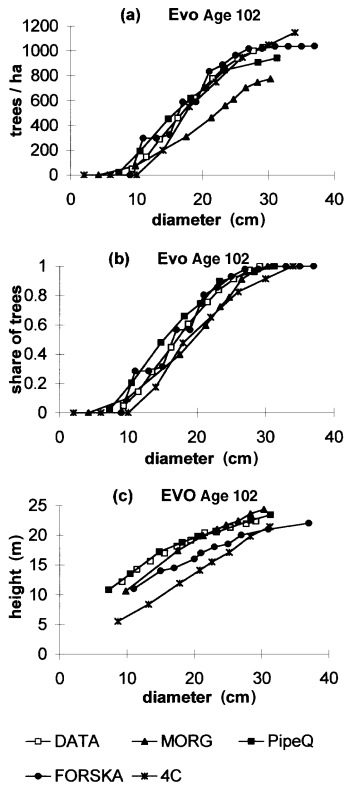
Figure 3. Predictions of stand structure for the Evo site at Age 102. (a) Cumulative diameter distribution, (b) relative cumulative diameter distribution, and (c) height–diameter relationship.
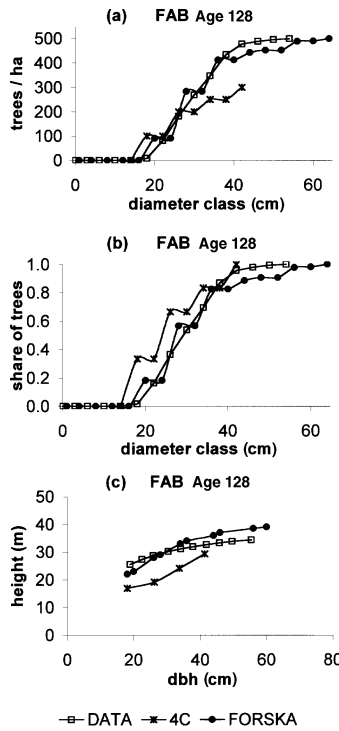

Figure 4. Predictions of stand structure for the Fabrikschleichach site at Age 128. (a) Cumulative diameter distribution, (b) relative cumulative diameter distribution, and (c) height–diameter relationship.

assessing stand structure at different times. Figures 3c and 4c complement the information obtained from the diameter distribution. Figures 3 and 4 give a clear picture of whether a model can reproduce stand structure at a particular time.

Volume growth and survival graphs   The stand structures indicated by Figures 3 and 4 depend on the relative growth and mortality of the trees in the size classes, manifested in the VGS graphs. To relate the predicted stand structure to the differences in growth and mortality implied by the models, these graphs were computed on two occasions during the simulation: Years 46 (Figure 5) and 78 (Figure 6) for Scots pine and Years 82 and 128 for beech (Figure 7). In these runs, the models were initialized with data for the respective year, to avoid differences caused by an accumulating deviation from the actual stand structure (Table 2). Survival graphs were not constructed for beech, because the field data did not distinguish between natural mortality and thinning.

Results and discussion

Currently, a key question in process-based forest growth modeling is how tree growth responds to the variable local environments in a stand. One of the response mechanisms is thought to be the allocation of growth, such that a certain reduction in intercepted light, or annual net photosynthesis, may not necessarily result in a similar reduction in growth if trees

of a stand are compared (Albrektson and Valinger 1985). To validate our model results, we must therefore be able to test the distribution of relative growth implied by the model between trees of different size and position. We illustrate such a
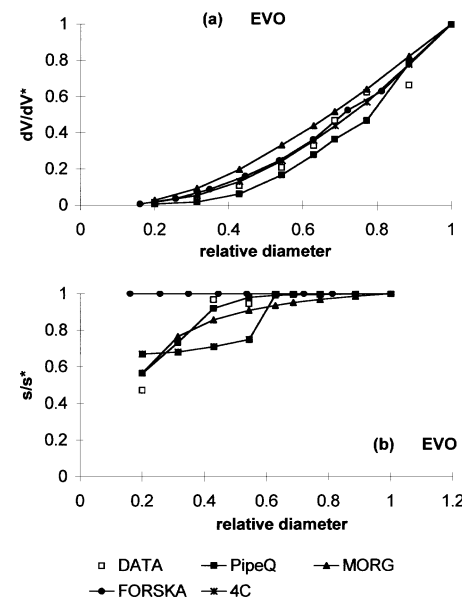

Figure 5. VGS graphs in the models compared with the Evo data at Age 46. (a) Volume, and (b) survival.
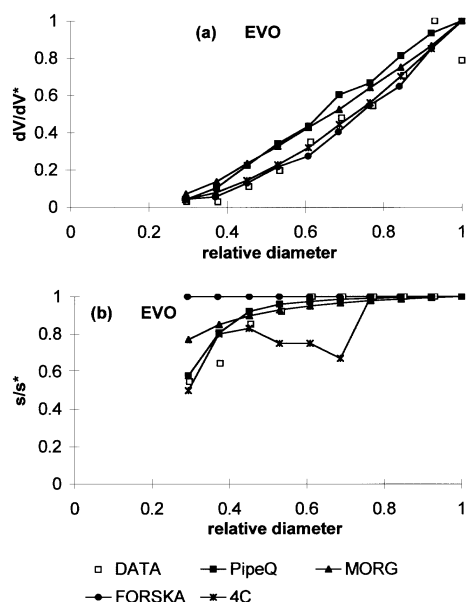
Figure 6. VGS graphs in the models compared with the Evo data at Age 78. (a) Volume, and (b) survival.

test using the VGS graphs developed by Sievänen et al. (2000).

We conclude that stand-level tests are not sufficient for evaluating an individual-tree based model. This is most clearly illustrated by the results of MORG and PipeQual, which provided fairly accurate predictions for the stand-level variables shown here, but failed to reproduce the shape of the diameter distribution after a 56-year simulation. PipeQual overestimated the proportion of small trees, probably because it underestimated their relative growth rate in the early phase of the simulation (Figure 5a). The model MORG erred in the opposite direction: the proportion of small trees was underestimated, whereas growth of small trees was disproportionately
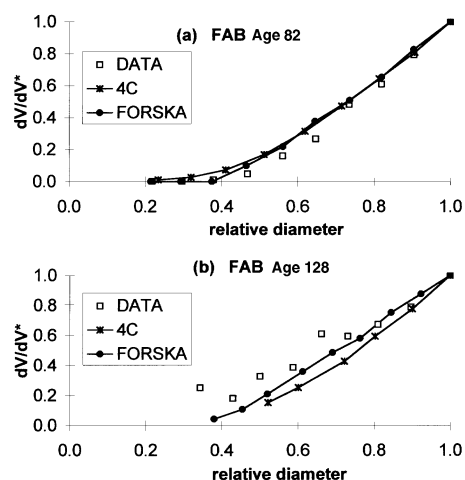
large compared with growth of the larger trees.

In contrast, the results with FORSKA illustrate that an accurate prediction of the diameter distribution or the VGS graphs is not sufficient for the model to perform adequately at the stand level. For the Evo runs, FORSKA showed good agreement with data for the VGS graphs for volume and reproduced the measured diameter distribution, but the prediction of total volume was grossly underestimated (Figure 3). The reason for the underestimation of stem volume is seen in the graph of tree height versus diameter (Figure 3): the predicted tree height of FORSKA is far too low, probably because the allocation between height and diameter was parameterized for the Central European rather than the northern pine region. This emphasizes that the VGS graphs represent relative growth and survival of trees, whereas model predictions of absolute growth rates have to be tested by other means. Further, because mortality occurs in pulses in FORSKA, the rather flat VGS graphs for mortality are unrepresentative of average mortality in the model. The pulses are also the cause of the step-like size distribution.

The FORSKA results indicate that the VGS graphs do not give a complete picture of stand dynamics. Because they are concerned with volume growth, no information on how this growth is distributed between diameter and height increments can be inferred. The graph of tree height versus diameter is therefore a useful additional tool for the analysis of stand structure, as noted by Lindner et al. (1997). This is further emphasized by comparison of the results obtained with PipeQual and MORG with those obtained with FORSKA and 4C. Figure 3 shows that PipeQual in particular, but also MORG, produced a realistic description of the allocation between height and diameter growth. This seems to override the discrepancies between the measured and predicted VGS graphs for volume (Figure 5 and 6) in those models, such that the overall model predictions of PipeQual and MORG are more in keeping with the test data than those of FORSKA and 4C which, however, are more accurate in their predictions of the VGS graphs. This is probably caused by the propagation of error from stand structure to the VGS graphs in model simulations, whereas a realistic stand structure will give rise to more realistic VGS graphs. Indeed, VGS graphs based on data from PipeQual and MORG remained quite similar to those based on measurement data throughout the long-term simulations, unlike the VGSs based on data from FORSKA and 4C.

The discrepancies between the models and the data can be analyzed further by investigating the contributions of tree size, photosynthesis, respiration, and allocation to the form of the VGS graphs. This can be done using the concept of growth efficiency (GE) (Waring and Schlesinger 1985), defined as the growth rate of stem volume (G_s) per unit foliage mass (or area) (W_f). Stem volume growth is hence

$$G_s = GE W_f. \tag{4}$$

Foliage mass represents the impact of tree size on volume growth, whereas GE incorporates the combined, size-specific effect of photosynthesis, respiration, and allocation of total growth to stems. These depend on a variety of factors, includ-

Figure 7. VGS graphs for volume in the models compared with the Fabrikschleichach data. (a) Age 82, and (b) Age 128.

ing shading, acclimation of specific leaf area, and the ratio of respiring biomass to foliage. A description of these relationships is an integral part of any process-based model, but the methods of implementation vary greatly among models. Foliage mass, on the other hand, is usually a straightforward state variable (e.g., in all the models used here), or an algebraic variable computed from stem dimensions (e.g., Shugart 1984).

In both the Evo and Fabrikschleichach data, the relationship between diameter and volume growth resembles a power function. Additionally, the relationship between foliage mass and diameter is known to be of similar form (e.g., Landsberg 1986). We studied this proposition in PipeQual and MORG and found that variation in foliage mass explained most of the variation observed in volume growth in the models. Furthermore, the differences observed in the VGS graphs for volume between PipeQual and MORG could be attributed largely to the different initialization procedures in the two models concerning foliage mass. On the other hand, the strong correlation between foliage mass and volume growth largely disguised the difference between the two models in the relationship between GE and tree size. However, the significance of foliage for volume growth was probably larger than normal because the size range of the stand was large.

We conclude that actual data on foliage mass or area are necessary for a stringent test of the VGS graphs in process-based models. Preferably, the different foliage processes that contribute to volume growth should be analyzed separately. It is necessary for the model to maintain a realistic proportion of foliage in each tree relative to its height, diameter, and other indicators of size, just as a realistic height:diameter ratio is necessary, to simulate stand structure correctly, and hence to reproduce the development of the VGS graphs over time.

An analysis of the component processes contributing to the VGS graphs can be useful not only in model evaluation but also in model development and improvement. The VGS graphs have already been used as a tool for structural improvement in the 4C and PipeQual models. For example, PipeQual was first run based on the assumption that crown length is an attribute of photosynthetic efficiency through a postulated reduction of water availability in the crown (Hellkvist et al. 1974, Tyree 1988, Mäkelä 1997), but this led to gross underestimation of the relative volume growth of larger trees in the stand. When this assumption was relaxed, the VGS graphs derived from the model became more consistent with the measurement data. Similarly, in a former version of 4C, the growth VGS indicated that the growth of small and intermediate tree cohorts was underestimated relative to that of the dominant tree cohort. This behavior was traced to the growth model and its parameterization. Consequently, some sensitive and highly uncertain parameters (e.g., the sapwood senescence parameter and the parameter describing the relation between height growth and foliage growth) were improved and changes to the growth model were carried out: height growth is now modified by stand density (similar to the approach of Lindner et al. 1997), and the calculation of light absorption is a function of crown projection area.

As a result of this analysis, it is evident that all four models can be improved. In PipeQual and MORG, some of the important issues will be the initialization procedure for foliage, as well as an analysis of the photosynthesis submodels, to improve the VGS graphs for volume. The mortality functions clearly need improvement with respect to the mortality of the smaller trees. Further, the comparison of simulated and measured height–diameter relationship (Figure 3) indicates that height growth in MORG, which is driven by height of the crown base, does not work well on the Evo plot, indicating the need for re-examination of this model component.

In FORSKA, the VGS graphs for volume are satisfactory, especially for the Evo data, but the height–diameter relationship requires attention. The problem in the case of Evo may be solved by re-parameterizing the model for the Finnish pine. In Fabrikschleichach, FORSKA overestimates the height and diameter of dominant trees and underestimates those of suppressed trees. Accordingly, the VGS graph for growth at Age 128 (Figure 7b) indicates an underestimation of growth of small trees. This could be explained by the simplification of the photosynthesis model in FORSKA, which uses only one light response parameter set for beech, although it is well known that shaded beech leaves are more efficient than unshaded leaves (e.g., Schulze 1970). The overestimation of stand volume of beech at Fabrikschleichach may be partly explained by differences in the definition of volume: the measurements show only stem volume, whereas FORSKA simulates (aboveground) biomass, which includes branches.

Although 4C produces satisfactory VGS graphs for volume, the main concern is the underestimation of growth in the smaller tree cohorts, which also corresponds to an overestimation of mortality of smaller trees, as indicated by the VGS graphs for survival. A thorough analysis of the different submodels of 4C (light interception, photosynthesis and allocation) is necessary, therefore, to explain the unsatisfactory growth behavior of the small and intermediate tree cohorts.

Use of the VGS evaluation method assessed here requires data on individual tree growth and mortality in a stand. However, as it is stem volume growth that is of interest, suitable data can be derived from forest inventories. Furthermore, a snapshot of growth and mortality over a period of no more than 5 years may be all that is required. This method is therefore easy to use and provides insight into model properties.

Individual-tree, process-based growth models consist of numerous interrelated model components that make thorough model validation difficult. Our analysis has shown that VGS graphs are useful in model evaluation because they show how deviations from observed stand dynamics can be attributed to the growth and mortality components in a process-based model. In particular, if used in combination with indicators of stand structure, such as the height:diameter ratio, they provide additional information on the relative growth of different size classes of trees that is of great value in model development and improvement.

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