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Simulation of tree and stand development under different environmental conditions with a physiologically based model

R. Grote^{a,*}, M. Erhard^b

^a*Institute for Forest Growth Research, University of Munich, Am Hochanger 13, D-85354 Freising, Germany*

^b*Potsdam Institute for Climate Impact Research, P.O. Box 60 12 03, D-14412 Potsdam, Germany*

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Abstract

A simulation approach is used to describe annual tree growth and tree mortality from the output of a physiologically based model (FORSAANA). Height and diameter growth are calculated directly from the amount of carbon allocated to sapwood by considering an optimum height/diameter ratio, which depends on stand density. Tree mortality is defined by means of a relation between net primary production and carbon loss due to compartment senescence. Thus, all responses to environmental conditions considered in the physiological part of the model are implicitly considered in the stand development description. The dynamic simulation of stand properties, on the other hand, is required to apply the physiological based process description to long-term assessments.

The model is used to describe height and diameter development of three Scots pine (*Pinus sylvestris* L.) stands in eastern Germany which are exposed to different levels of nitrogen deposition and SO₂ air pollution. Results are compared with tree ring analysis covering a period of 27 years. For further evaluation, the model is initialised with forest inventory data of 288 pine stands and is run over 23 years using daily weather and deposition data as well as fertilisation information as input. The results are compared to data from a second inventory of the same stands. This comparison is conducted separately for regions exposed to high and low deposition.

The model represents annual height and diameter development at two of the three selected sites. With respect to the third site, considerable disturbances in the early years of stand development are assumed to be responsible for the unusual growth trend. The regional evaluation of the model yields correlation coefficients with forest inventory data between 0.57 and 0.86, with a generally better fit on diameter and stemwood volume than height. The approach demonstrates the uncertainty of estimations which are based on investigations at only few sites, and is discussed as a possible method for regional assessment of forest development under environmental change. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Environmental change; Nitrogen; Air pollution; Tree growth; Mortality; Modelling

1. Introduction

The uncertainty in future climate conditions and atmospheric deposition increases the demand for appropriate tools that are able to evaluate the effect

*Corresponding author. Tel.: +49-8161-71-4711; fax: +49-8161-71-4721; e-mail: Ruediger.grote@lrz.uni-muenchen.de

of projected changes on forest development (Fosberg, 1990; Kräuchi, 1993). The question how forests will respond to long-term impacts of changed environmental conditions is currently addressed with a number of different approaches, including statistical procedures (Pan and Raynal, 1995), canonical models (Voit and Sands, 1996), gap models (e.g. Bowes and Sedjo, 1993; Lindner et al., 1997), distance dependent whole-tree models (Kahn, 1995), or physiologically based models (e.g. Hunt et al., 1991; Sheriff et al., 1996). In all of these approaches, except the physiologically-based model, growth responses are directly calculated from environmental variables rather than from their impacts on the various physiological processes. Thus, they can hardly account for feedback reactions, which may develop dynamically within the system in response to new combinations of influences.

Physiologically based models are able to consider interrelations between plant processes in a multitude of possible impacts (Chen et al., 1994; Constable et al., 1996; Sadanandan Nambiar, 1995; Thornley and Cannell, 1996). However, since their focus is on short-term behaviour, they generally neglect feedback between the tree and the stand level (Cropper and Gholz, 1993; Friend et al., 1997; Oja and Arp, 1997; Sheriff et al., 1996). This has been considered a major source of errors in long-term assessments (Bassow et al., 1990) and, since measurements of physiological processes over decades are not carried out, the long-term evaluation of these models is not possible. Thus, procedures, which describe stand development mechanistically in relation to the underlying physiological processes are needed.

In order to produce output that can be used by the forest practitioner, attempts have been made to modify empirical functions of height and diameter growth in terms of their dependence on physiological output variables (Chen et al., 1994; Mohren et al., 1993). This has been applied in more detail by Bossel (1994), who calculated dimensional changes of trees explicitly from the carbon increase of the sapwood compartment, and Korol et al. (1995), who additionally included a mechanistic description of tree mortality.

This paper describes the representation of annual stand processes (height and diameter growth, tree mortality) from cumulated daily physiological variables, as implemented in the new forest growth model FORSANA. The simulation of daily processes, includ-

ing the dependency on stand properties, is described elsewhere (Grote, 1998; Grote and Suckow, 1998).

To evaluate the stand growth model, simulations of diameter increase, based on detailed information about soil, weather, and deposition conditions at three Scots pine (*Pinus sylvestris* L.) stands in eastern Germany are compared with tree ring analyses, extending 27 years back in time. For further evaluation of the representation of stand developments, the model was initialised with forest inventory data of several hundred pine stands within the same region, and forest development was simulated in daily timesteps during a period of 23 years. The results are separately compared for regions exposed to high and low deposition with data from a second inventory of the same stands.

2. Study sites and methods

2.1. Study region

The investigation area for the evaluation of the model – the Dübener Heide – is located in eastern Germany, south of Berlin and north-east to the main industrial centre of the former German Democratic Republic. It includes about 450 km² of forests, with more than 70% being even-aged stands of pure Scots pine growing on sandy, anhydromorphic soils with less than 5% clay. The climate is characterised by relatively dry conditions (550 mm precipitation per year) and annual mean temperatures of 8.0–8.5°C. Until the year 1989 the area was highly impacted by industrial emissions from power plants and chemical industries. Industrial production was based on burning lignite without using pollution reduction technologies. Thus, annual average atmospheric SO₂ concentrations reached about 150 µg m⁻³ in the western part and about 75 µg m⁻³ in the eastern part of the area. Bulk deposition of nitrogen was about 1.5–2.5 g m⁻² a⁻¹. To compensate for forest damage, nitrogen fertiliser was applied, mainly in the western part of the area, during the seventies and eighties.

For the regional evaluation of the model, site data were entered into a geographic information system (GIS – ARC/INFO). Forest inventory, soil, and topographic maps were digitised. Attribute data sets and additional information such as soil profile data and soil chemical analyses were joined by importing the digital

data into the relational data management system of the GIS.

To provide the forest growth model with a unique set of site condition parameters for each stand, so-called spatial homogenous units (SHUs) based on even-aged forest patches were calculated using the overlay and interpolation functions of the GIS. Time series of SO₂ concentrations for every forest stand are based on the results of a Gaussian model approach calculating daily SO₂ deposition for the year 1989 using a 500 m × 500 m grid size. Inter-annual variability was estimated using the annual trend of SO₂ emissions considering point and non-point sources in the area and about 100 km around (Schaller, pers. commun., 1996).

A random subsample of 288 pine forest stands older than 40 years was selected, representing different combinations of SO₂ levels and nitrogen loads. The data set contains forest inventory data (age, height, diameter, stemwood volume) as well as a soil description for the particular site (porosity, field capacity, pH

value, C and N contents for each soil horizon) for the years 1970 and 1992, respectively (Table 1).

2.2. Study sites

Three Scots pine stands are used for the evaluation of the annual change in stand dimensions. These are 'Rösa' in the western part of the area, 'Taura' in the eastern part, and the reference site 'Neuglobsow,' about 100 km north of Berlin. All stands are similar in height (except Rösa) and diameter (Wenk, in Anonymus, 1997), but they represent a gradient of air pollution and deposition. Different amounts of additional nitrogen was applied through fertilisation between 1970 and 1985. Soil water capacities are also considerably different at each site. Rooting depth is about 60 cm and the ground water level is below the rooting zone. Stand density is highest and ground vegetation (dominated by *Avenella flexuosa* in Neuglobsow and Taura, and *Calamagrostis epigeios* in Rösa) has the smallest biomass at the least polluted

Table 1

Site and stand statistics of stands used for regional model evaluation, grouped by highly (+N+S), medium (-N+S and +N-S), and moderately (-N-S) influenced sites

Variable	1970		1992		Number of stands
	Mean	Standard deviation	Mean	Standard deviation	
<i>Tree age (years)</i>					
+N+S	53.3	10.8	75.3	10.8	87
+N-S	53.1	10.0	75.1	10.0	90
-N+S	51.0	6.9	73.0	6.9	9
-N-S	51.8	9.4	73.8	9.4	102
<i>Stem diameter (cm)</i>					
+N+S	16.7	3.2	24.4	2.9	87
+N-S	16.6	3.2	24.5	2.8	90
-N+S	18.0	2.8	25.8	2.4	9
-N-S	16.9	3.8	24.8	3.3	102
<i>Tree height (m)</i>					
+N+S	13.1	1.9	17.0	1.5	87
+N-S	14.2	2.4	18.3	2.2	90
-N+S	14.3	1.9	18.9	2.3	9
-N-S	14.5	2.2	19.1	1.9	102
<i>Stemwood volume (m³ ha⁻¹)</i>					
+N+S	110.6	30.0	153.7	30.7	87
+N-S	138.5	36.9	194.4	38.2	90
-N+S	131.3	19.5	195.3	39.3	9
-N-S	141.4	33.5	211.1	34.8	102

-N: fertilised more than twice during the investigation period; +S: average annual SO₂ concentration of 1993 above 75 ppb.

Table 2
Site and stand data of the three intensively investigated stands

	Neuglobsow	Taura	Rösa
Age (1993)	60	41	64
Average height (m)	20.1	18.0	16.0
Average diameter at 1.3 m (cm)	21.0	20.6	20.7
Stemwood volume (m ³)	339	242	208
Stem number (ha ⁻¹)	1043	852	788
Soil water capacity (%)	125	215	170
Nitrogen content of current needles (%)	1.43	1.80	2.10
Estimated fertilisation from 1970–1985 (kg N ha ⁻¹)	200	100	900
Annual average SO ₂ air concentration 1989 (μmol m ⁻³)	50	86	130
Annual average SO ₂ air concentration 1994 (μmol m ⁻³)	12	34	57

site, Neuglobsow. More detailed data concerning the sites and their history are presented in Table 2 and are documented in Hüttl et al. (1995).

Tree ring analyses for model evaluation were performed in 1995 on stem discs of five harvested trees from each stand, with each of the five trees belonging to a different diameter class (10–15, 15–20, 20–25, 25–30, >30 cm). The results were weighted by the stem number within each class at each site. Daily weather records from 1967 through 1993 were obtained from the weather stations Neuglobsow (for Neuglobsow) and Wittenberg (for Rösa and Taura) of the German weather service. Deposition was estimated by the methods described above.

Initial stand data for the long-term simulation of the three intensively investigated sites were not available. Thus, they were estimated from stand age with empirically developed functions of height, diameter and stand volume, based on the forest inventory data of a representative forest district. The soil data were initialised as measured in 1994, but total nitrogen content was reduced by the amount of total fertilisation at the specific site. Additional gains from nitrogen deposition or losses, for example, due to percolation were not considered.

No information about thinning in the simulated stands were available except general management rules for foresters. Thus, a thinning procedure is implemented in the stand growth model which mimics the conventional forest practice by decreasing tree number at intervals which depend on the height

growth of the stand. The intensity of a thinning is set to decrease with stand age. Fertilisation, which generally had been applied as urea (CO(NH₂)₂), is considered by the model as additional deposition of 100 kg N in the form of ammonium, equally distributed throughout the year of application.

2.3. Model description

In the modelling approach it is assumed that the stand is horizontally homogeneous and that stand processes can be described by means of the average stem. The model does not account for differences in tree individuals and is thus only suitable for uniform forest plantations. Since not all trees are of the same size even in a plantation, the stem number calculated by the model from stand volume is only virtual and does not intend to represent the actual number of trees.

Since the physiological part of the model is explained in two separate papers (Grote, 1998; Grote and Suckow, 1998), this part of the model is only roughly explained. Nevertheless, some basic or new features of the model are given in the Appendix A to make the rationale easier to understand. The stand development is described in more detail, including the presentation of the parameters used in the equation (Table 3).

Table 3
Stand model parameters

Name	Meaning	Value	Unit
ΔH_{cri}^a	Height growth interval after first thinning application	1.8	m
D13 _{max}	Max diameter	0.4	m
DENS	Wood density	0.45	kg dm ⁻³
FBRA _{min}	Final branch fraction on sapwood	0.14	–
FCRT	Coarse root fraction on sapwood	0.2	–
FPSN ^a	Thinning intensity parameter	0.07	–
FTHIN ^a	Biomass relation of average harvested tree to average tree	0.07	–
H_{min}^a	Height at which first thinning is applied	13	m
KB	Exponential parameter	10	–
QCDD	Crown/diameter ratio	13.3	–
QHD _{max}	Max height diameter ratio	130	–
QHD _{min}	Min height diameter ratio	40	–
SLO_V	Slope of tree mortality function	0.3	–

^a Regional evaluation, in year-to-year evaluation adjusted according to the specific stand.

2.4. Physiological components

The physiological model separately describes the canopy light climate according to the Beer-Lambert law for diffuse and direct radiation in a number of canopy layers (Spitters et al., 1986). The estimation of net primary production is taken from the FORGRO model (Mohren, 1987; Mohren et al., 1993), which calculates gross photosynthesis from an exponential dependency on light (Spitters, 1986) and maintenance respiration from temperature and mineral content of each organ. Maximum photosynthesis is limited by the nitrogen content of the foliage (Aber et al., 1996) as well as CO₂ and SO₂ concentrations (Mohren et al., 1992). Temperature affects the CO₂-compensation point and water stress development in dependence on potential evaporation (Monteith, 1965) relative to maximum transpiration. The latter is calculated explicitly from soil water content, considering root biomass and distribution, ground vegetation competition, and sapwood water storage (Grote and Suckow, 1998). Carbon and nitrogen allocation to foliage (which is further divided by foliage age classes), woody compartments (sapwood, heartwood, branches and coarse roots), regenerative tissue, fine roots, and reserve carbohydrates is determined on daily time steps using a source/sink-related approach. The sink strength of compartments is basically defined according to the principle of functional balance by their relationship to foliage biomass, but this relationship is allowed to vary according to water and nitrogen supply (Grote, 1998). New foliage growth is supplied from the reserve pool with dependence on temperature sum. Foliage mortality is calculated from the relationship between net carbon gain and maintenance respiration. Fine root mortality increases with decreasing soil water content. Two pathways are considered on nitrogen uptake. Soil nitrogen uptake depends on water uptake and the concentration of different nitrogen species in the soil solution. Canopy uptake is estimated from deposition data (Grote, 1998). Soil processes are described with a mechanistic submodel based on an agricultural model (Kartschall et al., 1990; Suckow, 1986).

2.5. Height and diameter growth

First, the annual stemwood increase per hectare (G_{STE}) is calculated from (virtual) tree number per

hectare (N) and the annual sum of sapwood growth of the stand (G_{SAP}), simulated by the physiological part of the model.

$$G_{STE} = \frac{G_{SAP}}{N} \times (1 - FBRA - FCRT) \quad (1)$$

It is assumed that the coarse root fraction (FCRT) does not change in time, whereas the branch fraction (FBRA) increases with stem diameter at breast height ($D13$) in relation to the parameterized maximum diameter ($D13_{max}$), minimum branch fraction ($FBRA_{min}$), and an exponential parameter (KB) (equation from Bossel, 1994).

$$FBRA = FBRA_{min} + (1 - FBRA_{min})e^{(-KB(D13, D13_{max}))} \quad (2)$$

In the next step, the new diameter at breast height and tree height (H) are calculated from the increase in stemwood biomass (G_{STE}). Therefore, the contributions of diameter and height increment ($dD0$ and dH) to stem increment are differentiated with respect to time (for equation theory see Bossel, 1994):

$$\begin{aligned} G_{STE} &= \frac{CMV \times d(D0^2 \times H)}{dt} \\ &= CMV \times D^2 \times \left(2 \times \frac{HP}{D0} \times d + D0 \times dH \right) \quad (3) \end{aligned}$$

with

$$CMV = DENS \times FORM \times \frac{\pi}{4} \quad (4)$$

With DENS being a parameter for wood density and FORM denoting the relation between a cylinder derived from $D0$ and H and the actual stem form. In contrast to Bossel, we assume the tree stem as a cone. In this case, the form parameter is always one-third and $D0$ refers to the base diameter instead of the diameter at breast height. From Eq. (3), the maximum diameter increase can be obtained, if height growth is assumed zero:

$$GD0_{max} = \frac{G_{STE}}{2 \times CMV \times H \times D0} \quad (5)$$

On the other hand, the maximum height growth can be derived by assuming no diameter growth:

$$GH_{max} = \frac{G_{STE}}{CMV \times D0^2} \quad (6)$$

Without a change in the relation between diameter and height, Eq. (3) yields the following description of diameter growth:

$$GD0 = \frac{G_{STE}}{3 \times CMV \times H \times D0} \quad (7)$$

However, if the deviation between height and diameter growth should be described in dependence on environmental conditions, Eq. (7) can be transformed to include a variable height/diameter relationship (QHD_{var}).

$$GD0 = \min \left(GD0_{max} \times \frac{G_{STE}}{3 \times CMV \times QHD_{var} \times D0^2} \right) \quad (8)$$

QHD_{var} shifts between parameterized borders (QHD_{min} and QHD_{max}) in dependence on stand density, which is described by the crown area index (CAI). CAI stands for the fraction of crown-covered area in relation to total stand area and is derived from the stem number, average diameter and the parameterized ratio between breast height diameter and crown diameter (QCDD).

$$QHD_{var} = \min(QHD_{max}, QHD_{min} + (QHD_{max} - QHD_{min})CAI) \quad (9)$$

$$CAI = (D13 \times QCDD)^2 \times \frac{\pi}{4} \times \frac{N}{10000} \quad (10)$$

Due to the assumptions made about the stem form, the new height and the diameter at breast height can be simply calculated from the diameter increment and the old dimensions.

$$H = H + GH_{max} \left(1 - \frac{G \times D0}{G \times D0_{max}} \right) \quad (11)$$

$$VIT = \frac{\sum POOL}{\sum (M_{NDL} + M_{FRT} + M_{SAP} + M_{CRT} + M_{BRA} + M_{REN} + G_{EXS})} \quad (13)$$

$$D13 = (G \times D0 + D0) \times \frac{(H - 1.3)}{H} \quad (12)$$

The representation of tree stems as cone-shaped is somewhat unconventional in forest biometry. The model has the advantage that a continuous change in height and diameter development can be repre-

sented in dependence to changing environmental conditions. However, it is assumed that the relationship between base diameter and stem volume is constant (1/3), what is actually not the case. In yield tables, a set of empirically found form factors is used to describe tree volume in dependence on diameter at breast height. Compared to estimations based on these numbers the model yields almost 20% less stand volume if the height, diameter and stem number of the investigated stands are used. However, since the actual form factors of the sampled trees have been found to be considerably smaller than those in the yield tables (Wenk, unpublished data), the estimated volume seems to be only about 10% smaller than the actual one – the same magnitude of error as produced by the yield table method. This error is not constant but depends on the actual tree form and decreases with decreasing height/diameter relationship as well as increasing diameter. Since stand volume and not tree number is used as an initial value, virtual tree number is somewhat increased by this error and thus there is only a small effect on stand volume increase. Nevertheless, in young stands with small diameter and relatively large height, the error leads to a considerable different tree mortality. This is why no stands younger than 40 years are used in this study.

2.6. Tree mortality and harvesting

A vitality index (VIT) is introduced to characterise tree health. It is calculated by dividing net primary production (POOL) by total annual compartment mortality (M, foliage = NDL, fine roots = FRT, coarse roots = CRT, branches = BRA, regenerative tissue = REN) including core wood formation (M_{SAP}) and exudation losses (G_{EXS}).

By means of VIT and the slope parameter SLO_V , the probability for natural tree mortality (FTOT) is calculated.

$$\begin{aligned} FTOT &= 1 - VIT^{SLO_V}, & \text{if } VIT < 1 \\ FTOT &= 0, & \text{if } VIT \geq 1 \end{aligned} \quad (14)$$

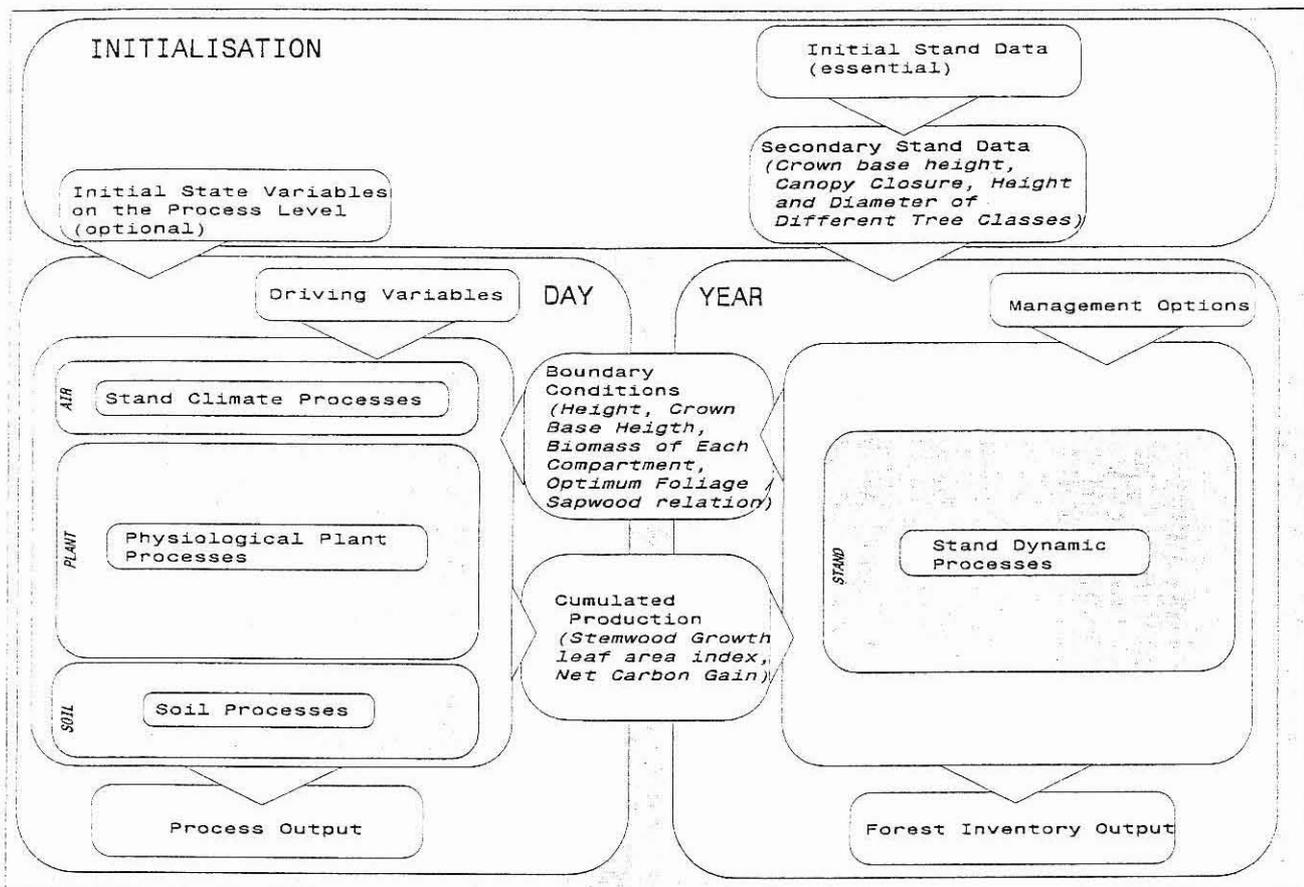


Fig. 1. Interrelations between daily and annual modules in FORSANA.

If the net primary production of the stand is smaller than the overall amount of carbon losses, the tree number as well as every single biomass compartment and all nitrogen pools are reduced to the same amount. Thus, it is assured that no further change of average tree dimensions takes place. As demonstrated in Figs. 1 and 2, small values of SLO_V provide for only small changes in annual stem mortality until the VIT decreases to very small values. Such conditions, indicating a very severe stress, however, will lead to a substantial stem reduction.

If thinning is applied, it has to be considered that trees are generally not selected randomly by the forester, but that the average size of removed trees can be smaller or bigger than the average size of all trees in the stand. In the model, the kind of thinning can be determined by the parameter FTHIN, which indicates the size of the removed trees in relation to the average tree in the stand. This parameter is used only

for the calculation of the relative tree number reduction (FHAR), but not for the reduction of tree compartment biomass (wood, foliage, roots, reserve pool) (FTOT).

$$\text{FHAR} = 1 - e^{(-\text{FPSN} \cdot \text{FTHIN} \cdot \Delta H)} \quad (15)$$

$$\text{FTOT} = 1 - e^{(-\text{FPSN} \cdot \Delta H)} \quad (16)$$

The following recalculation of height and diameter from the new stemwood and tree number values (assuming no change in height/diameter ratio) gives the average stand dimensions after thinning. Thinning occurs whenever a defined height (H_{\min}) has been reached (first disturbance) or if the height growth interval (ΔH) exceeds a certain height growth interval (H_{cri}). The intensity of the thinning is characterised by the parameter FPSN, which can be set by the model user separately for each harvesting event.

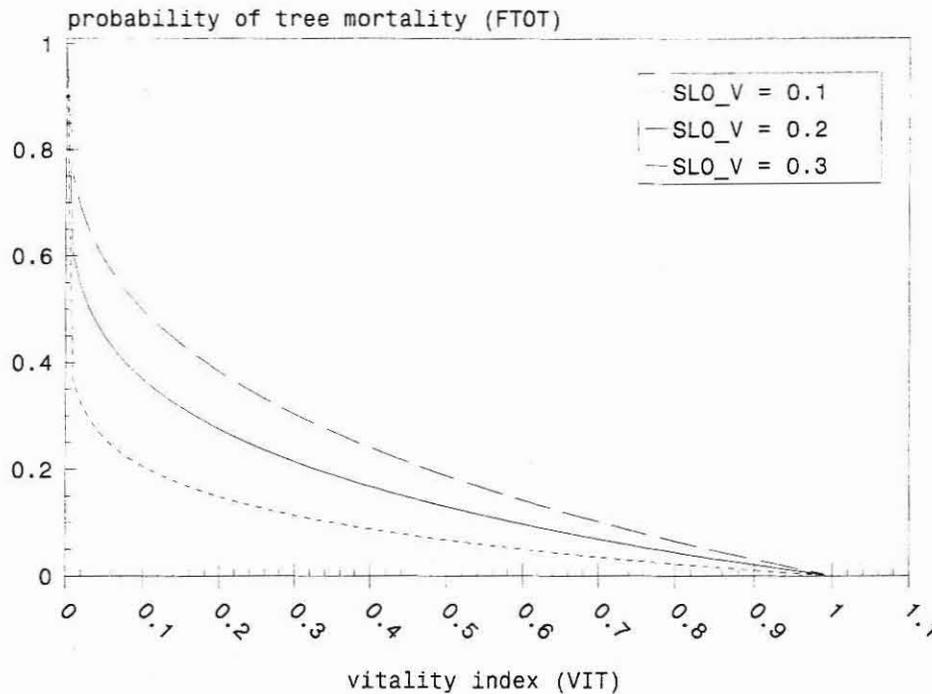


Fig. 2. Probability of tree mortality in dependence on VIT (relationship between net carbon gain and carbon losses) and the slope parameter (SLO_V).

3. Results

3.1. Simulation of annual stand growth

In Fig. 3(a–c), simulated diameter growth of the three stands is shown together with weighted averages obtained from the five harvested trees in each stand. The year-to-year development is generally very similar between the simulations of the average diameter growth and the weighted average of measured tree ring width. The absolute increase in tree ring growth decreases with increasing diameter and shows a considerable growth decline in drought years, for example, 1975–1976, 1989 (which is more expressed in the simulation than in the measurements). A significant growth increase after nitrogen fertilisation is observed only at Neuglobsow, the stand with the lowest nitrogen supply.

In the first decade, either larger (Neuglobsow, 1967–1970) or smaller (Rösa, 1967–1976) growth is simulated than is actually observed. In Taura, deviations from measurements are considerable during the whole period, with a change from underestimation to overestimation in the early 1980s. The general trend of

decreasing diameter growth with increasing age is most evident at Rösa, and is correlated with increasing air pollution at this site. With decreasing air pollution in the early 1990s, a recovery is indicated, although dry years in 1989, 1991, and 1993 are counteracting this development.

The simulated development of stemwood volume, height and average diameter from estimated initial stand conditions (Fig. 4(a–c)), are very close to actual measured stand conditions at Rösa and Neuglobsow (compare with Table 2). At Taura, the simulated stand values, which are initialised with considerably smaller heights and diameters because this stand is somewhat younger than the other ones, did not reach the actual observed stand dimensions.

In response to thinning, the average stem dimensions increase, because it is assumed that the average harvested tree is smaller than the average tree of the total stand. Thus, recalculation of stand dimensions after thinning yield a larger average tree. This effect is considerably greater in Taura than in Rösa and Neuglobsow because Taura is younger and the thinning intensity was assumed to decrease with stand age. Thinning occurs more frequently at Neuglobsow than

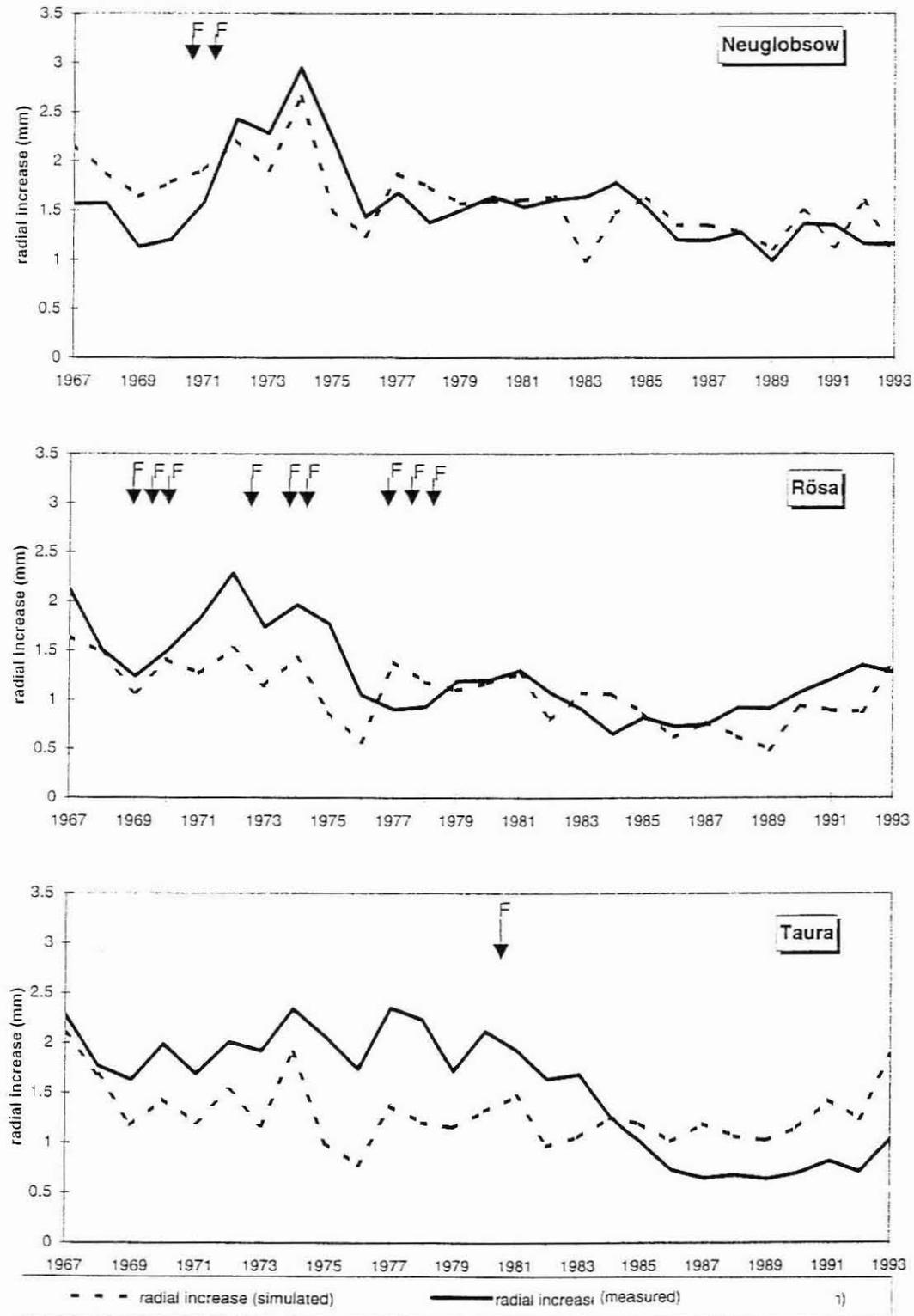


Fig. 3. (a–c) Simulated average tree ring width and estimated diameter growth from a sample of harvested trees at the three investigated stands from 1967–1993. Years in which fertilisation ($100 \text{ kg N ha}^{-1} \text{ a}^{-1}$) occurred are denoted with a capital F.

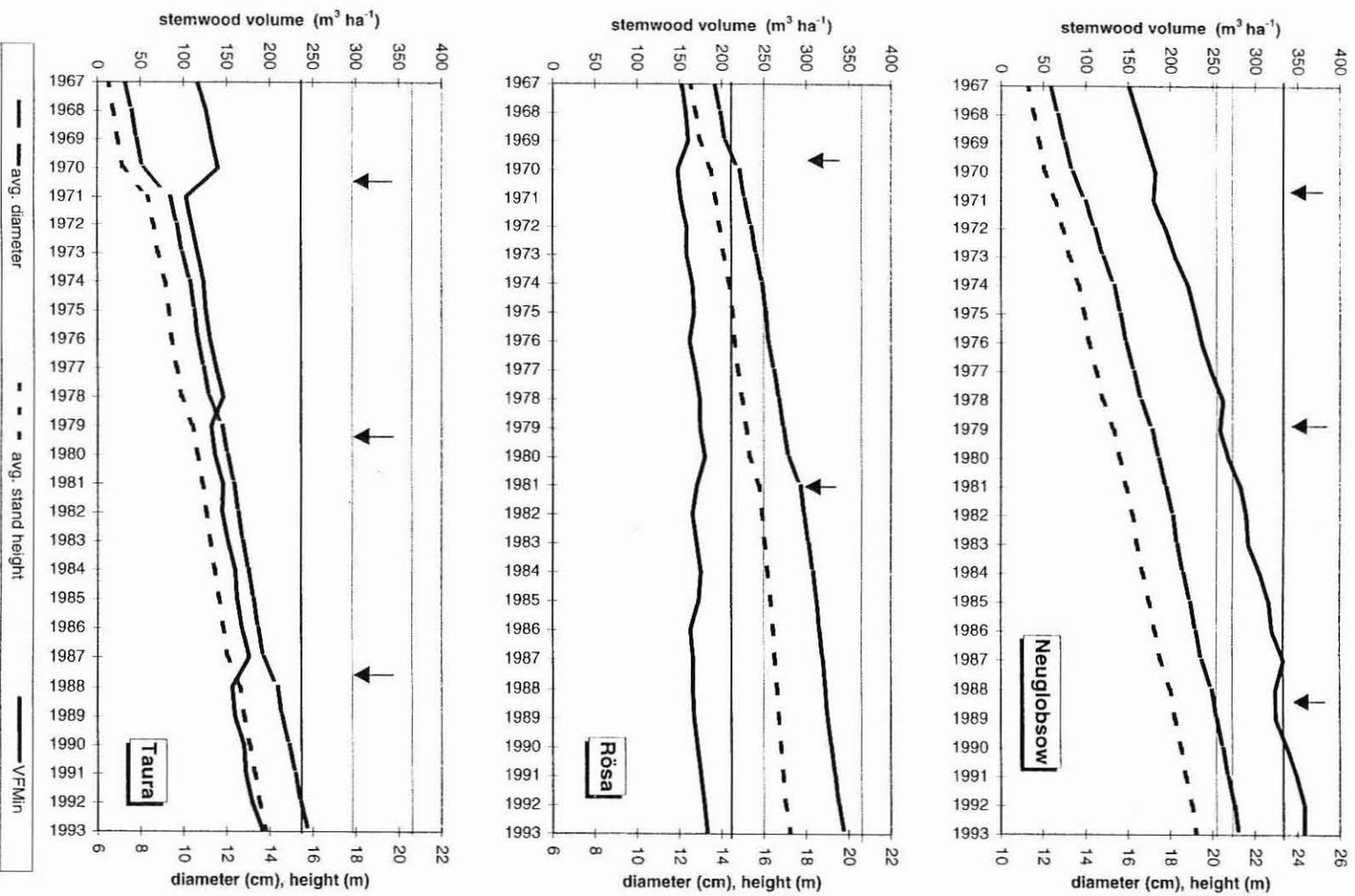


Fig. 4. (a–c) Simulated development of stemwood volume per ha (VF_{min}), height, and average diameter at the three investigated stands from 1967–1993. Years in which thinning occurred are indicated by an arrow. Straight lines indicate the measured values in 1993.

at Rösa, because higher natural tree mortality at Rösa leads to a reduced stand density (indicated by smaller stemwood volume). This prefers diameter growth over height growth and consequently leads to fewer thinning events, which are coupled to height growth.

3.2. Regional simulations

The comparison of simulated stand properties with forest inventory data shows that all four investigated groups of forests (+N+S, +N–S, –N+S, –N–S) could be more or less represented by the model (Fig. 5(a–c) and Table 4). Height, diameter growth, and stemwood volume are slightly underestimated, indicating that the actual competition is slightly smaller than assumed in the simulation. This could possibly

be due to a too small tree mortality in the model which may result partly from the simplified tree growth assumptions (see also stand model description). The development of diameter and stemwood volume are better represented as is height growth. In fertilised stands which are exposed to only low levels of SO₂, simulated values are very close to measurements, whereas they are somewhat smaller than the inventory data in stands exposed to high SO₂ levels. However, stands with simulated tree heights between 17 and 20 m are distinctly closer to the measured values as are stands with smaller tree heights. This could possibly indicate that the bias in simulation results vanishes in taller stands (Fig. 5(b)) and that only one empirical relation, like that implemented in the model, may not be sufficient to represent the damaging effect for every

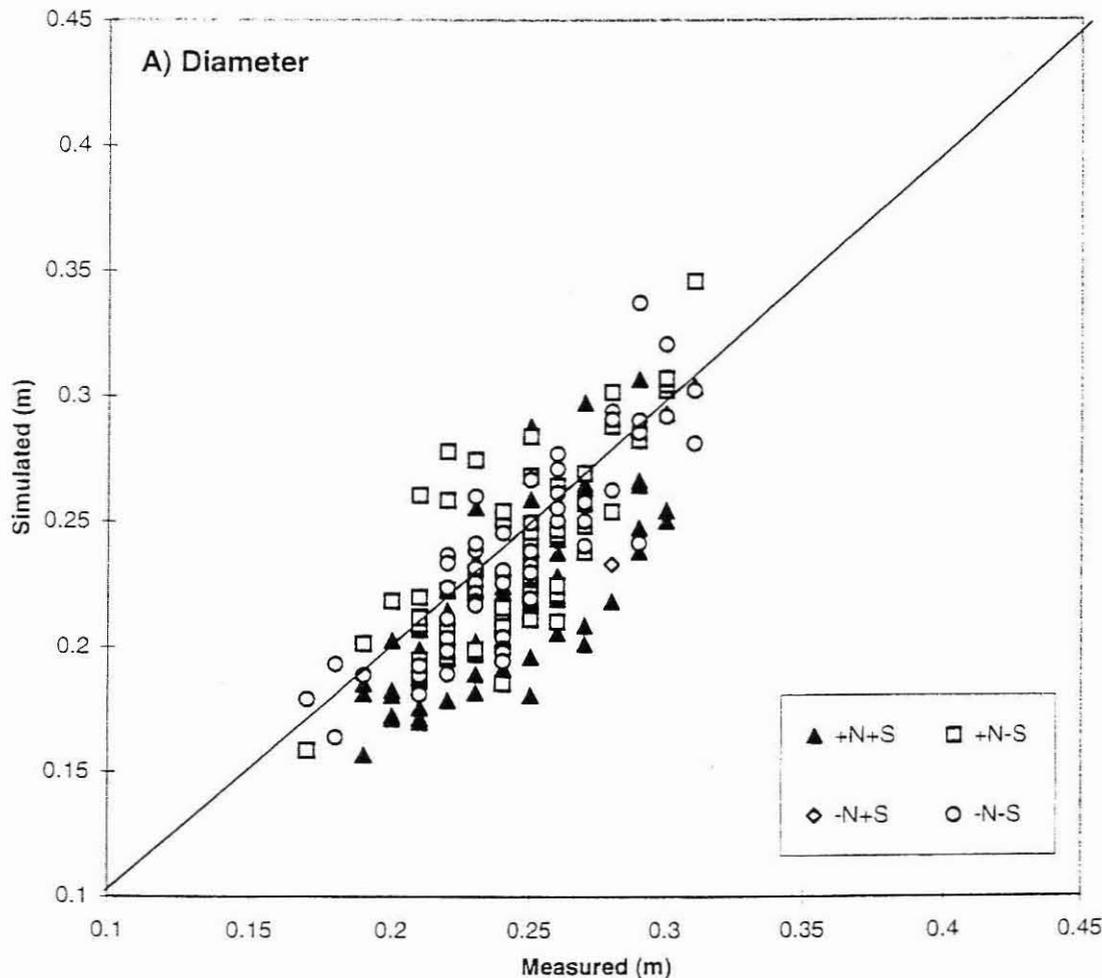


Fig. 5. (a–c) Comparison of simulated and measured average stand diameter, stand height, and stemwood volume per ha in stands exposed to different anthropogenic influences (+N+S, –N–S, –N–S, see text for more information).

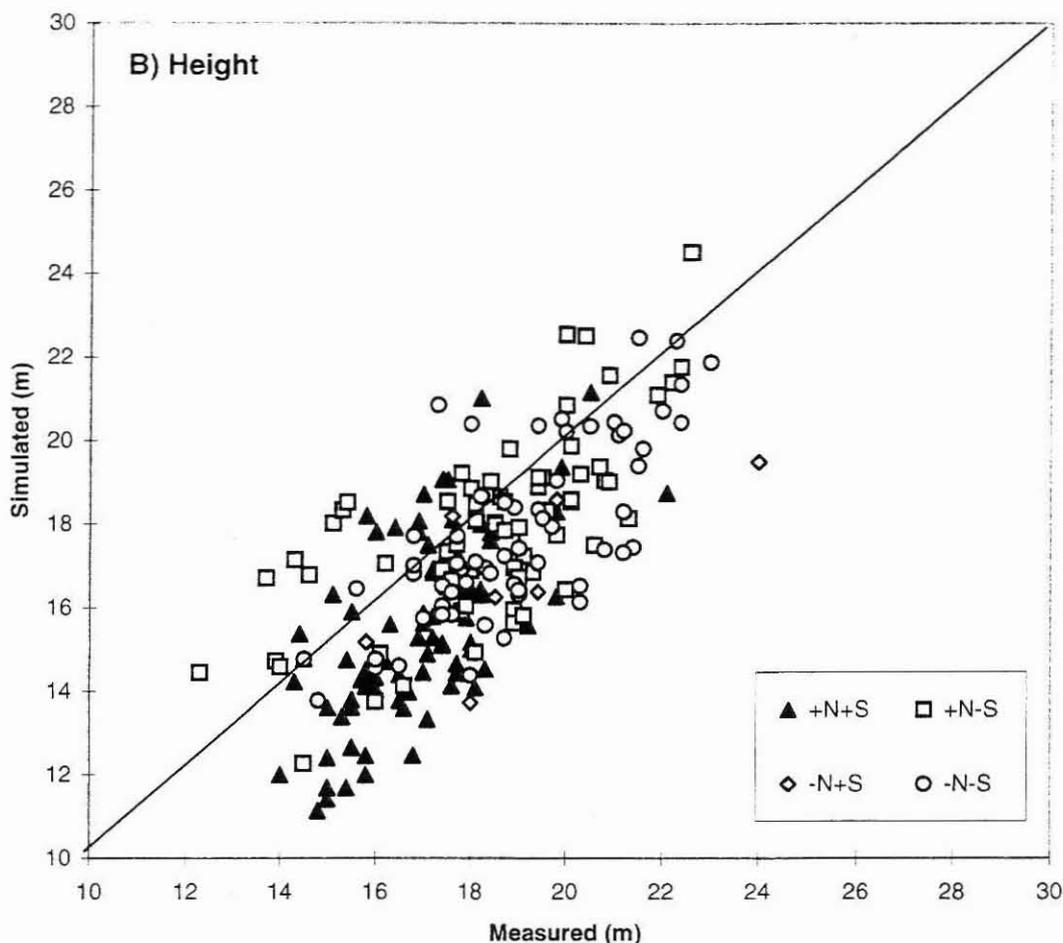


Fig. 5 (Continued).

tree age. However, too few stands taller than 20 m are available to decide if there is actually a trend in the simulation results.

In both simulations and measurements, height and stemwood volume in the highly impacted group of

stands (+N+S) is smaller than in the 'background' group (-N-S). Height growth in this group is significantly different even to each other group (Table 5). On the other hand, no differences in diameter growth are apparent. In the group of stands which is only

Table 4

Correlation coefficients and mean differences between simulated and measured stand dimensions

	+N+S	+N-S	-N-S	-N+S	Total
<i>Mean differences</i>					
Diameter (cm)	2.9	0.7	2.5	0.8	1.6
Height (m)	1.4	0.4	2.1	1.2	0.9
Stemwood volume (m ³ ha ⁻¹)	10	2	29	14	4
<i>Correlation coefficients</i>					
Diameter	0.80	0.74	0.79	0.86	0.79
Height	0.64	0.68	0.67	0.74	0.72
Stemwood volume	0.76	0.75	0.70	0.57	0.78

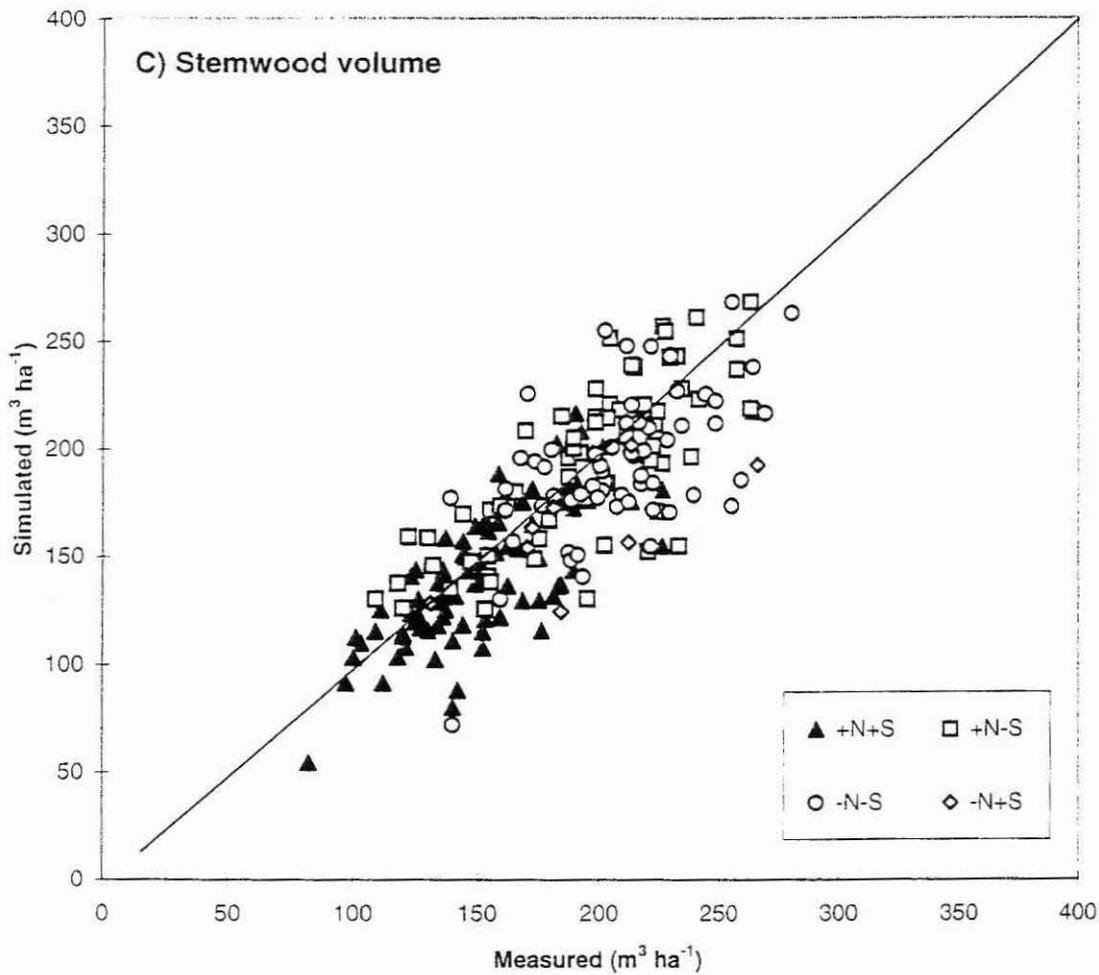


Fig. 5 (Continued).

Table 5

F-values and levels of significance between highly (+N+S), medium (-N+S and +N-S), and moderately (-N-S) influenced sites (+N, fertilised more than twice during the investigation period. +S, average annual SO₂ concentration of 1993 above 75 ppb)

	1970			1992		
	+N-S	-N+S	-N-S	+N-S	-N+S	-N-S
<i>Tree age</i>						
+N+S	1.18	2.49	1.32	1.18	2.49	1.32
+N-S	-	2.11	1.12	-	2.11	1.12
-N+S	-	-	1.88	-	-	1.88
<i>Diameter</i>						
+N+S	1.02	1.30	1.40	1.09	1.50	1.28
+N-S	-	1.32	1.38	-	1.38	1.39
-N+S	-	-	1.82	-	-	1.91
<i>Height</i>						
-N+S	1.52 ***	1.04 *	1.36 ***	2.26 ***	2.35 **	1.63 ***
+N-S	-	1.59	1.12	-	1.04	1.38 **
-N+S	-	-	1.41	-	-	1.44
<i>Stemwood volume</i>						
-N-S	1.51 ***	2.37 **	1.25 ***	1.54 ***	1.64 **	1.28 ***
+N-S	-	3.58	1.21	-	1.06	1.20 **
-N+S	-	-	2.96	-	-	1.27

$p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

fertilised (+N–S), the whole range of tree dimensions and stand volume occurs that was investigated, and the simulation could represent each kind of growth equally well. The non-fertilised group, which has been exposed to high SO₂ concentration (–N+S), cannot be judged in comparison to the other groups because its case number is too small (compare also with statistics in Table 1).

4. Discussion

In general, the simulations at the selected sites gave satisfactory results. Particularly, at Neuglobsow the 'background' site, simulations and measurements are in good agreement over the whole time period. At Rösa, stand development could be represented by the simulation, although the site had been exposed to multiple influences which varied substantially in time. The simulated growth in Taura, however, is too small compared to the actual growth and dimensions of the stand.

The simulation of year-to-year changes in growth could be represented in a very realistic fashion, regardless of the dominating impact (N or S). Most of the growth dynamics in this respect could be explained by changes in water supply, which lead to a decreased growth, particularly when two dry years occurred sequentially (1975–1976). The simulated effect of decreasing SO₂ concentration on growth is apparent particularly at Rösa. This effect is known from laboratory experiments (e.g. Mooney et al., 1988; Tesche et al., 1989), but is also in general accordance with field observations (McLaughlin et al., 1982; Sterba and Eckmüllner, 1988; Shaw et al., 1993). Similarly, increased growth with additional nitrogen supply in nitrogen-limited systems, as is particularly true for Neuglobsow, is well-known (e.g. Mälkönen et al., 1990; Niefnecker, 1985). This is consistent with a decreasing benefit from additional nitrogen at the well-supplied sites like Rösa and Taura, which is also well-documented in literature (Bergmann and Flöhr, 1989).

One of the problems comparing simulated tree growth with measurements (Fig. 3(a–c)) is connected to the kind of measurements that are available. Tree ring width can be measured only on trees that have survived until 1995. Thus, only the most competitive

trees are represented, whereas the growth of trees which died due to natural reasons or which are harvested are not included. In the simulation, however, stand growth is calculated as the average of all trees that were actually present in the stand. This means that also the less vigorous trees are included in the simulation as long as they are assumed to live at all. Since the fraction of trees that die during one year is usually only 1–2 percent, the deviation between simulated and measured tree ring width on an annual basis is generally small. It can be considerable, however, if the mortality is increased due to particular stress events (in Rösa 6% mortality is simulated in the mid 1980s due to high air pollution), or if the continuous selection of less competitive trees leads to a shift in genetic growth potential or diameter distribution. Thus, under stress conditions (Rösa and Taura > Neuglobsow) and early in the simulation period, measured diameter increment is usually greater than the increment of the actual average tree.

Initial stand properties of Rösa, Taura and Neuglobsow are estimated only from stand age. This is a very coarse estimation and most of the deviation between measurement and simulation during the first (3–5) years may be attributed to errors in initialisation. It should be noted that the simulation results are particularly sensitive to initialisation errors in the height/diameter ratio, because this ratio determines the distribution of stemwood growth. Additionally, the particular weather and deposition conditions may sometimes deviate from the measurement records used in the simulation (which is probably more important for Rösa and Taura than for Neuglobsow).

Other sources of errors are disturbances, like diseases or storm damage that are not accounted for in the simulation. It is known that pest infestations have occurred several times at Neuglobsow, which may explain that the simulation sometimes indicates a higher growth than that actually observed.

That the simulation failed to represent stand development at Taura may be due either to some kind of disturbance or extraordinary stand dimensions at the beginning of the simulation, since the stand is now less dense than that at Neuglobsow, although it is 19 years younger. It is assumed that the stand has been subject to severe stem reduction in the past, which increased the availability of light and nutrients and thus growth of the remaining trees. This theory is supported by the

observation that the regional average dimension for stands of the same age is 13.6 m height and 15.4 cm in diameter, which is very close to the simulated results (Fig. 4(c)).

Considering the multitude of possible impacts that could not explicitly be taken into account, the result of the regional evaluation can also be considered satisfactorily. The growth reducing effect of air pollution, which is particularly effective on height growth, is simulated quite well. The higher sensitivity of height growth, compared to diameter increase, is apparently related to the altered density of the polluted stands and could be shown here for the first time in both measurements and simulation. Also, the growth increasing effect of nitrogen fertilisation, which is stronger for stand volume increase than for height or diameter growth, is met in the simulation. Thus, it can be assumed that a mechanistical representation of tree mortality is indeed necessary if all the different aspects of stand development should be estimated. It has to be admitted, however, that only the nitrogen effect at the less polluted sites can be discussed here, because the number of cases in the $-N+S$ group was too small to yield significant results.

In stands which are only moderately exposed to anthropogenic influences ($-N-S$), the difference in stemwood volume between the simulated and measured data is higher. The reason for this is still unclear. Possibly, it is due to the fact that disastrous influences (e.g. wind throw, diseases) have led to a replacement of many stands at polluted sites (which are thus not included in the data set anymore), while at less polluted sites the damage was less severe (but nevertheless lead to considerable deviations from the simulation). This effect, however, needs to be investigated further and requires more information about the site history at the simulated plots.

5. Conclusions

A stand growth model is mechanistically linked to a physiological model, which provides sensitivity to temperature, light, drought stress, CO_2 , air pollution, and nitrogen supply. The increase of the wood compartment as well as the relationship between total carbon gain and total carbon loss determine tree growth and mortality in the stand process model. Thus,

a feedback between individual tree physiology and stand level characteristics is established; this is required for long-term calculations where boundary conditions of the stands cannot be assumed to be constant.

Generally, a major advantage of coupling tree physiology and stand processes is the possibility of model evaluation on a broader scale in time and space. However, because of their large data requirements, physiologically based models have seldom been applied on a regional scale. When this has been done, either hypothetical boundary conditions were assumed which were not intended to represent actual conditions (Friend et al., 1997), or only very few sites were simulated along a gradient of conditions that were assumed to be representative of the whole region (Running, 1994). It has been demonstrated, however, that the evaluation of a very sophisticated model at a single site is cumbersome and may be by no means representative. Based on this conclusion, the present approach offers an alternative to (medium scale) regional assessments, because initialisation with forest inventory data and coarse soil information allows the simulation of a large number of stands. Furthermore, the stand development calculations, which are presented here, enable the model to be evaluated at the same scale.

The simplicity of the approach and the requirement of the underlying physiological model for more or less homogeneous canopy conditions, restricts the applicability of the current model to even aged, single species plantations. In young stands, additional problems arise from the assumption of a fixed stem form as well as from the fact that only stems above a certain diameter are counted as stemwood by general forest inventory practise. Very old or damaged stands, on the other hand, may be subjected to additional stress factors not accounted for in the model (e.g. storms and diseases).

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Appendix A

The water balance equation yields the soil water in a specific layer z from percolation, total uptake (from trees and ground vegetation), and ground evaporation.

$$\frac{\partial}{\partial t} (\text{WC}(z, t) - \text{FC}(z)) = \text{PERC}(z, t) - (\text{UPT}(z, t) + \text{EP}_s(z, t)) - \text{FCON}(z) \times (\text{WC}(z, t) - \text{FC}(z))^2 \quad (\text{A1})$$

WC, water content (mm); FC, field capacity (mm); PERC, percolated water (mm); UPT, total uptake (mm); EP_s, evaporation from the uppermost soil layer (mm); FCON, soil layer conductivity (texture-specific parameter).

The actual water uptake is limited by the canopy demand on transpiration and by the available water. The latter is defined as the sum of plant available soil water that can be transported into the canopy within one day and the net loss from the sapwood water.

$$\text{TRA}_{\max} = \sum \text{UPT}_{\text{pot}} \times \text{CREL} + \text{WCS} \times \text{FWCS} \quad (\text{A2})$$

TRA_{max}, maximum transpiration (mm); UPT_{pot}, potential water availability in one soil layer (mm); CREL, relative hydraulic conductivity of the stem; WCS, water content in the sapwood (mm); FWCS, relative amount of the sapwood water that is available for transpiration.

The potential water uptake of the trees is defined by the water supply. It is calculated separately for each soil layer and is limited by either the amount of water between wilting point and field capacity or the uptake capacity of fine roots in a specific layer.

$$\text{UPT}_{\text{pot}} = \sum \min \left(\frac{\text{UMAX}_{\text{FRT}}}{\text{HFC} \times (\text{WC} - \text{WP})} \times \frac{\text{UMAX}_{\text{FRT}}}{\text{UMAX}_{\text{FRT}} + \text{UMAX}_{\text{FRT-V}}} \right) \quad (\text{A3})$$

UMAX_{FRT}, maximum fine root uptake of trees (derived from fine root biomass and specific conduc-

tivity, mm); UMAX_{FRT-V}, maximum fine root uptake of the ground vegetation (mm); HFC, relative availability of soil water; WC, soil water content (mm); WP, wilting point (mm).

Growth in every compartment besides foliage is calculated according to the net carbon gain and the relative demand for carbohydrates of this particular compartment i . The demand is derived from a functional relation to foliage biomass.

$$G_i = \text{POOL} \times \frac{D_i}{\sum D_i} \quad (\text{A4})$$

$$D_i = \max \left(0, \frac{\text{WOPT}_i - W_i}{\text{WOPT}_i} \right) \quad (\text{A5})$$

G , growth (kgCH₂O day⁻¹); POOL, net carbon gain (kgCH₂O day⁻¹); D , relative demand for carbohydrates; W , biomass (kgDW); WOPT, optimum biomass (kgDW).

New foliage is grown from the reserve mass compartment by means of development function until a previously defined biomass growth is achieved. The total foliage growth is determined by a parameterised maximum leaf area index and stand density.

$$\text{DVS}_{\text{gro}} = 1 - e^{(-K_{\text{DVS}} \times (\text{TK} - \text{TK}_{\text{cri}}))}, \quad \text{if } \text{TK} > \text{TK}_{\text{cri}} \quad (\text{A6})$$

DVS_{gro}, development state of foliage growth; TK, temperature sum since the first of January (°C); TK_{cri}, critical temperature sum; K_{DVS}, curve parameter.

The relative fraction of foliage (and sapwood) mortality at each day is derived from the relationship between daily assimilation and respiration. Mortality increases with decreasing assimilation relative to respiration and is limited to a maximum of 5% of annual foliage mortality. The annual litterfall is predetermined as a fraction of the total foliage, which is empirically increased under the influence of SO₂.

$$\Delta \text{DVS}_{\text{mor}} = 0, \quad \text{if } \Sigma \Delta \text{DVS}_{\text{mor}} \geq 1$$

$$\text{or } \text{DVS}_{\text{mor}}(t) \leq \text{DVS}_{\text{mor}}(t-1)$$

$$\Delta \text{DVS}_{\text{mor}} = \min(0.05, K_{\text{mor}} \times (\text{DVS}_{\text{mor}}(t) - (\text{DVS}_{\text{mor}}(t-1))))), \quad \text{if } \text{DAY} < 364$$

$$\Delta DVS_{mor} = 1 - \Sigma \Delta DVS_{mor} \cdot \text{otherwise} \quad (A7)$$

$$DVS_{mor} = \frac{QRA - QRA_{min}}{1 - QRA_{min}} \quad \text{if } QRA_{min} < 1$$

$$DVS_{mor} = 0, \quad \text{if } QRA_{min} \geq 1 \quad (A8)$$

ΔDVS_{mor} , fraction of daily foliage mortality; DVS_{mor} , development state of foliage mortality; DAY, day of the year; K_{mor} , curve parameter; QRA, ratio between daily respiration and net assimilation; QRA_{min} , smallest QRA of the year.

The share of fine roots that die during a day develops between a parameterised maximum and minimum value according to the water-stress factor, which is calculated from the amount of water in a particular soil layer relative to the water content at field capacity.

$$FM_{FRT} = TO_{max} - (TO_{max} - TO_{min}) \times RW_{mor} \quad (A9)$$

FM_{FRT} , fraction of fine root mortality in each soil layer; TO_{max} , maximum daily turnover; TO_{min} , minimum daily turnover; RW_{mor} , water-stress factor.

Canopy nitrogen uptake is calculated from daily NO_x and NH_3 field deposition rates assuming that the deposition at forests is somewhat increased compared to the field and that a net uptake of nitrogen can only occur if foliage nitrogen concentration is below a certain threshold. Furthermore, canopy uptake is limited by a maximum uptake rate which is estimated from leaf area index and water stress.

$$UN_A = \min \left(\frac{UN_{spe} \times LAI \times RW_{sto}}{CNF_{opt} - CNF} \times (DEP_{NO_x} + DEP_{NH_3}) \times FDEP \right) \quad (A10)$$

UN_A , canopy uptake of nitrogen ($kg\ ha^{-1}$); UN_{spe} , daily maximum uptake of nitrogen ($kg\ m^{-2}$); LAI, leaf area index; RW_{sto} , water-stress factor, reducing stomatal conductivity; CNF, nitrogen concentration of foliage; CNF_{opt} , optimum value for CNF (calculated from parameterised maximum and critical values); CNF_{crit} , critical value for CNF; DEP_{NO_x} , daily deposition of NO_x ($kg\ ha^{-1}$); DEP_{NH_3} , daily deposition of NH_3 ($kg\ ha^{-1}$); FDEP, factor increasing field deposition (calculated from leaf area and stand density).

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Simulation of tree and stand development under different environmental conditions with a physiologically based model

R. Grote^{a,*}, M. Erhard^b

^a*Institute for Forest Growth Research, University of Munich, Am Hochanger 13, D-85354 Freising, Germany*

^b*Potsdam Institute for Climate Impact Research, P.O. Box 60 12 03, D-14412 Potsdam, Germany*

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