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A Model for Individual Tree Development Based on Physiological Processes

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Abstract: A tree growth model is presented which calculates the 3D development of trees and stands in dependence on their individual carbon, water and nitrogen balance. The availability of energy, soil water and nutrients is estimated from field data at the scale of crown and root system fractions, taking into account the individual neighbourhood. The model includes a simple estimation of radiation distribution and the simulation of carbon and nutrient exchange. Senescence is represented by compartment-specific turnover rates. Allocation of carbon and nitrogen into foliage, fine roots, branches, coarse roots, and the stem is calculated according to functional balance and pipe model principles. Dimensional changes are calculated annually according to the distribution of net assimilation. The model describes tree development as a response to individual environmental conditions and changes environmental conditions with individual tree development. Due to this feedback loop, environmental influences can be assessed in any kind of species mixture or stand structure. Furthermore, the physiological-based approach ensures that the model can be used for investigations of complex environmental changes, e.g. CO₂ concentration, precipitation, temperature and nitrogen deposition. Thus, it is particularly suitable to analyse field investigations and to support the cognition process on the ecology of forests. It could also be used, however, to estimate forest responses to given environmental scenarios.

Key words: Spatially explicit, tree growth model, mixed stands, stand structure, water consumption, competition.

Introduction

Within the framework of the integrated research programme "Growth and Parasite Defence", a forest trial plot has been established in southern Germany, where scientists of different disciplines investigate the growth efficiency and competition strength of mature beech (*Fagus sylvatica*) and spruce (*Picea abies*) in a mixed stand. The investigation is taking place over several years under natural as well as manipulated environmental conditions. Theories about underlying mechanisms

will be tested with the help of a new tree growth model which will also serve for scaling measurement results in time and space. Therefore, a model concept has been developed and implemented in computer code. The model has been parameterized with local investigations and reported values from literature and has been tested with various weather input and stand structures.

Forest practitioners have developed numerous tree growth models to support management decisions (e.g. Ek and Monserud, 1974^[10]; Hasenauer et al., 1995^[15]; Miina and Pukkala, 2000^[27]; Pretzsch et al., 2002^[34]). These models simulate tree dimensions and stand development as essential variables for management planning and are based on empirically derived growth response functions. Thus, they are not very well suited for the description of tree growth under conditions that have not yet been explicitly investigated. To overcome this drawback, more sophisticated models have been developed that represent growth as the result of biological and ecological responses to a broad range of environmental conditions. These models concentrate on either physiological processes (e.g., Bossel, 1996^[6]; Cropper, 2000^[8]; Running and Coughlan, 1988^[39]) or biogeochemical fluxes (e.g. Liu et al., 1992^[24]; Rastetter et al., 1991^[35]). However, stand structure is only marginally dealt with because the models are applied to homogenous stands only, or simulations are run over a short time, assuming that structural changes during this period can be neglected. Another approach involves gap modelling (Acevedo et al., 1995^[11]; Lindner et al., 1997^[21]) which is used to represent tree development during longer time periods but also assumes horizontal homogeneity on the spatial scale considered. To account for the important influence of structure, some models have recently been developed which concentrate on the structural change of woody plants in dependence on their individual environment (Balandier et al., 2000^[2]; List and Küppers, 1998^[22]; Perttunen et al., 1996^[30]). However, as far as we know, very few attempts have been made to describe the ecophysiological responses of large trees on a stand scale in dependence on their explicit individual conditions (but see Simioni et al., 2000^[42]; Williams, 1996^[45]).

In order to develop a model that describes individual growth in dependence on individual resource availability and utilization and that is nevertheless suitable to simulate the development of enough trees to represent a forest stand, we followed three basic principles. Firstly, we implemented a number of physio-

logical process descriptions that are supposed to be necessary to assess variations in climate, deposition and air pollution. Secondly, we calculated all processes at the scale of tree compartments (foliage, branches, etc.) within fractions of the crown or root system. This assures that dimensional changes can be calculated in dependence on physiological differences within the tree. Finally, development on different hierarchical levels, e.g. physiology, dimensional change and stand structure, is based exclusively on the output of the respective level below (see Fig. 1). This means that physiological processes are determined by meteorological and chemical conditions of their immediate surrounding, dimensional changes or death of a segment is directly based on biomass production, and that the new structure and species mixture can be described as the sum of tree development results. The latter, in turn, determines the new environmental conditions for each segment. Because of this feedback structure, a dynamic transition between an initialized equilibrium state and a new balance between environmental impacts and stand development can be simulated, which led us to the name of the new model: "BALANCE".

Model Description

General

As indicated in Fig. 1, the model is divided into three parts which are executed with different time steps. Firstly, the individual environment is calculated from daily weather conditions (minimum requirements are average temperature, radiation and precipitation sum) and initial tree dimensions (height, diameter at breast height, stem position). Light competition is determined three times a year (beginning of the year, start and end of vegetation period) with a simple radiation model. Absolute light availability is then calculated for each crown segment. The daily amount of water available for each tree is simulated with a water balance model and reduction of photosynthesis is determined by comparison with its current transpiration requirement. This indicator for drought stress is assumed to be the same in every part of the crown. Furthermore it is also assumed that temperature and air chemistry impacts are evenly distributed within the canopy. All environmental conditions are averaged into monthly values.

All physiological and biogeochemical processes (carbon and nutrient uptake, respiration, senescence, allocation) are calculated monthly, leading to a net change in biomass of each of the tree compartments: stem wood, foliage, buds, fine roots, branches, and coarse roots. All compartments, except stem wood, are differentiated into fractions of the crown and the root system. Stem wood and branches are divided into dead and living parts, with only the latter contributing to respiration. Additionally, a reserve compartment is introduced to fulfill the respiration requirement during times of negative carbon balance.

Tree dimensions are updated at the end of the year according to the biomass changes of the stem wood, branch, and coarse root compartment. Height and diameter growth are defined by the increase in stem wood and a given height/diameter relation. The model user currently prescribes this relation but in later model versions it will depend on individual resource availability. The distribution of the total amount of branch (and coarse root) growth into each fraction of the crown (and

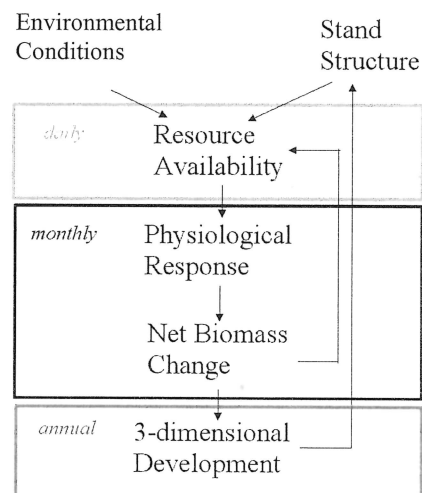


Fig. 1 Hierarchy of processes as represented in BALANCE.

root system) depends on the relative amount of net carbon (and nitrogen) assimilation in each fraction.

The model is implemented in DELPHI programming language with a Windows-based user interface. The length of one simulation depends on tree number and size, as well as on output options. For example, the simulation of 100 trees, initialized as described in the text, took about 30 min to run over 10 years on a Pentium IV PC (1400 MHz). The pictures in Fig. 12 are computed with the TreeView software, developed at the Chair of Forest Yield Science in Munich (Seifert, 1998^[40]). The graphical output of the maximum crown area that is also given in Fig. 12 is a part of the BALANCE programme.

Tree structure

The structure of a tree as assumed by the model is illustrated in Fig. 2. Stem height and diameter at breast height (*dbh*) have to be initialized. Height of crown base (*hcr*), rooting depth, and horizontal extension (r_{max}) of the crown and root system in k ($= 4$ or 8) directions are taken from measurements or are estimated from stem dimensions and stand density. The canopy, as well as the root system, is divided in discs of equal but adjustable thickness. These discs are further divided into k segments. The radius length (r) in any height (h) is related to r_{max} according to Equation 1. It is estimated from relative height within the crown (*relH*) and crown length (*lcr*) (or depth within the soil and total rooting depth). To calculate crown volume and cover, any two neighbouring radii in the same layer are connected by means of ellipsoidal equations. Radii arranged above each other are connected stepwise, without vertical interpolation.

$$r_h = r_{max} \cdot \frac{relH \cdot f(h)}{\max[relH \cdot f(h)]} \quad (1a)$$

$$relH = \frac{lcr - (h - hcr)}{lcr} \quad (1b)$$

$$f(h) = ps \left(100 \cdot \frac{(h - hcr)}{lcr^2} \right) \quad (1c)$$

ps: shape parameter

The stem of a tree is divided into two sections: above and below crown base height. Below crown base, the stem is described as a truncated cone with the diameter dbh at 1.3 m height and a given diameter decrease with height. The upper part is represented by a cone with a basal area equal to the top area of the lower stem part.

Biomass distribution

Compartment biomass is initialized from tree dimensions, considering the particular competition situation of the tree. Firstly, foliage biomass during the vegetation period (M_{fol}) in every crown segment is calculated from the segment volume (V), the fraction that is actually foliated (F_{fol}), foliage density (δ_{fol}), and specific foliage area of the segment (sFA) (Equation 2). F_{fol} , d_{fol} and sFA are calculated in dependence on a competition factor (CF) which is the sum of all segment volumes that are classified as competing segments according to the same procedure as used to calculate light extinction within the canopy (see further down).

$$M_{fol} = \frac{V \cdot F_{fol} \cdot \delta_{fol}}{sFA} \quad (2a)$$

$$sFA = sFA_{max} - (sFA_{max} - sFA_{min}) \cdot \exp(-psla \cdot [CF+1]) \quad (2b)$$

$$F_{fol} = \min \left[1, \frac{V_{fol_{max}} / (CF+1)^{0.3}}{V} \right] \quad (2c)$$

$$\delta_{fol} = \delta_{fol_{max}} \cdot \exp(F_{fol}/pdens) \quad (2d)$$

$psla$, $pdens$: scaling parameter; $\delta_{fol_{max}}$, sFA_{max} , sFA_{min} : parameterized maximum and minimum values; $V_{fol_{max}}$ is calculated from the maximum foliated radius (parameter lg_{max}) and the angle between the k segments of one disc, considering the segment as part of an ellipse (Röhle and Huber, 1985^[37]).

These calculations result in an increase of sFA and a decrease of δ_{fol} from the top to the bottom of the crown, consistent with investigations described in the literature (Hendrich, 2000^[17]; Kellomäki and Oker-Blom, 1981^[20]). The foliated fraction of the segment volume generally decreases with crown depth, but the calculation allows also for fully foliated crown segments in suppressed trees with small crowns.

The crown volume is also used to estimate branch biomass (M_{bra}). This compartment consists of a "twig" fraction which is linearly related to foliage biomass ($=M_{fol} \cdot ptwg$), and a "coarse branch" fraction for the residual branch wood (branch volume $V_{bra} \cdot$ branch density δ_{wod}). The branch volume of one segment is calculated from the sapwood area needed to supply the foliage within this segment ($=M_{fol} \cdot psap$), the length of the average branch and the increase of branch thickness with length. This is a modification of the approach from Raulier (1998^[36]) and is well in accordance with the principles of the pipe model theory (Shinozaki et al., 1964^[41]). The length of the "pipe" depends on the size of the segment, the insertion point of the coarse branch within the foliated volume ($=r - prel \cdot$ foliated radius length) and the average angle of branch insertion (α_{avg}). The basal area of the branch, and thus branch volume, is calculated assuming a constant increase of branch diameter with length ($pbra$), which accounts for branch wood

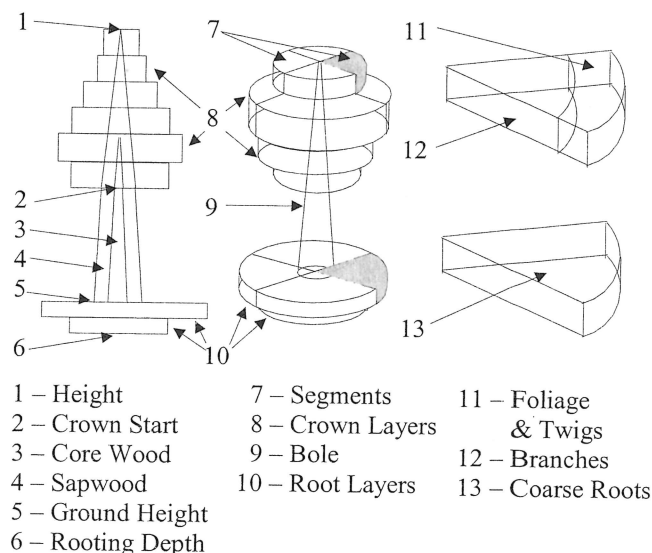


Fig. 2 Representation of the tree structure in BALANCE.

that is built for branch stability or that has been produced for water transport into now unfoliated crown parts. Only the twigs and the wood necessary to build the "pipe" are considered as living tissue.

According to the functional balance principle (Mäkelä, 1990^[25]), fine root biomass is initialized as a certain fraction of the foliage biomass. The relation between both depends on their supply from soil resources, but is held constant in the presented simulations. Coarse root biomass is estimated similarly to branch biomass, assuming that the same amount of conducting xylem area is required and that this area can be distributed across the root segments according to their relative segment volume. The length of the "root pipe" is assumed to be equal to the average radius of the segment and a form factor (p_{prt}) is used to account for their taper development.

The carbon and nutrient pool stored in buds is introduced to provide flushing of foliage in springtime. At the beginning of the year it contains the carbon necessary to produce the foliage required according to Equation 2 and is refilled thereafter according to the demand of the foliage compartment. The reserve pool accounts for the free available carbon within the tree and is defined as a fraction of living woody tissue. This compartment is used to supply the carbon for respiration requirement in times with negative net assimilation.

Total stem wood is calculated from the two geometric figures that represent the stem, assuming a constant wood density. The amount of living sapwood in the lower stem fraction is calculated from crown height and sapwood area at crown base, which is determined from total foliage biomass, using the same relation between sapwood area and foliage as applied for branch sapwood. Since the top fraction of the stem is represented as a cone and sapwood area at the base of this cone is known, living sapwood in this fraction can be calculated assuming that the core wood forms an inner cone with the same height/diameter relationship as the outer cone.

Individual environmental conditions and competition

Competition for resources depends on tree dimension and biomass distribution. Nutrient and water availability is determined by the amount of occupied soil volume, as well as fine root density. It also depends on local temperature, which drives mineralization and decomposition processes (see below). Aboveground, CO₂ concentration, radiation and temperature are the major driving forces for photosynthesis and respiration, which also depend on the crown size and foliage distribution within the canopy. Thus, the model can be used to calculate the availability of all necessary energy and matter resources. In a first attempt, however, we concentrate on the most variable effects – soil water content and radiation interception. Other influences are assumed to be constant within the canopy (temperature, CO₂) or do not change with time (nutrient supply).

The available soil water is calculated from precipitation, interception, throughfall, soil water movement and percolation. The interception capacity of a tree is determined by its foliage area and its specific interception capacity (int_{spe}), and the amount of intercepted water per day is calculated from precipitation, total interception capacity and potential evaporation (Liu, 1997^[23]). The fraction of precipitation that falls directly on the ground is derived from the relation between crown-covered area and total stand area. In a first approach, the exchange of water is described as a flow from unrooted to rooted soil volume once a day until the water content of both compartments are equal. Finally, percolation is calculated using a "bucket model", which means that the amount of water that exceeds the holding capacity of one soil layer flows into the layer below.

Radiation availability could be estimated by the ray tracing method which calculates the light intensity at a particular point from the energy loss of a number of sample light rays which are followed through the canopy (Brunner, 1998^[7]). However, this method is computational expensive and thus has been used only in combination with very few physiological processes (Genard et al., 2000^[11]) or a very simple tree structure (Bartelink, 2000^[5]). In order to reduce the computational effort for the presented simulations, we applied a procedure originally proposed for calculation of whole tree competition (Pretzsch, 1992^[31]) to estimate the light intensity at each canopy segment (I_s) in dependence on global radiation (I_0).

$$I_s = I_0 \cdot \exp(1 - [Fc_s + 1]^{kext}) \quad (3a)$$

$$Fc_s = \sum_{i=1}^n (Vfol_i \cdot LA_i \cdot pclu) \quad (3b)$$

$kext$: extinction coefficient; $pclu$: clustering parameter

The competition that one segment s experiences is expressed as the relative light availability Fc , which is determined from the foliated volume ($Vfol$) of every competing segment n and the leaf area (LA) within this segment (Fig. 3). Competing segments are those that are located within a cone above segment s . This cone is characterized by the base angle β_1 and its insertion point in the middle of the foliated segment volume. Thus, if the angle (β_x) between the insertion point in segment n and the reference point in segment n (= centre point of the upper surface

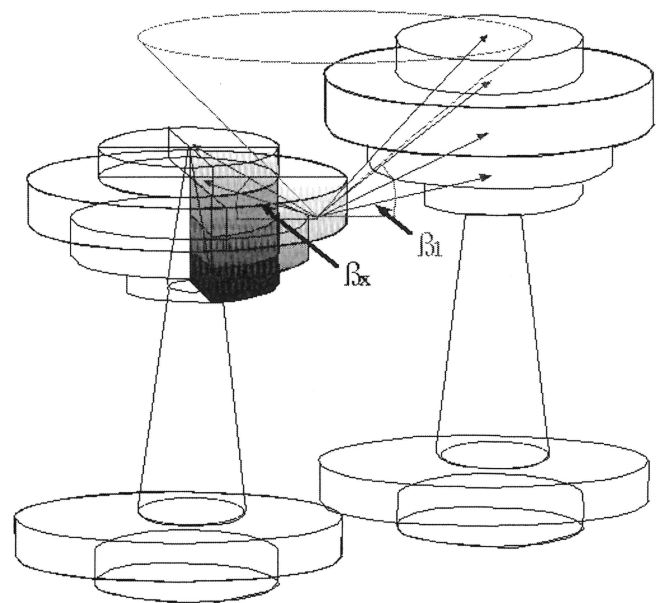


Fig. 3 Illustration of the competition procedure used for estimating relative light availability. The angle β_1 determines the size of the cone that is used to calculate relative radiation availability of a segment. A segment will be considered as a light reducing segment if the angle β_x between this segment and the segment of interest is larger than β_1 . (Only four layers and four radii are drawn for reason of simplicity. Layers of the central tree are shaded in one direction to a different degree to indicate the loss of light with increasing crown depth.)

of the foliated segment volume) is smaller than β_1 , n is considered in the calculation. Parameter $kext$ refers to the degree of radiation extinction in analogy to the Beer–Lambert law (see Fig. 4 for illustration), and $pclu$ is the fraction of the segment that is actually occupied by foliage (Bartelink, 1998^[4]). Because of the more clustered structure of spruce foliage, this factor is higher for beech.

Process description

Water balance

The most important impact of water availability is the decrease of photosynthesis by means of stomatal closure. However, stomatal width is not modelled explicitly, but is assumed to allow actual transpiration (T_{act}) to be as high as potential evaporation demand (T_{pot}) as long as sufficient soil water (T_{max}) is available (Grote and Suckow, 1998^[14]). The only plant properties that have to be considered are maximum CO₂ conductivity of the canopy (g_{max}) and leaf area, which both are used in the Penman–Monteith equation to determine T_{pot} (Monteith, 1965^[29]). T_{max} is defined as the smaller value of either soil water within the rooted soil volume (UW_{pot}) or the uptake capacity (UW_{max}). Whereas the calculation of UW_{pot} depends on rainfall, soil water movement and uptake as described above, UW_{max} is determined by the amount and specific uptake rate of the fine roots and their biomass in each soil layer. If T_{act} is less than UW_{pot} water uptake is distributed between the soil layers according to the amount of available water per fine root surface area (see Fig. 5).

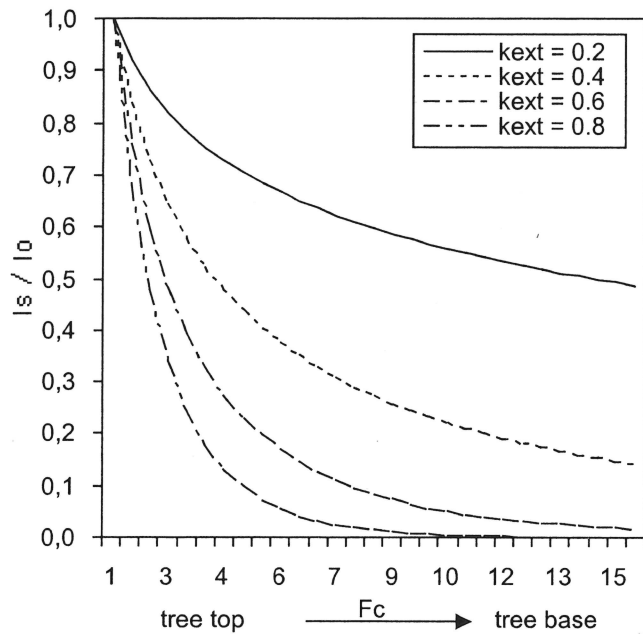


Fig. 4 Development of relative light intensity at one tree canopy segment (I_s/I_0) in dependence on the competition factor (F_c , see text for further explanation) and the extinction parameter k_{ext} .

These processes are calculated with a daily time step and require daily precipitation, temperature and radiation data as input. This is necessary because the pattern of water availability depends strongly on the distribution of precipitation within a particular period. The impact of water availability on carbon balance is expressed with the monthly average of the relation between T_{act} and T_{pot} . In order to use this relation to represent drought stress in every crown segment, T_{act} is weighted according to foliage area ($M_{fol} \cdot \delta_{fol}$). The relation between T_{act} and T_{pot} at the segment level is used to decrease photosynthetic carbon gain, which is based on the assumption that average stomatal width is linearly related to gross carbon assimilation on a time scale large enough to allow for physiological adjustment. Thus, we assume that physiological reactions, e.g. the delay of stomatal responses due to water transport resistance and the depletion of stem water reserves, are able to compensate the over-estimation of drought stress that results from averaging values obtained from days with different carbon gain.

Nutrient balance

In contrast to aboveground processes, it is hardly possible to describe nutrient uptake with high spatial resolution and small time steps. This is mainly because of the high spatial heterogeneity of soil conditions and the difficulties in assessing this heterogeneity, which prevents a realistic initialization in three-dimensional models. Also, the understanding of below-ground processes is less developed than that for aboveground processes. Despite these difficulties, it is important to consider nutrient cycling in tree growth simulations, e.g. to describe the response of tree growth on deposition or the decline in plant productivity with stand dimension (Johnsen et al., 2001^[19]). The modelling concept includes the uptake of nutrients, their distribution within the plant, their input into the

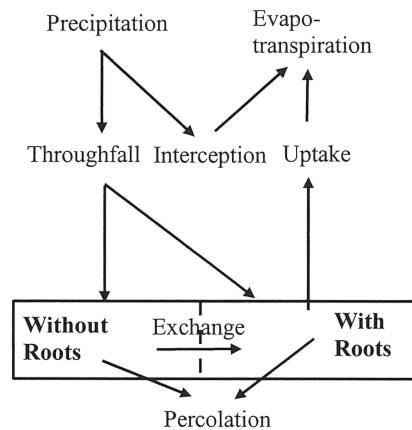


Fig. 5 Water balance.

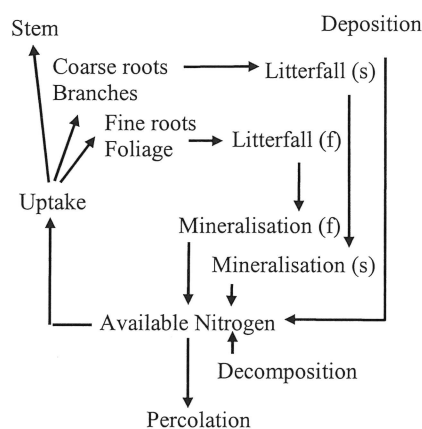


Fig. 6 Nutrient balance.

soil by deposition and litterfall, and mineralisation (Fig. 6). However, the current implementation is not yet suitable for long-term simulations since mineralization response to temperature is kept constant and soil water only plays a role in the distribution of nitrogen. It is thus described here as a basis for further refinement.

Nutrient uptake (UN_{act}) is calculated similarly to water uptake. It is limited by the smaller of the three values tree demand (N_{pot}), maximum uptake rate (UN_{max}) and nutrient availability (UN_{pot}) (Grote, 1998^[13]). N_{pot} is defined as the sum of compartment deficiencies that are derived from biomass and specific optimum nutrient concentration. UN_{max} is calculated as the fine root surface multiplied by its specific uptake rate for the nutrient. UN_{pot} is derived from the mineralization rate of two litter compartments (material from branches or coarse roots, and foliage or fine roots), weathering and deposition. Only the uppermost soil layer gets direct input from deposition and litter (except root litter, which emerges in the soil layer where the root died). Transport of nutrients is assumed to occur only with percolation from the upper into the deeper soil layers and with uptake from the soil into the plant. If the total nutrient requirement is less than UN_{pot} , nutrient uptake is distributed between soil layers according to the ratio between fine root surface and nutrient content in each soil layer. Once taken up, nutrients are distributed into the different compartments relative to their demand. The nutrient content of the litter is that of the living tissue in the case of the roots and branches but is

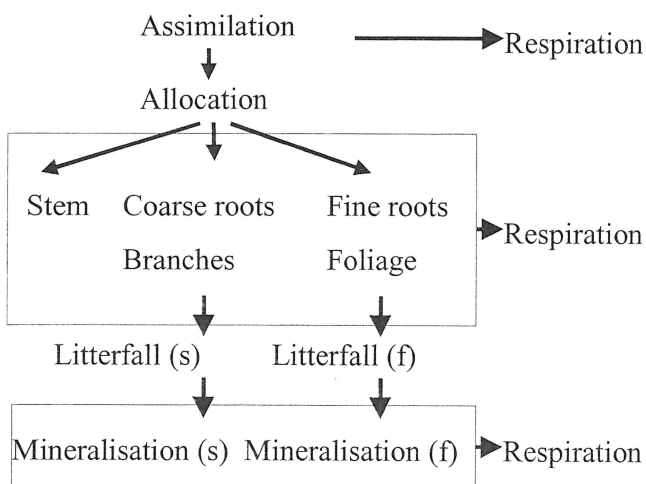


Fig. 7 Carbon balance (s and f are indicating compartments with slow and fast decomposition properties).

reduced for foliage. The retranslocated nutrient amount is then distributed into the other tree compartments to supplement uptake as long as any deficiencies occur and is otherwise put into the reserve compartment to supply new foliage growth.

In principle, various nutrient cycles could be represented within the presented framework. However, very few mechanistic process descriptions concerning mineralization and nutrient uptake are currently available and the sensitivity of these processes to environmental variations is not known in many cases. Thus, nitrogen is the only nutrient currently considered. Since nutrient availability belongs to the environmental conditions, it is calculated in daily time steps. The summed nitrogen uptake is used in the physiological part of the model, where the distribution and the influence on respiration and photosynthesis are described in monthly time steps.

Carbon balance

The carbon balance of every plant is determined by its assimilation, the distribution of carbon within the plant in different compartments, and carbon losses by respiration and litterfall (Fig. 7). Eventually other carbon sinks also have to be considered, e.g., exudates, mycorrhiza, or grazing. Both environment (e.g. radiation) and foliage properties (e.g. photosynthetic capacity, compensation point, and specific leaf area) vary a lot within the canopy and also change during the year and between years. This makes it difficult, if not impossible, to simulate these processes on the same scales as investigations are usually performed, particularly for whole stands and over periods relevant for forest development. However, theoretical concepts exist that link climatic conditions and physiological foliage properties, assuming an adaptation of the plant to optimize its carbon gain. The concept proposed by Haxeltine and Prentice (1996^[16]) assumes basic biochemical properties (e.g. temperature dependency of enzyme activity in photosynthesis) as constant, which makes it possible to determine photosynthesis from average radiation, temperature and CO₂ concentration, independent of tree species. However, a species-specific reduction factor (Φ_c) is introduced that accounts for

sub-optimal adaptation responses. The procedure requires time steps large enough to allow for physiological adjustments and is used here to calculate the maximum assimilation rate on a monthly basis. The actual gross carbon gain is derived after the application of reduction factors referring to various kinds of stress (drought, sub-optimal nutrient content, direct pollution effects).

Gross carbon gain is diminished by growth and maintenance respiration. Growth respiration is considered as a constant fraction of gross assimilation, whereas maintenance respiration (RM) is calculated for each compartment according to its biomass (B), specific respiration rate (R_{spe}) and temperature (T), as shown in Equation 4. To account for nutrient dependencies, the specific respiration rate is calculated from nitrogen concentration of the compartment (N_c).

$$R = B \cdot R_{spe} \cdot q_{10}^{\left(\frac{T - T_{ref}}{10}\right)} \quad (4a)$$

$$R_{spe} = pres \cdot \left(1 - \frac{N_c}{N_{c_{opt}}}\right) \quad (4b)$$

q_{10} : base coefficient of the exponential function; T_{ref} : reference temperature to which the specific respiration is related; $N_{c_{opt}}$: optimum nitrogen concentration; $pres$: scaling parameter

The remaining amount of carbon is used to increase biomass in the different plant compartments. It is distributed in order to hold or obtain functional relationships which are derived from commonly accepted principles (Grote, 1998^[13]). The relations depend on mineral nutrition (foliage – fine roots) (Mäkelä, 1990^[25]) or dimension (foliage – branches – stem – coarse roots) (Shinozaki et al., 1964^[41]) and are disturbed by senescence and by the occurrence of new foliage during flushing. Senescence is described in a preliminary form with given turnover rates for foliage (which is assumed to be the inverse value of foliage longevity) and fine roots ($tofol$, $tofrt$). Twigs that are supposed to supply foliage biomass within foliated parts of crown segments are shed in proportion to the loss of foliated volume and foliage density. If the segment no longer contains foliated volume, also the remaining coarse branch biomass of this segment is considered dead and transferred into the litter compartment.

Bud biomass is completely converted into foliage biomass at the beginning of the vegetation period, and foliage is reduced by litterfall at the end of this period. The model user currently sets both values. Respiration and assimilation in the month where the start or the end of the vegetation period occurs are weighted according to the fractions with and without new foliage.

Dimensional development

Height and diameter development

A prescribed height/diameter relationship is insufficient to describe individual growth responses to changing conditions over a long time period because the relative carbon investment in different parts of the stem is likely to depend on internal

variation of physiological plant processes (Deleuze and Houllier, 1997^[9]; Thornley, 1999^[43]). Nevertheless, we preliminarily applied a constant height/diameter relationship because the derivation of individual environment, as well as the physiological processes, is not yet well enough evaluated to allow for a better representation. Based on this assumption, the total increase in stem biomass is distributed around the stem, provided that the sapwood area increase is the same at any height below the crown base. The amount of dead wood in both compartments is updated once a year according to the development of foliage biomass and the necessary sapwood in crown segments and stems.

This procedure leads implicitly to changes in stem form if the height of the crown base increases – representing slim stems if crowns are short, whereas thick stems develop otherwise, which is in accordance with general findings. The crown base shifts upward by the height of the lowest foliated crown layer if all segments within this layer are lost. Since a crown layer dies only if negative net assimilation is obtained, crown base development depends on the individual environment of the tree, as well as its physiological properties. If all layers are lost, the tree is considered dead.

Horizontal extension and crown form

The horizontal extension of each crown (and root system) segment is described directly in dependence of the biomass distributed into each segment for branch growth. This biomass is derived by distributing the annual increase of the branch (coarse root) compartment (ΔB) according to the specific net carbon (nitrogen) assimilated in the particular segment (NA_{spe}), as described in Equation 5. The respiration term ($Rfbs$) in this equation includes the annual respiration of foliage and branches within this segment, as well as that of the stem sapwood needed to supply the particular crown fraction. Because the growth of new segments cannot be determined from their responses to past environmental conditions, their fraction of total biomass increase is calculated in relation to the efficiency of the uppermost old segments. Branch (and coarse root) biomass growth is then converted to volume increment according to the relationship between them which has been described above.

$$\Delta B_s = \Delta B \cdot \frac{NA_{spe}}{\sum NA_{spe}} \quad (5a)$$

$$NA_{spe} = \frac{A - Rfbs}{Vfol} \quad \text{old segments} \quad (5b)$$

$$NA_{spe} = NA_{spe} \cdot \frac{h - hs_{old}}{hs_{new} - hs_{old}} \quad \text{new segments}$$

$hs_{old,new}$: stem height (before and after annual height growth);
 h : height of the new segment

To account for mechanical competition effects (i.e. wind-induced branch damage due to crown contact), the largest radius in a particular direction is restricted by r_{pot} . This annually updated maximum value is determined according to the distance (D_{ij}) of the central tree i to the nearest tree j within the angle of the two segments that enclose the radius (Equation 6).

$$r_{pot} = D_{ij} \cdot \frac{dbh_i}{dbh_i + dbh_j} \quad (6)$$

Parameterization

Since the processes described in the model are not yet evaluated, BALANCE is considered as a conceptual model. Nevertheless, model testing has been executed with respect to some properties, using a mixture of directly measured, fitted and estimated parameters, with estimations based on field information, as well as literature studies (Table 1).

Field information has been obtained from measurements at a trial plot in Southern Bavaria, Germany. The plot has a size of 5312 m² and consists of 522 49-year-old spruce (*Picea abies*) and 307 56-year-old beech (*Fagus sylvatica*) trees per hectare, planted in a group mixture. 14 trees per hectare belong to other tree species e.g. pine, larch, maple and aspen (reference year 1999). More detailed information can be obtained from Pretzsch (1998^[33]). Diameter and stem position of all trees were measured in 1994. Tree heights and crown base heights of the trees have been estimated from height growth curves, elaborated from a sample of 86 trees (43 spruce and 43 beech). Crown radii are measured for 215 trees in 8 directions (by visual estimation from the ground). Height and diameter measurements have been repeated in 1999. The scaling parameters $pdens$ and $psla$, which describe the development of foliage density and specific leaf area in dependence on light competition, have been estimated to be in accordance with investigations of Hendrich (2000^[17]) in the same stand (Fig. 8). Also, foliage longevity has been derived from litter sampling at this area (Riedel, pers. comm.) and maximum and minimum values of specific foliage area are estimated from measurements made by Reiter (pers. comm.).

Most allometric parameters are determined from a number of sample trees (5 beech, 6 spruce), harvested in the close vicinity of the experimental site. This includes the direct derivation of lg_{max} , α_{avg} , $prel$, $ptwg$ and $psap$. Also, the crown shape parameter ps , which is used to initialize the older trees in the simulation (young spruce are initialized with a perfect cone shaped crown), has been determined from the average value of each of these trees (0.018 for spruce and 0.076 for beech, not given in Table 1 because ps is only used for initialization). Samples of foliage, branch wood, and coarse root biomass were weighed and the obtained dry mass values were extrapolated to obtain total tree biomass for these compartments. Furthermore, simulations were executed using the tree dimensions (height, diameter at breast height, crown radii) of the same trees, as well as their nearest neighbours that were determined before harvest. Estimations from measurements and simulation results were compared and used to fit the parameter δfol_{max} , $pbra$ and $pcrt$ in order to obtain a 1 : 1 line between simulations of whole tree foliage, branch wood, and coarse root biomass, respectively. The resulting correlation coefficients are presented in Fig. 9.

Start and end of the vegetation period, as well as canopy conductivity (g_{max}), was determined by comparing simulated and measured water content in the upper 20 cm of the soil (Fig. 10). The measurements were executed with 6 equi-tensiometers (ecomatic, Dachau) that were placed under the beech and

Table 1 Parameter values used in the simulation

Abbreviation	Description	Spruce	Beech	Reference
α_{avg}	average branch angle (between tree top and branch insertion)	90	45	*
$\delta\text{fol}_{\text{max}}$	maximum foliage density ($\text{m}^2 \text{m}^{-3}$)	1.13	0.57	**
g_{max}	max foliage conductivity (m s^{-1})	0.012	0.035	**
int_{spe}	specific foliage interception capacity (mm m^{-2})	0.5	0.5	***
l_{gmax}	maximum foliated crown radius (m)	4.9	8.5	*
p_{bra}	branch diameter change with length (m m^{-1})	0.019	0.006	**
p_{crt}	coarse root form factor	3.1	1.1	**
p_{dens}	scaling parameter for foliage density development	2	6	**
p_{rel}	relative coarse branch insertion within the foliated crown segment	0.7	0.3	*
p_{sap}	foliage biomass per sapwood area (kg cm^{-2})	0.0577	0.0148	*
p_{sla}	scaling parameter for specific foliage area changes	0.01	0.015	*
p_{twg}	twig biomass per foliage biomass (kg kg^{-1})	0.3919	7.47	*
r_{spfol}	specific respiration rate of foliage at 25 °C (kgC kgDW^{-1})	0.004	0.006	****
s_{famax}	maximum specific foliage area ($\text{m}^2 \text{kg}^{-1}$)	8	45	*
s_{famin}	minimum specific foliage area ($\text{m}^2 \text{kg}^{-1}$)	2.5	9	*
t_{ofol}	annual turnover of foliage	0.1667	1	*
t_{ofrt}	annual turnover of fine roots	1	1	*****
v_{egend}	last day of the vegetation period	290	310	**
v_{egstart}	first day of the vegetation period	130	130	**
δwod	wood density ($\text{kg dry matter m}^{-3}$ fresh volume)	380	560	*****

* estimated directly from measurements; ** fitted with measured data; *** Running and Coughlan, 1988^[39]; **** Mohren et al., 1993^[28]; ***** Jansen et al., 1995^[18]; ***** Grosser, 1995^[12].

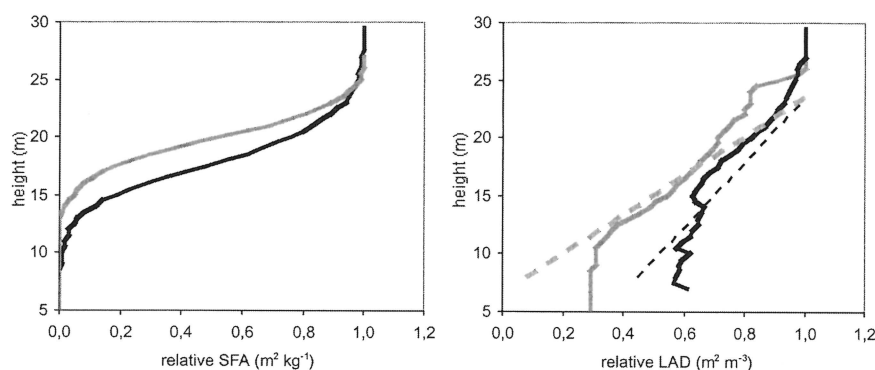


Fig. 8 Simulated development of specific foliage area (sFA) and leaf area density (LAD) throughout the canopy profile of the investigation plot "Freising 813/1" for spruce (black lines) and beech (grey lines). The broken lines are measured relations calculated from Hendrich (2000^[16]).

spruce canopy, within the area of the experimental forest described above. The water tensions are recorded every 30 min, converted into water content values and averaged over one day. The simulations were initialized with the tree dimensions measured in 1999 and were run with the climate information obtained from the Freising weather station of the Bavarian Forest Research Station that is close to the trial plot. The squared correlation coefficients between the daily average values of simulated and measured water availability were 0.79 (spruce) and 0.72 (beech). However, it is apparent that the largest deviations occur under beech during spring and autumn. This indicates that further improvement can be expected if the appearance and loss of foliage is described in a more sophisticated way.

Finally, Φ_c is adjusted in order to fit simulated stem wood growth to measurements. Therefore, tree development of the 215 trees that have been repeatedly measured in 1994 and 1999 is simulated over five years. The simulation has been started with the tree data from 1994. 137 additional trees with similar dimensions to the simulation trees were artificially po-

sitioned around the plot to exclude boundary effects. The procedure to create position and dimension of these trees was taken from the stand simulator SILVA (Pretzsch, 2001^[32]), and will not be further discussed here. Climate information for the years 1995 until 1999 was again taken from the Freising weather station of the Bavarian Forest Research Station. The trees that died during this period were excluded from the simulation run at the estimated year of tree death. Because the height/diameter relation was kept constant in the simulation, simulated stem wood volume, which combines height and diameter increase, is compared with the volume increase calculated from the measurements that are executed in autumn 1994 and 1999. Only surviving trees with a measured positive dimensional increase are considered in the comparison. The simulation was repeated with different values of Φ_c until the 1:1 line was obtained (Fig. 11). As could be expected from the preliminary state of the model, the scattering is quite large and the growth of small trees tends to be over-estimated compared to the growth of large trees, particularly for beech. Nevertheless, we gained an obvious relation between simulation results and the stem volume calculated with measurements.

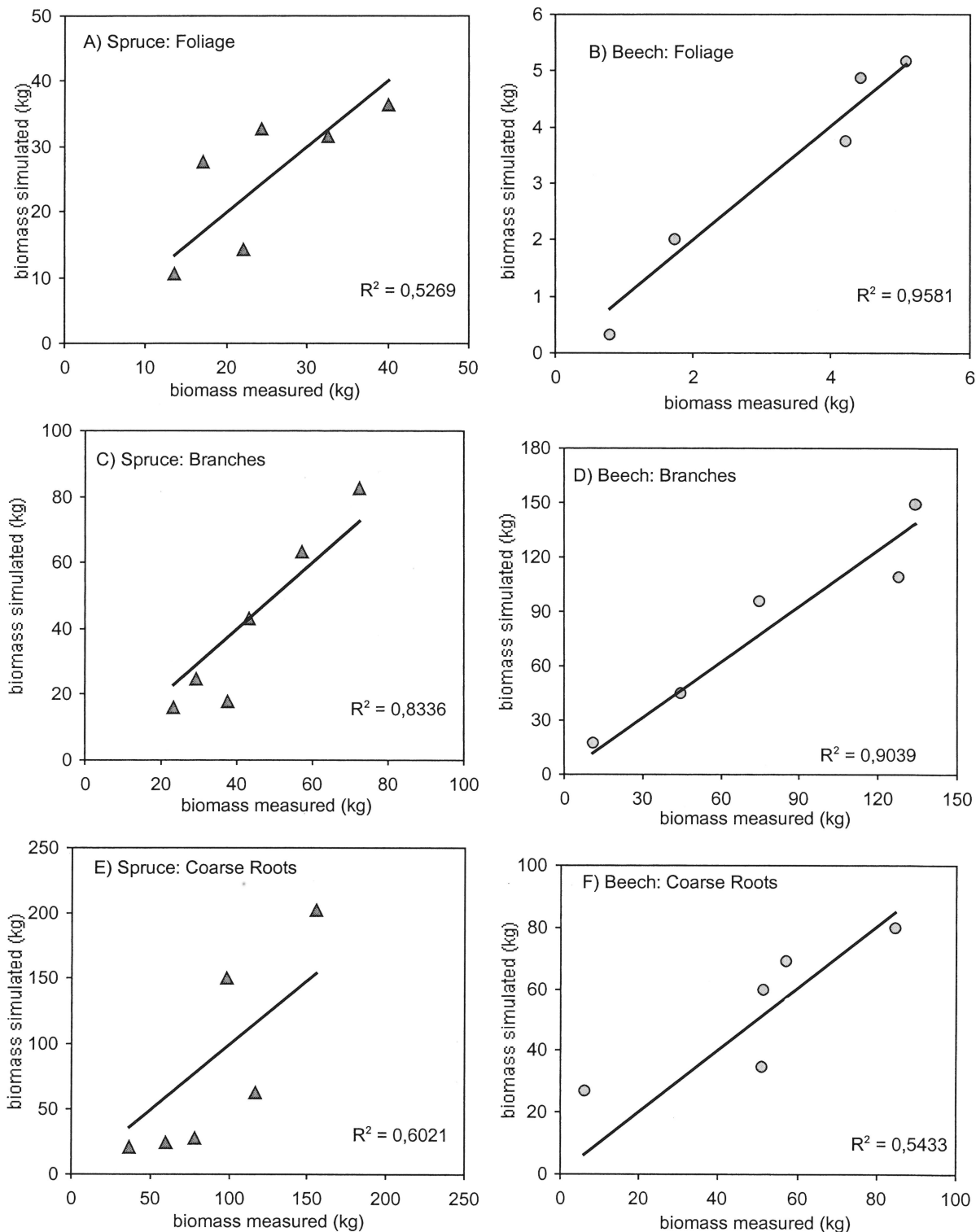


Fig. 9 Simulated vs. measured foliage, branch, and coarse root biomass of 6 spruce and 5 beech, collected in the vicinity of the long-term experimental plot "Freising 813/1".

Model Testing

Based on the parameters that are measured, estimated or taken from literature, three scenarios have been set up to test the presented model. The first run is simply initialized with two trees (one spruce and one beech) to demonstrate growth and

crown development without or with little competition. Both trees are initialized with 1.4 m stem height within a distance of approximately 2 m of each other. The trees are simulated over 10 years, each year using the weather conditions of 1997, which is selected as a typical year from the climate data used for parameterization. During this period, both trees develop

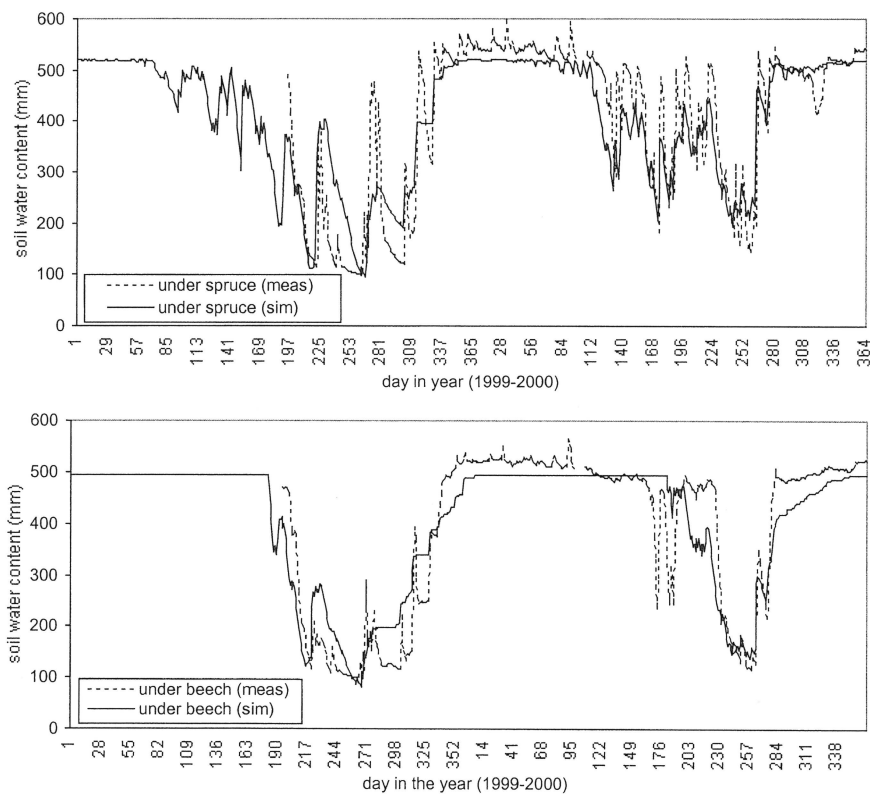


Fig. 10 Simulated vs. measured water content in the upper 20 cm of the soil under spruce (top) and beech (bottom) at the long-term experimental plot "Freising 813/1".

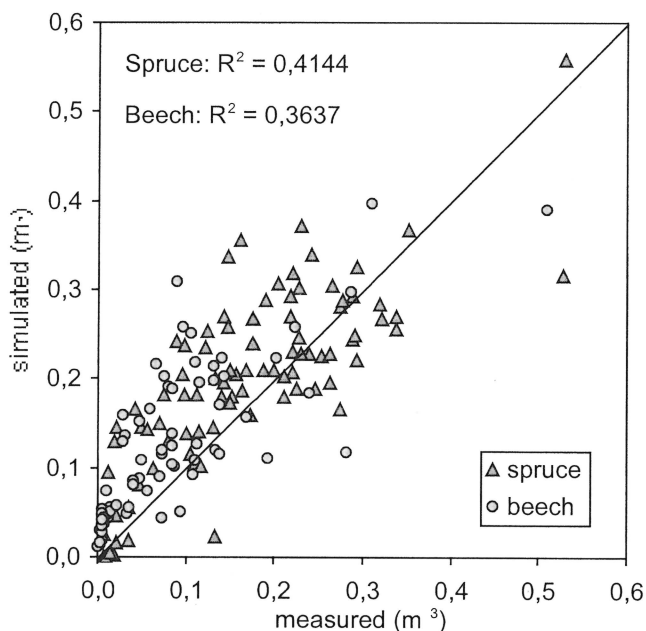


Fig. 11 Simulation results vs. measurements of volume increase from single stems of spruce (triangles) and beech (circles) at the long-term experimental plot "Freising 813/1" during 5 years (see text for further information about the simulation run).

realistic crown shapes, as shown in Fig. 12, which show the three-dimensional view and the crown covered area of the trees after 1, 5 and 10 years of simulation. It is also apparent that horizontal crown extension becomes asymmetric as the

crowns come closer together. This is partly due to the competition for light but mostly because of the mechanical limitation imposed by Equation 6.

With the second simulation set-up we intended to demonstrate the effect of stand structure on tree development. Two artificial stands were initialized: in both stands, 100 young trees with randomly distributed heights of 1.8 ± 0.4 m and height/diameter relations of 110 are positioned at 1×1 m distance on a square plot. In the first case, spruce and beech are positioned in rows, whereas in the second case, 24 beech were positioned in the centre of the square, which is surrounded by spruce. In both cases we excluded the 36 border trees from the results. The simulation is executed over 20 years, using the repeated weather data of the year 1997 that has also been used in the former simulation runs. The simulation results are presented in Fig. 13. It is apparent that beech height growth is generally smaller under the initialized conditions. This is in good accordance with observations of growth patterns in southern Germany (e.g. Rothe and Kreutzer, 1998^[38]). In the row mixture, beech height growth becomes marginal after some years and foliage biomass per tree declines. In contrast, beech trees in the group mixture can continue to increase in height because most trees around the average beech are also beeches, which are smaller and have less light consuming leaf area than the spruce. Thus, the resource availability for beech is generally better in the group mixture. In turn, they have higher growth and are more competitive, which leads to less spruce growth in this run. The average growth of spruce, as well as beech, declines after canopy closure, which occurs after approximately 8–10 years. Thereafter, foliage biomass per tree increases only slowly or even decreases, which is in good

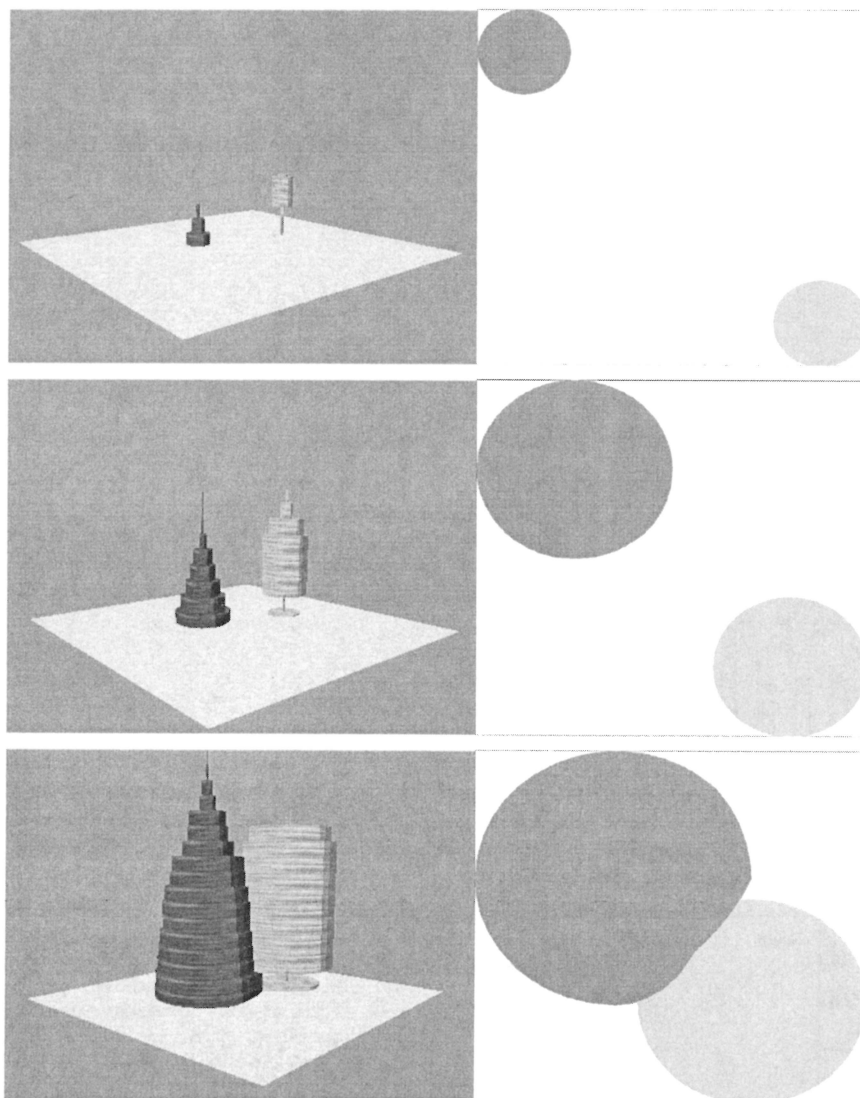


Fig. 12 Development of two trees (dark grey: spruce, light grey: beech), standing together. Pictures show the stage of the trees after 1, 5 and 10 years of simulation in three-dimensional view and as crown cover pictures.

accordance with general considerations (Mäkelä and Hari, 1986^[26]). However, contrary to expectations, no trees died during the simulated time span, whereas in literature the onset of mortality is generally assumed to start with canopy closure according to the self-thinning rule (e.g. Weller, 1987^[44]). Although the beech in the row mixture show a continuously increasing crown base in the last 5 years of the simulation, which indicates the onset of tree mortality, it remains to be investigated if the mortality assumptions in the model have to be redefined.

Finally, the simulation set-up used for parameterization of the assimilation reduction factor of 215 trees was applied to examine sensitivity to weather conditions. This time we ran the simulation with repeated weather data of the year 1996, which was the coolest in the observation period (6.3 °C) but relatively dry (annual precipitation of 745 mm). The results are compared with those of a second simulation run using the same tree and soil properties for initialization. For this run, weather data from a relatively warm and wet year (the year 2000 with 8.7 °C and 891 mm) were applied. As an example

for the simulation results, the cumulative height growth of both runs is presented in Fig. 14, together with the growth development as simulated with the actual weather record of 1995 to 1999. For both species, the weather conditions in 2000 were more favourable than in the year 1996 because higher temperatures increase photosynthesis and the negative impact on water availability is overcompensated due to higher precipitation. The difference between these two runs is considerably larger in spruce than in beech, indicating that the drier conditions in 1996 may affect spruce growth more than beech. However, a closer analysis revealed that the water availability for beech and spruce was not considerably different from each other in 1996. Instead, the reason that the conditions of the year 2000 were less favourable for beech than for spruce was that the average temperature in July 2000 was more than 2 °C below the average July temperature of the years 1995 to 1999, despite the higher annual average temperature. The effect of the conditions during one summer month is different in the two species because the total period in which a net carbon gain is possible is different. Thus, beech perform best under average conditions (7.8 °C, 796 mm), whereas

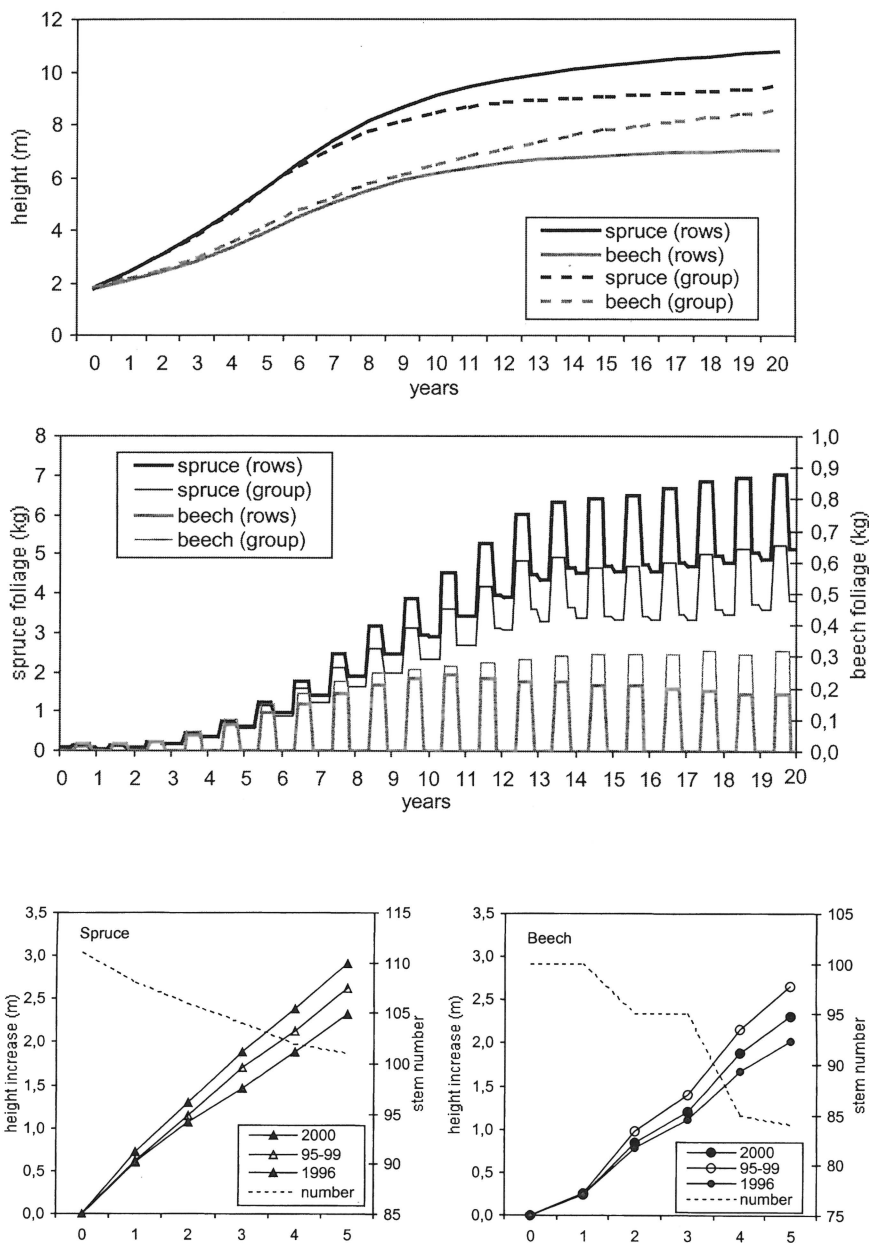


Fig. 13 Average height development (top) and foliage biomass development (bottom) of 100 trees (dark: spruce, grey: beech), positioned in row mixture (thick lines) or group mixture (broken or thin lines). Simulation is executed over 20 years with repeated weather conditions.

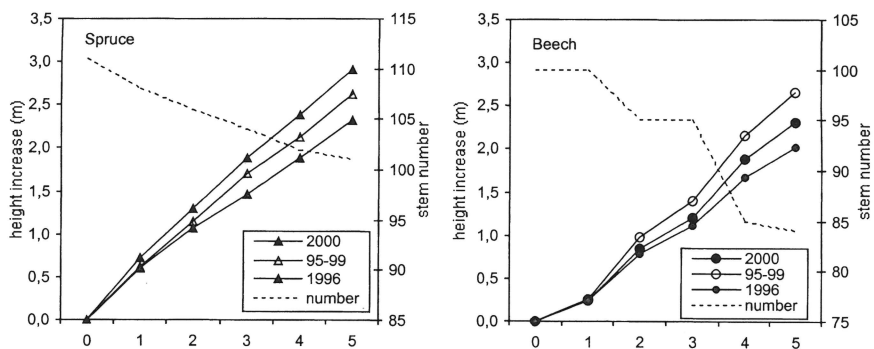


Fig. 14 Average height development of spruce and beech at the long-term experimental plot "Freising 813/1" during 5 years with different weather conditions (1995–1999: actual weather conditions, 2000: repeated conditions of the year 2000, 1996: repeated conditions of the year 1996). Additionally, the imposed development of tree number is presented.

spruce show the highest growth under the conditions of the year 2000. Indeed, stem wood growth as derived from girth band measurements was found to be exceptional high in spruce during the year 2000, whereas beech showed a less than average growth (girth band measurements were executed for all trees since 1996).

For all simulations, crown layer heights of 0.5 m, soil layer extensions of 0.2 m were used. The number of considered cardinal directions was 8 and the competition angle β_1 was set to 70 degrees. Furthermore, the weathering rate was adjusted in order to provide optimum availability of nitrogen over the whole simulation period and other stress factors like parasites or pollution effects were neglected.

Discussion

As far as can currently be judged, the model can reproduce single tree growth in dependence on climatic driving variables, although the variation in the comparison of measured vs. simulated dimensional changes is still quite large. Hopefully, this variation can be decreased by elaborating the processes that describe the individual environmental conditions (i.e. light conditions), as well as the physiological responses. It is also possible that within the observed 5-year period, the influence of nutritional changes should not be neglected, as had been assumed.

However, despite these large uncertainties, we learned from the simulation exercises that the model is already capable of reproducing reasonable development of trees in vertical, as

well as horizontal, directions over medium-term simulations. Longer simulations occasionally result in unrealistic crown shapes, particularly for spruce trees, which tend to grow into column-shaped rather than cone-shaped crown forms. This, in turn, produces shorter crowns since the self-shading effect increases. However, this behaviour only demonstrates that the relation between individual environment, physiology and three-dimensional growth is linked more or less correctly. The difficulty in this case is probably due to the simple light competition model that seems to predict a too small light availability in the lower parts of solitary trees.

In this study, only a small range of an indefinite number of individual environmental combinations could be assessed that develop from environmental conditions outside the stand but also from stand structure. Thus it is very likely that specific stress factors or certain environmental combinations will result in much larger tree responses than obtained from the presented simulation. Since new combinations of environmental influences can be expected that have not yet been observed, the challenge for ecophysiological models is to predict the resulting impact on tree development from the combination of major effects. The presented modelling exercises have shown that BALANCE is already capable of weighting different environmental influences in a reasonable fashion. Furthermore, the simulations underlined the importance of considering stand structure, if the suitability of tree species to certain environmental conditions should be judged.

Although the general behaviour of the model seems to be in accordance with field observations, the simulation results revealed a need for model refinements. As already indicated, a sensitive response of tree development to environmental conditions should include a distribution of stem growth between height and diameter increase in dependence on physiological differences within the tree crown. In order to use the model with a variety of different stands, the currently used constant relationship should be replaced because it depends on the specific resource availability of a tree (Baldwin et al., 2000^[3]). A very promising approach had been suggested by Thornley (1999^[43]), which relates the relative growth of height and diameter (dHD) to the difference in activity in foliage and stem tissue. Since this could not easily be simulated, we suggest calculation of the efficiency at the top and bottom parts of the plant (eff_{top} and eff_{bot}) which could be represented by net carbon gain – a value already calculated in every crown segment of the tree (see Equation 5). The height/diameter relationship could then be defined as:

$$dHD = HD_{max} \cdot \frac{q}{1+q} \quad (7a)$$

$$q = \left(phd1 \cdot \frac{eff_{top}}{eff_{bot}} \right)^{phd2} \quad (7b)$$

HD_{max} is a given maximum height/diameter growth relationship, $phd2$ describes the slope of the response and $phd1$ is a scaling parameter. If the difference between net carbon gain at the top and at the bottom of a tree is large, as can be expected in dense stands, height growth will be favoured over diameter increase, whereas the opposite is true after intensive thinning or in solitary trees.

As described in the introduction, the final model is intended to support the objectives of the joint research project. Thus, a close cooperation with several other groups has been established. For example, the computation of canopy structure from available tree dimension data will contribute to more sophisticated modelling of radiation distribution in other groups but is also a good basis for further improvements of BALANCE itself. Furthermore, it is important that physiological processes are represented on a scale at which they can be easily compared with measurements. On the one hand, these measurements serve for parameterization and further refinement of the model, and on the other hand, the model can be used for scaling the results and judge their importance for impacts on the stand level. A major condition to scale these results, not only in space but also in time, is the model's ability to derive crown extension from physiological processes. However, in order to be compatible with the overall aims of the joint research, the sensitivity of the model to parasites and symbionts, as well as other environmental stresses (e.g. ozone), has to be increased. Thus, respiration losses as indicators for damage mitigation will be represented in a more mechanistic way and the strategic role of the free available carbon pool in the plant will be given a lot more attention.

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