Improving the simulation of stand structure in a forest gap model

Marcus Lindner [a,*], Risto Sievänen [b], Hans Pretzsch [c]

[a] Potsdam Institute for Climate Impact Research, P.O. Box 601203, D-14412 Potsdam, Germany
[b] Finnish Forest Research Institute, Vantaa Research Station, P.O. Box 18, FIN-01300 Vantaa, Finland
[c] Chair of Forest Yield Science, Faculty of Forest Science, University of Munich, Hohenbachernstr. 22, D-85354 Freising, Germany

Abstract

There is currently great interest in improving the applicability of forest gap models to changing environmental conditions, in order to facilitate the assessment of possible impacts of climatic change on forest ecosystems. Moreover, for the development of mitigation strategies, it is necessary to include forest management options in the models. Both the simulation of transient effects of climatic change and of forest management regimes require a realistic representation of stand structure in gap models, since tree species respond to variations in stand density in characteristic ways, depending on their ecological strategies.

In this study, we compared the effect of five different height growth functions that are sensitive to stand density on simulated stand structure of the FORSKA forest gap model. We used long term observation data from a beech thinning trial at Fabrikschleichach, Bavaria, to test the alternative functions. First, we compared simulation results of the original FORSKA model with measured stand development from 1870 to 1990. Whereas simulated stand level variables (e.g. biomass, mean diameter and height) showed good correspondence with observations, individual tree dimensions and simulated stand structure were quite unrealistic. After calibrating parameters of the height growth functions with data from a lightly thinned plot at Fabrikschleichach, we ran the model with data from a heavily thinned plot for validation. All five functions considerably improved the simulation of height/diameter relationships and stand structure. However, there were distinct differences between functions. The best correspondence with measurements was shown by a function which uses the relative radiation intensity in the centre of a tree crown as an indicator of the competition status of the tree. This function is rather simple and needs only two growth parameters, which can be derived for different functional types of species, according to their shade tolerance.

With the new, flexible height growth function it should be possible to extend the applicability of gap models to more realistic simulation experiments including forest management and natural disturbances. To our knowledge, this was the first attempt to employ long term forest observation data for the calibration and validation of a forest gap model. The results suggest that such data could be very useful in model testing and improvement. © 1997 Elsevier Science B.V.

Keywords: Forest gap model; Stand structure; Height/diameter relationship; Competition effects; Climate change impact analysis

---

* Corresponding author. E-mail: lindner@pik-potsdam.de.

1. Introduction

Forest gap models have been applied to simulate forest development and long term forest succession in many studies over more than 20 years (Botkin et al., 1972; Shugart, 1984; Shugart and Smith, 1996). In most of these investigations the focus has been on the simulation of species composition and forest productivity in terms of biomass production. Stand structure (here defined in a broad sense as the vertical and spatial mixture of species, and size and age distributions of trees) has been considered to be response of species composition to environmental conditions. With increasing concern about the possible impacts of a changing climate on forests, gap models have been used to analyse forest dynamics under climatic change (e.g. Solomon, 1986; Pastor and Post, 1988; Kienast, 1991; Shugart and Smith, 1996). However, there are still many uncertainties, especially concerning the transient effects of climate change (Kirschbaum et al., 1996). These are important, e.g. for the calculation of the carbon balance and the role of forests as a source or sink of CO_2 (King and Neilson, 1992; Dixon et al., 1994).

There are several reasons why stand structure deserves greater attention in the analysis of transient effects of climate change. Urban et al. (1993) have shown that over shorter time spans the transient effects on species composition and succession are very sensitive to the initial composition of forest stands. In mixed stands, short term forest dynamics could also depend on stand structure and density. For example, if biomass on a forest patch is strongly reduced due to environmental stress, both the surviving trees and possible new invaders will probably respond differently if there are few large or many small trees remaining. Furthermore, stand structure is an important factor with regard to the susceptibility of forest stands to disturbances. Many authors expect changes in the disturbance regimes under a changing climate (Overpeck et al., 1990; Cammel and Knight, 1992; Baker, 1995; Volney, 1996), and secondary damages are often observed in stressed forests. In such situations, the size distribution of trees, that is, stand structure may play an important role. Finally, the development of forest management strategies will also require the consideration of possible changes in stand structure.

A model comparison of two gap models at sites in northeast Germany revealed that in simulations with low stand density, individual trees grew much too fast (Lasch and Lindner, 1995b; unpublished results). Especially after thinning, simulated stand structure became unrealistic compared with observations or yield tables. This is at least partly attributable to the density independent relationship between height and diameter in the models (Botkin et al., 1972; Prentice and Leemans, 1990). We therefore believe that, in order to represent forest structure in forest gap models more realistically, it is necessary to improve the description of height growth in the models.

In the following we analyse the effect of incorporating flexible height/diameter increment functions into the FORSKA forest gap model (Prentice et al., 1993). The model in question is presented in Section 2.1, and suitable height growth functions are discussed in Section 2.2. In Section 3.1, the simulated stand growth of the original approach is compared with observations. In Sections 3.2 and 3.3, the general effects of the new functions on model behaviour are analysed.

2. Materials and methods

2.1. Simulation model

The FORSKA model 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. FORSKA shares the common gap model structure with many other models (Shugart, 1984; Bugmann et al., 1996), but it includes more mechanistic formulations of tree growth than most earlier gap models. The model was described by Prentice et al. (1993), and a detailed documentation of the tree growth functions can be found in Leemans and Prentice (1989). In this study we are using a version of FORSKA with slight modifications made by Lasch and Lindner (1995a) for applications to northeast Germany.

In the following we briefly summarise the major growth equations of FORSKA. Carbon allocation and allometry are dealt with in Section 2.2.

Net growth rate of a tree is calculated in terms of

tree-volume index, D^2H, which is directly proportional to stem volume. It is obtained by integrating the balance between net assimilation of the leaves of one crown layer and the maintenance costs of the sapwood up to this layer through the crown

$$d(D^2H)/dt = bf\int_B^H S_L\left[m_G \Gamma P(z) - m_R rz/C\right]dz \tag{1}$$

where D is diameter at breast height, H is tree height, B is bole length of the tree, S_L is leaf area per unit height z, Γ is a growth scaling constant which is proportional to the maximum net assimilation rate, $P(z)$ is a reduction factor for the net assimilation rate of the canopy layer at depth z, C is the initial ratio between leaf area and sapwood area, r is a sapwood maintenance cost factor, m_G and m_R are environmental multipliers, and bf is a function to account for resource depletion as the forest gains biomass (Lasch and Lindner, 1995a)

$$bf = 1 - e^{-0.01(W - W_{max})} \tag{2}$$

where W is total biomass per patch and W_{max} is a site specific maximum biomass.

Biomass of the patch is the sum of stem dry weights, w, which are obtained from the tree-volume index

$$w = qD^2H \tag{3}$$

where q is a wood density and form factor.

2.2 The height growth function in FORSKA and some possible alternatives

The FORSKA model specifies the growth increment primarily in terms of mass of the whole tree (or stand). Thus, the task to convert the mass increment of the whole tree to values of dimensional variables (diameter, height, etc.) ensues. In FORSKA this is accomplished in the following way: the photosynthesis submodel produces the increment of tree-volume index $\Delta(D^2H)$ (cf. Eq. (1)). Differentiation of D^2H yields

$$\Delta(D^2H) = 2DH\Delta D + D^2\Delta H \tag{4}$$

Assume further that the increments of D and H have the relationship $\Delta H = f_h \Delta D$, where f_h is a function which depends on tree size, stand conditions, etc. When this relationship is substituted in Eq. (4), it can be solved for ΔD, giving

$$\Delta D = \frac{\Delta(D^2H)}{2HD + f_h D^2} \tag{5}$$

and consequently

$$\Delta H = \frac{f_h \Delta(D^2H)}{2HD + f_h D^2} \tag{6}$$

Introducing the functional relationship between height and diameter increments makes it thus possible to transform biomass increment into diameter and height increments.

The FORSKA model was developed for unmanaged natural forests, where tree height can be approximated as a function of diameter

$$H = 1.3 + (H_{max} - 1.3)$$
$$\times \left(1 - \exp\left[-sD/(H_{max} - 1.3)\right]\right) \tag{7}$$

where H_{max} is the maximum height and s is a parameter specifying the initial slope (at $D = 0$) of the function. In this case, function f_h is defined simply as $f_h = dH/dD$ and

$$\frac{dH}{dD} = s\exp\left[-sD/(H_{max} - 1.3)\right] \tag{8}$$

Most gap models use similar relationships between height and diameter and thus the height increment of a tree depends only on its current diameter. However, it is known that the competition experienced by a tree affects height growth and consequently dH/dD. For example, after thinning diameter growth increases and height growth may even decrease (Kramer, 1988; Oliver and Larson, 1990).

To include such competition effects in FORSKA, it is necessary to modify the height growth function of the model. It is desirable that the modified h/d increment function is a modification of the dH/dD equation above. The right-hand side of Eq. (8) can also be expressed in terms of H and then reads

$$\frac{dH}{dD}\bigg|_{D=D(H)} = s\cdot\left(1 - \frac{H - 1.3}{H_{max} - 1.3}\right) \tag{9}$$

where $D(H)$ is D as a function of H solved from Eq. (7). Eq. (9) has two parameters, H_{max} and s. Maximum tree height, H_{max}, is a species specific parameter which should not be affected by competi-

tion. Hence we incorporate the effect of competition into parameter s and redefine it by

$$f_h = s(K)\left(1 - \frac{H - 1.3}{H_{max} - 1.3}\right)$$	(10)

where K denotes a measure of competition.

What would be a suitable measure of competition? The function to account for competition should reflect the effect of stand density and the relative size of the tree in the stand. In the following we present five possible functions. In all equations, s_{min} is the minimum value of s (low competition pressure) and e_1 and e_2 are parameters, which have their own meaning in each function.

2.2.1. Function 1

Sievänen (1993) used a function where f_h was dependent on the ratio B/H (B is height of the crown base)

$$s = s_{min} + e_1 \frac{B}{H}$$	(11)

The B/H ratio reflects stand density since it tends to be larger in denser stands and also reflects the relative size of the tree if small trees have higher B/H than tall ones. This tends to be the case in even-aged pure stands, since the height of the crown base is approximately the same for all trees. This condition also holds for the present FORSKA simulations of beech stands. However, for uneven-aged stands this condition does not hold and the function has to be reformulated.

2.2.2. Function 2

Whereas the B/H ratio responds only slowly to abrupt changes like thinning, the relative change of the height of the crown base responds faster. Considering the latter, we formulated the function

$$s = s_{min} + e_1 \frac{\Delta B}{H}$$	(12)

Its logic is the same as that of function 1: in a dense stand the height of the crown base increases rapidly, and for small trees the relative speed is greater than for tall ones. In the case that the height of the crown base does not increase, the stand is obviously rather sparse, the competition pressure is low and there is no need for rapid height growth.

2.2.3. Function 3

Nikinmaa (1992) used an h/d increment function that was dependent on the change of radiation intensity between the top and bottom of the crown. It is based on the reasoning that when a tree is in danger of being overtopped, it experiences a rapid change of radiation conditions within its crown. Increasing height growth in proportion to diameter growth is an obvious way to counteract overtopping by others. This consideration gives the function

$$s = s_{min} + e_1 \frac{I_u - I_l}{H_u - H_l}$$	(13)

where I_u and I_l are relative radiation intensities (local intensity divided by intensity at the top of the stand) in the centres of the upper and lower third of the crown, respectively, and H_u and H_l are the corresponding heights. The relative radiation intensities were calculated using the radiation extinction model (Lambert-Beer and assumption of even distribution of leaf area between the top of the stand and the crown base) used in FORSKA.

2.2.4. Function 4

Instead of the steepness of change in radiation conditions, the relative radiation intensity itself can be used as a measure of competition pressure. Korol et al. (1995) used a step function assuming that when the photosynthetically active radiation (PAR) available to an individual tree is less than 50% of the above-canopy PAR, height growth is favoured over diameter growth. We adopted a more flexible function which utilises the relative intensity of the radiation in the centre of the tree crown, I_c

$$s = s_{min} + e_1\left(\frac{1}{I_c} - 1\right)$$	(14)

2.2.5. Function 5

The last function that we analysed is based on traditional mensurational measurements

$$s = s_{min} + e_1 G + e_2(max[1, H_d/H] - 1)$$	(15)

where H_d is the dominant height of the stand and G denotes stand basal area.

2.3. The data

Research plot data from a beech (*Fagus sylvatica* L.) thinning trial at Fabrikschleichach in Bavaria

Table 1
Summary of the Fabrikschleichach research plot data

Plot	Thinning treatment	Research plot data 1870				Research plot data 1990			
		Density (ha^{-1})	Dg (cm)	Hd (m)	Basal area (m^2 ha^{-1})	Density (ha^{-1})	Dg (cm)	Hd (m)	Basal area (m^2 ha^{-1})
P1	Light	6220	7.6	15.9	28.2	407	41.1	36.5	53.9
P2	Moderate	3831	9.4	14.9	26.3	302	46.7	37.4	51.9
P3	Heavy	2440	10.5	14.8	21.3	206	52.9	38.1	45.3

Dg, quadratic mean diameter; Hd, dominant height.

(Franz et al., 1993) were used to initialise and test the model variants with different height growth functions. The trial consists of three plots with light, moderate and heavy thinning from below. It was started in 1870 at a stand age of 48 years with subsequent stand measurements every 5–15 years; the last inventory was taken in 1990. Data from the plots are summarised in Table 1.

2.4. Simulation experiment

First, we used the initial stand description of the lightly thinned plot (P1), where only dead and heavily suppressed trees were harvested, to initialise the model with alternative height growth functions. The parameters of the height growth functions (Table 2) were estimated in a series of simulations. The values were adjusted iteratively by comparing simulated and observed stand characteristics visually. We ran the model only with stress-induced mortality (see Prentice and Leemans (1990) about mortality functions in FORSKA), because there was no major mortality caused by disturbances in the plots during the observation period. Nevertheless, the simulated stand density declined faster than in reality, because mortality of suppressed trees was overestimated (Fig. 1). Since stand density has a strong influence on tree dimensions and stand structure, it was difficult to

compare the different height growth functions as long as mortality was estimated incorrectly. We decided to repeat the experiment without the mortality functions. Instead, we applied a thinning routine analogous to the observed stand development, thus ensuring that stem numbers would be comparable to the control plot. Finally, we ran a validation experiment with initial data from the heavily thinned plot (P3). Again we ran the FORSKA model without mortality except for the prescribed thinning regime.

Size distributions in terms of diameter and height were used to compare simulated stand structure against observations. The effect of stand structure on individual trees was analysed by comparing height/diameter relationships within the stand using stand-height curves at different stages of stand development.

Comparison of simulation results and research plot measurements
FORSKA original (plot P1)

Table 2
Parameter values of the five height growth functions

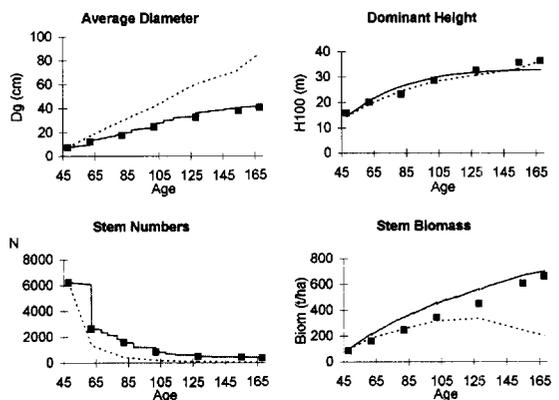| Function	s_{min}	e_1	e_2
1	0.4	3.0	–
2	0.4	250.0	–
3	0.4	40.0	–
4	0.4	0.4	–
5	0.3	0.005	7.5

Fig. 1. Simulated (lines) and measured (squares) stand level variables for Fabrikschleichach plot P1 (light thinning): Dg, average diameter; Hd, dominant height; Biom, stem biomass and stem number. Original FORSKA (dashed line) and the same model with prescribed stem number (solid line).

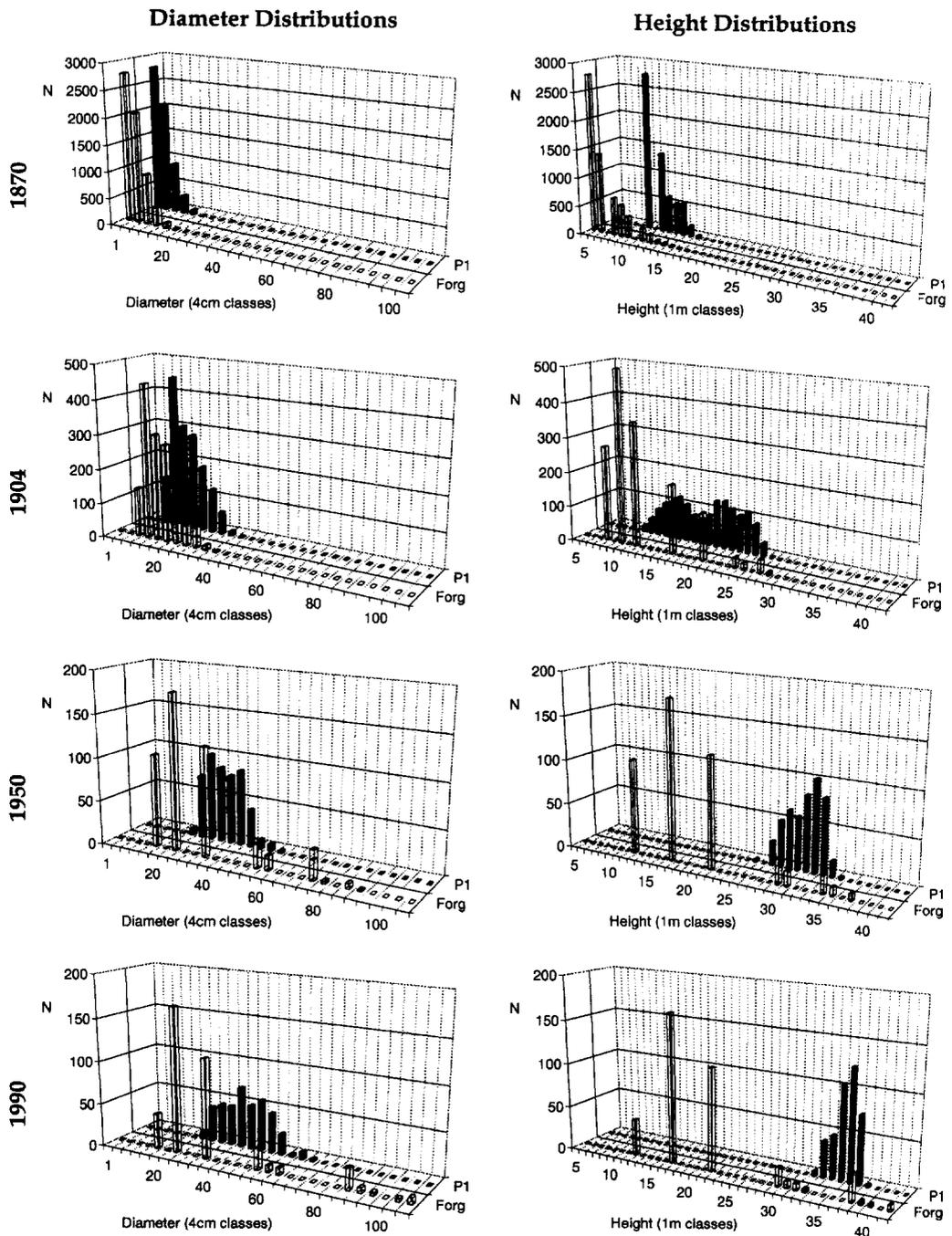## Diameter Distributions   Height Distributions

Fig. 2. Measured (P1) and simulated (Forg) diameter and height distributions in Fabrikschleichach plot P1 in 1870, 1904, 1950 and 1990. Original FORSKA using prescribed stem numbers.

3. Results

3.1. Stand growth simulation of the original FORSKA model

3.1.1. Control run without thinning

The original growth function in the FORSKA model was calibrated to produce realistic projections mainly for stand biomass and basal area of natural mixed stands without management (Prentice and Leemans, 1990). Owing to rather high estimated mortality rates the model results for the pure even-aged beech stand deviate from observed stand level variables with increasing age of the stand (Fig. 1). Simulated stem numbers are significantly below ob-
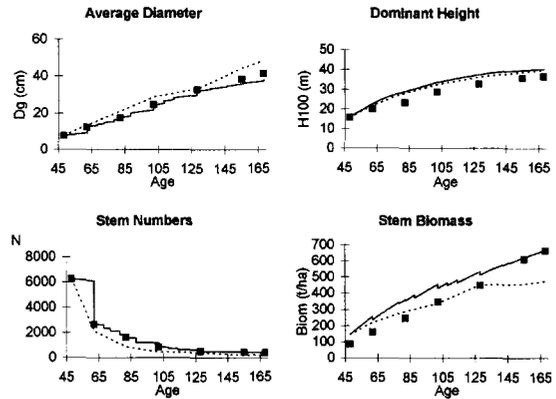

Fig. 4. Simulated stand level variables for Fabrikschleichach plot P1 with height growth function 4 (dashed line, model run with simulated mortality; solid line, stem numbers forced from observations) compared with measurements (squares). *Dg*, average diameter; *Hd*, dominant height; stem number; biom, and stem biomass.

served values and without regeneration, stand biomass and basal area decline; dominant height over age is fairly realistic, whereas mean diameter is overestimated.

3.1.2. Simulated stand development with prescribed stem density

The introduction of prescribed stem numbers to FORSKA improved the agreement with the stand level observations at Fabrikschleichach (Fig. 1). However, stand structure analysis revealed that strong differences remain. The simulated beech stand is much less homogeneous than in reality (Fig. 2). Furthermore, the height growth function of the original FORSKA gives rise to a constant height/diameter relationship independent of stand age or stand density, whereas the measured height/diameter curve becomes almost flat with increasing age (Fig. 3).

3.2. Effect of incorporating the h / d increment function

All five height growth functions improved the estimations of FORSKA in a qualitatively similar way. However, function 4 (Eq. (14)) turned out to be the best of the alternatives. We first present the general results only in terms of function 4, and then

Fig. 3. Tree height vs. diameter from 1870 (diamonds) to 1990 (circles) in Fabrikschleichach plot P1. Measured data (top) vs. simulation results of the original FORSKA (centre) and FORSKA using height growth function 4 (bottom).
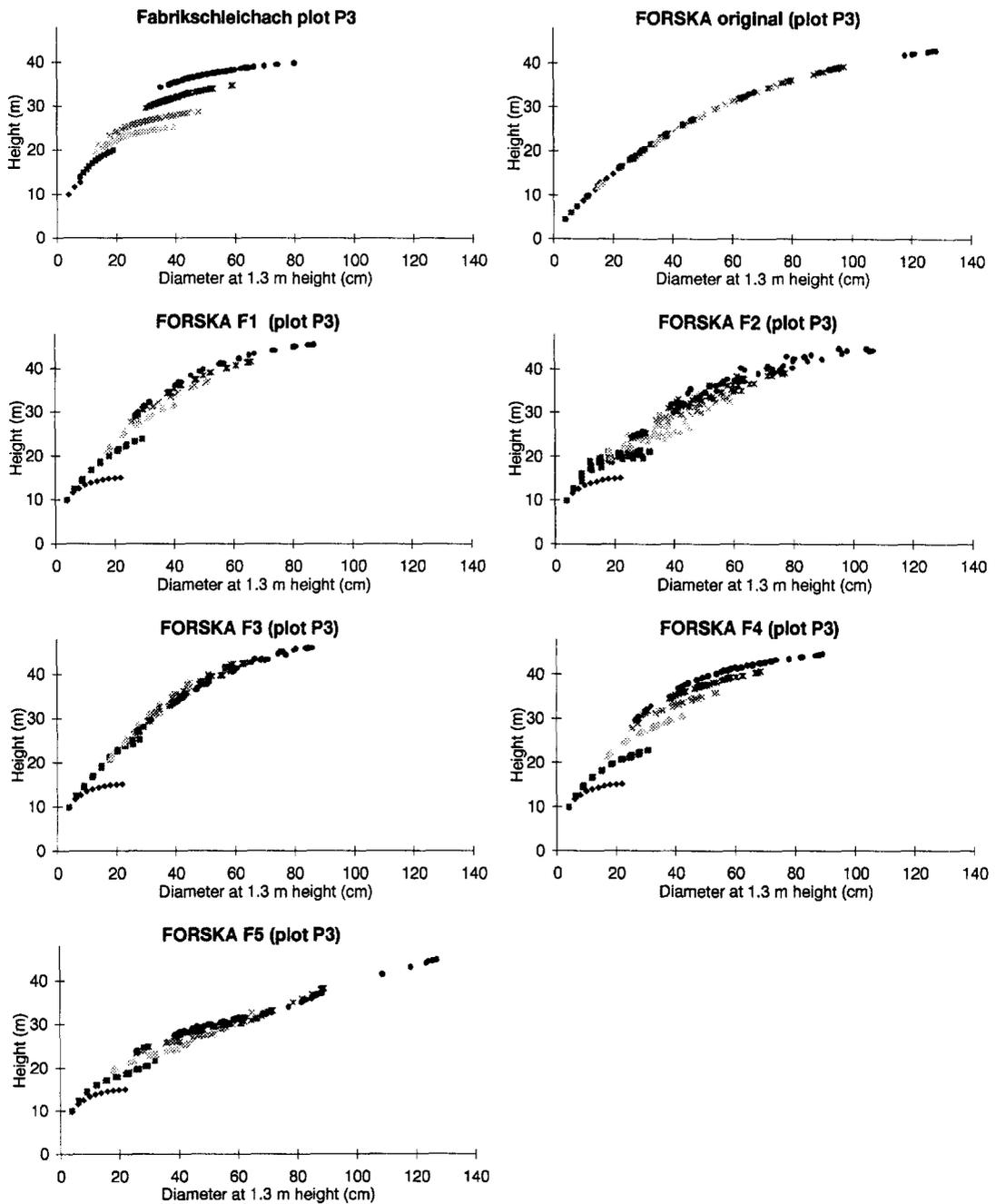
Fig. 5. Tree height vs. diameter from 1870 (diamonds) to 1990 (circles). Measured data at Fabrikschleichach plot P3 and simulation results of FORSKA, using the original height growth function (FORSKA original) and height growth functions 1–5 (Forska F1–F5).

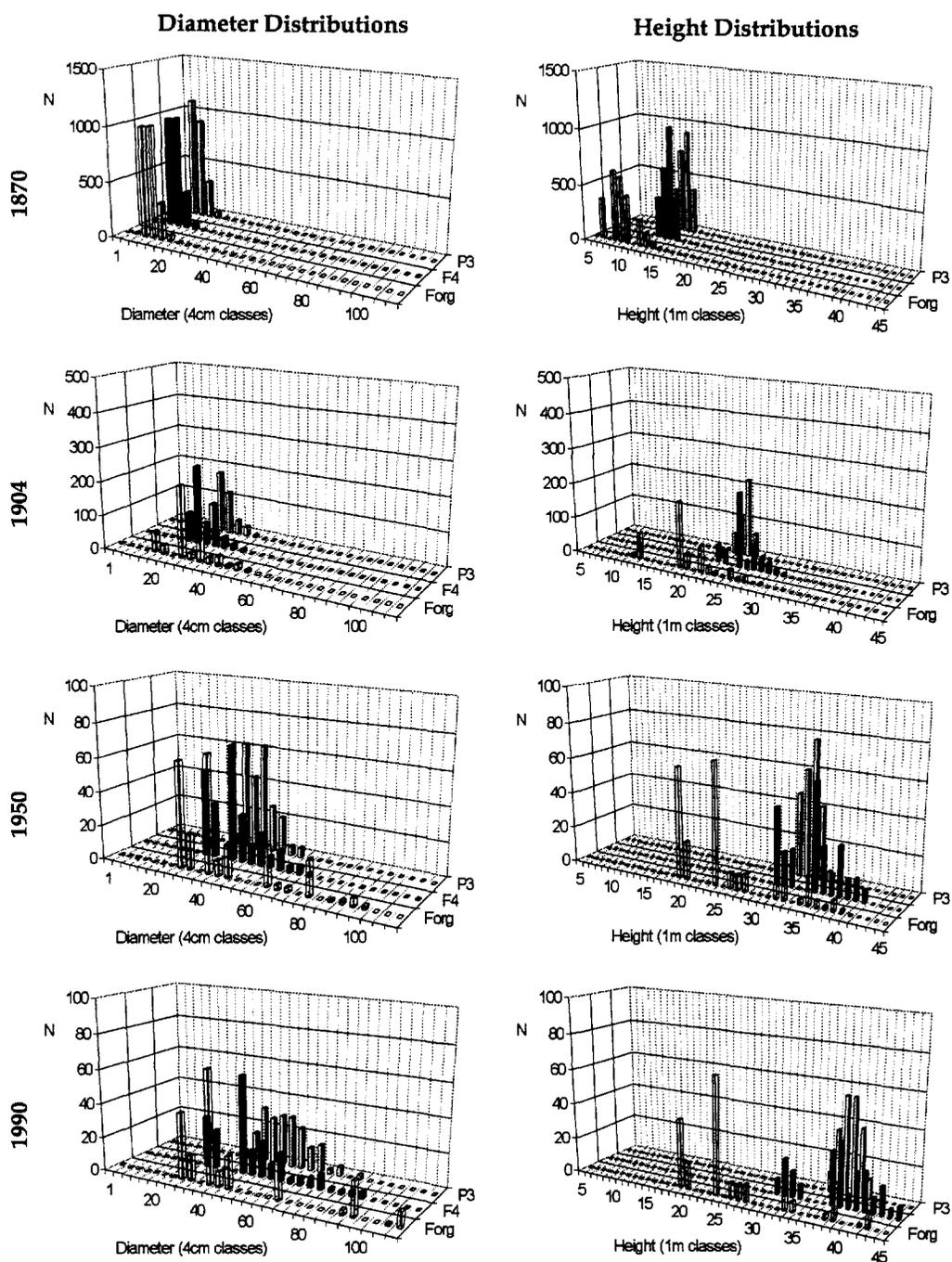## Diameter Distributions

Height Distributions

Fig. 6. Diameter and height distributions measured at Fabrikschleichach plot P3 (P3), simulated with the original height growth function (Forg) and with function 4 (F4). Stem numbers were prescribed.

describe differences between the alternative functions exemplified in the stand-height curves of the validation experiment.

3.2.1. Calibration run (plot P1)

3.2.1.1. Stand level variables.
The flexible height growth function also modifies mortality rates, because it forces suppressed trees to increase height growth, to avoid being overtopped by dominant trees, thus postponing mortality. Therefore, we first ran the FORSKA model with the new height growth function without thinning. Simulated stand level variables (Fig. 4) are significantly more realistic than with the original height growth approach. However, stem numbers are still slightly underestimated, consequently average diameter is overestimated and biomass is underestimated at stand ages above 125 years.

In the simulation experiment with the prescribed stand density, agreement with observations is generally good over the whole observation period (Fig. 4). Average diameter is slightly underestimated in the old stand, whereas dominant height and biomass are slightly overestimated most of the time. Interestingly, simulated biomasses match the observations in the last two inventories.

3.2.1.2. Individual tree variables.
Height growth function 4 modifies the simulation of individual tree variables significantly. There is a distinct influence of stand structure on the h/d ratio of individual trees which depends on their position within the stand. Simulated h/d ratios in plot P1 are much more realistic compared with the original FORSKA (Fig. 3). Simulated stand height curves at the six dates of measurements on the research plots are similar to observations and show that the model is now able to produce more realistic responses of individual trees to their stand environment.

3.2.2. Validation run (plot P3)

In plot P1 stand density remained relatively high throughout the observation period. In the heavily thinned plot P3, dominant trees were frequently released from competitors, which led to quite different growing conditions in the stand. Therefore, the P3 simulation series provides a good test for the alterna-

tive functions. In general, the performance of the height growth functions was even better in comparison with the original FORSKA than at the lightly thinned plot. Height/diameter relationships of individual trees were closer to observations (Fig. 5, FORSKA F4 cf. Fig. 3). Moreover, height and diameter distributions also improved significantly (Fig. 6).

3.3. Comparison of height growth functions

All height growth functions (functions 1–5) modified height growth in comparison with the original approach in FORSKA and improved the correspondence of simulated to observed values. This is true for stand level variables (Fig. 4), height–diameter relationship (Fig. 5) and diameter and height distributions (Fig. 6). There were differences between the results obtained with these functions, exemplified in the development of stand-height curves (Fig. 5). Functions 1 (Eq. (11)) and 4 (Eq. (14)) produce results which are qualitatively very similar to the observations. Other functions show some characteristic differences in comparison with observations: function 2 (Eq. (12)) leads to strong individual variations in h/d relationships, function 3 (Eq. (13)) underestimates height growth of suppressed trees and the height–diameter relationship of function 5 (Eq. (15)) is clearly different from the observed one.

4. Discussion and conclusions

In this study we tested the FORSKA model with five alternative height growth functions in order to improve the representation of stand structure in the model. The comparison of simulation results with the 120 year long record of observations from a beech thinning trial at Fabrikschleichach has shown that all functions improved simulated stand structure considerably.

Since stand density has a strong influence on tree growth (e.g. Oliver and Larson, 1990), we had difficulty in separating the effect of the height growth functions from density effects on tree growth. Part of the deviation from observed values was caused by the mortality function of FORSKA which overestimates mortality in comparison with the present data.

Therefore, we changed the stochastic mortality function into a deterministic thinning regime that guaranteed stem densities that are comparable to observations on the research plots. If stand density is estimated correctly, the original model simulates quite realistic stand level variables (mean diameter, dominant height, basal area and biomass), but stand structure analysis reveals that individual tree sizes within the stand still deviate from observed ones.

The new height growth functions resulted in general improvement of the distributions of tree diameters and heights, especially those of tree heights. The most obvious effect is a distinct change in the height growth of intermediate and suppressed trees. Simulated height/diameter relationships have improved with all five height growth functions. However, noticeable differences remain; simulated size distributions still deviate considerably from observations in the mature beech stand which show almost classic Gaussian bell shapes.

4.1. Effect of alternative height growth functions on model performance

The comparison of five height growth functions showed that different formulations of competition within a forest stand may lead to very distinct responses in model performance. Our study did not allow for a full quantitative comparison of the different approaches and changes in parameterisation could undoubtedly lead to slightly different results. Moreover, the observed model behaviour could also be influenced by features of FORSKA other than height growth. However, some differences in model performance seem to be less sensitive to parameterisation and could also be explained by the characteristics of the selected height growth functions.

The increase in crown height of individual trees due to shading is more variable in time and occurs much faster than changes in social position within the stand. Therefore, function 2 results in more individualistic growth developments of individual trees than all other approaches. It is the only function where trees of initially comparable size may show quite different growth development after only a few decades.

The approach based on traditional stand growth variables (function 5) resulted in non-asymptotic

stand height–growth curves, because the function assumes that increasing stand basal area has an effect on the height growth of every tree in the stand. Maybe because of the extraordinarily high stand basal areas on the research plots at Fabrikschleichach (over 150% of yield table values), the high absolute volume growth rate of dominant trees resulted in unrealistic simulated height growth of the mature stand. Fitting of this function with research plot data could possibly improve the performance of this approach.

Function 4, which showed the best results in our investigation, is a rather simple, but still mechanistic approach. It is based on the relative radiation intensity in the centre of a tree crown and should be valid for all kinds of forests, not only for pure even-aged stands like function 1, which is based on somewhat similar ecological reasoning (relative radiation intensity in the centre of a tree crown is closely correlated with relative bole length in pure even-aged stands) and also performed well in this study. Another advantage of function 4 is the fact that there is considerable knowledge about species-specific responses to light, and/or to radiation gradients. Therefore, it should be possible to derive parameters for different groups of species (functional types). In further investigations we will test the assumption that the responses of different species are related to their shade tolerance.

4.2. Limitations of the selected approach

The results have shown that the flexible height growth function 4 strongly improved the simulation of stand structure in FORSKA. The remaining differences may be due to several factors. Korol et al. (1995) reported that in the process-based tree growth model Tree-BGC dominant trees were also allocated too much of the stand level net photosynthesis unless photosynthesis efficiency of the leaves was modified according to the position within the canopy. Furthermore, they introduced a competition factor that incorporates the hydraulic architecture of trees, because leaf water potential decreases as tree height increases, thus reducing the photosynthetic capability of the tree (Korol et al., 1995). The FORSKA model is less detailed than Tree-BGC and in the current version only one set of photosynthesis parameters is

used for each tree species. It is known that beech, especially, shows adjustments of light and shade adapted leaves to available photosynthetically active radiation. Since in FORSKA all leaves have the same light response parameters, the production potential of intermediate and suppressed trees is underestimated. Consequently, simulated stress for intermediate trees is higher than in reality and these trees show reduced volume growth. The underestimation of biomass (and shading leaf area) of intermediate trees in turn increases available light for suppressed trees, which are able to survive longer than in the real stand. Another possible explanation could be the overestimation of site quality in the model, except for the last decades, when enhanced height growth on the research plots might reflect recent changes in European growth trends (Pretzsch et al., 1994; Spiecker et al., 1994).

4.3. Validation of gap model results

Although gap models have already been in use for more than 20 years (Botkin et al., 1972; Shugart and Smith, 1996) they have rarely been validated with observations, mainly because appropriate data are difficult to obtain. Doyle (1981) compared simulated density–diameter distributions and species abundance with field data in tropical rain forest and found no significant differences. In other gap model applications, validation was attempted qualitatively, using general patterns of species composition in natural old growth forest stands (Shugart, 1984) or remotely sensed data (Weishampel et al., 1992). Whereas stand level characteristics have been found to agree with observations fairly well, individual tree variables showed more uncertainty (Leemans and Prentice, 1987). Our investigation was, to our knowledge, the first attempt to employ long term forest observation data for the calibration and validation of a forest gap model. This exercise suggests that such data could be very useful in model testing and improvement. We do not believe that forest gap models could (or even should) have comparable precision with empirical forest stand simulation models (e.g. Pretzsch, 1992). Gap models should be more general and in the context of climate change it is more important to achieve plausible model performance under a broad range of environmental conditions.

However, empirical data could be used to validate important model assumptions (e.g. mortality functions) qualitatively.

4.4. Conclusions

We conclude that the implementation of a density dependent height growth function in the FORSKA gap model makes simulated stand structures much more realistic. The selected function needs two species specific growth parameters, which are related to fairly well known ecological responses to light gradients. With this approach more realistic simulation experiments, including forest management or natural disturbances, become feasible.

Acknowledgements

References

Baker, W.L., 1995. Longterm response of disturbance landscapes to human intervention and global change. Landscape Ecol. 10, 143–159.

Botkin, D.B., Janak, J., Wallis, J., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Bugmann, H., Yan, X., Sykes, M.T., Martin, P., Lindner, M., Desanker, P.V., Cumming, S.G., 1996. A comparison of forest gap models: model structure and behaviour. Climatic Change, 34, 289–313.

Cammel, M.E., Knight, J.D., 1992. Effects of climatic change on the population dynamics of crop pests. Adv. Ecol. Res. 22, 117–162.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

Doyle, T.W., 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest

succession model. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, pp. 56–73.

Franz, F., Röhle, H., Meyer, F., 1993. 120jährige Beobachtung des Durchforstungsversuches Fabrikschlaichach 15: Wachstumsgang und Ertragsleistung der Buche. Allg. Forstzeitschr. 48, 262–267.

Kienast, F., 1991. Simulated effects of increasing atmospheric CO_2 and changing climate on the successional characteristics of Alpine forest ecosystems. Landscape Ecol. 5, 225–238.

King, G.A., Neilson, R.P., 1992. The transient response of vegetation to climate change: A potential source of CO_2 to the atmosphere. Water, Air Soil Pollut. 64, 365–383.

Kirschbaum, M.U.F., Fischlin, A., Cannell, M.G.R., Cruz, R.V.O., Cramer, W.P., 1996. Climate change impacts on forests. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. (Eds.), Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific–technical Analyses. Contribution of WG II to the Second Assessment Report of the IPCC. Cambridge University Press, Cambridge, pp. 95–129.

Korol, R.L., Running, S.W., Milner, K.S., 1995. Incorporating intertree competition into an ecosystem model. Can. J. For. Res. 25, 413–424.

Kramer, H., 1988. Waldwachstumslehre. Paul Parey, Hamburg/Berlin, 374 pp.

Lasch, P., Lindner, M., 1995a. Application of two forest succession models at sites in Northeast Germany. J. Biogeogr. 22, 485–492.

Lasch, P., Lindner, M., 1995b. Wirkung von Klimaveränderungen auf Waldökosysteme. Abschlußbericht zum BMBF-Forschungsvorhaben DLR 01 LK 9109. Potsdam Institute for Climate Impact Research, PIK-Report, 12, 73 pp.

Leemans, R., Prentice, I.C., 1987. Description and simulation of tree-layer composition and size distribution in a primeval *Picea–Pinus* forest. Vegetatio 69, 147–156.

Leemans, R., Prentice, I.C., 1989. FORSKA, A General Forest Succession Model. Department of Plant Ecology, Uppsala University, Uppsala, Sweden. Meddelanden från Växtbiologiska Institutionen, Uppsala, 1989 (2).

Nikinmaa, E., 1992. Analyses of the growth of Scots Pine; matching structure with function. Acta For. Fenn. 235, 1–68.

Oliver, C.D., Larson, B.C., 1990. Forest Stand Dynamics. McGraw-Hill, New York, 460 pp.

Overpeck, J.T., Rind, D., Goldbeck, R., 1990. Climate induced changes in forest disturbance and vegetation. Nature 343, 51–53.

Pastor, J., Post, W.M., 1988. Response of northern forests to CO_2-induced climate change. Nature 334, 55–58.

Prentice, I.C., Leemans, R., 1990. Pattern and process and the dynamics of forest structure: a simulation approach. J. Ecol. 78, 340–355.

Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol. Modelling 65, 51–70.

Pretzsch, H., 1992. Konzeption und Konstruktion von Wuchsmodellen für Rein- und Mischbestände. Forstl. Forschungsber. München 115, 332 pp.

Pretzsch, H., Röhle, H., Foerster, W., 1994. Buchen-Durchforstungsversuch Fabrikschleichach 015. Exkursionsführer, Lehrstuhl für Waldwachstumskunde der LMU München, Freising.

Shugart, H.H., 1984. A Theory of Forest Dynamics. Springer, New York, 278 pp.

Shugart, H.H., Smith, T.M., 1996. A review of forest patch models and their application to global change research. Climatic Change 34, 131–153.

Sievänen, R., 1993. A process-based model for the dimensional growth of even-aged stands. Scand. J. For. Res. 8, 28–48.

Solomon, A.M., 1986. Transient response to CO_2-induced climate change: simulation modeling experiments in eastern North America. Oecologia 68, 567–579.

Spiecker, H., Mielikäinen, K., Köhl, M., Untheim, H., 1994. Growth trends of European forests—has site productivity changed? Working Paper No. 4, European Forest Institute, Joensuu, Finland, 68 pp.

Urban, D.L., Harmon, M.E., Halpern, C.B., 1993. Potential response of pacific northwestern forests to climate change, effects of stand age and initial composition. Climatic Change 23, 247–266.

Volney, W.J.A., 1996. Climate change and management of insect defoliators in boreal forest ecosystems. In: Apps, M., Price, D.T. (Eds.), Forest Ecosystems, Forest Management and the Global Carbon Cycle. Springer, Berlin, pp. 79–87.

Weishampel, J.F., Urban, D.L., Shugart, H.H., Smith, J.B., 1992. Semivariograms from a forest transect gap model compared with remotely sensed data. J. Veg. Sci. 3, 521–526.