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**Tree growth and resource allocation in forest stands: Empirical
evidence substantiated by scenario simulations**

**Baumwachstum und Ressourcenallokation in Waldbeständen:
Empirische Nachweise untermauert durch Szenariosimulationen**

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Keywords: Eco-physiological modeling; size-symmetry; competi-
tion; Norway spruce; European beech

Schlagwörter: Ökophysiologische Modellierung, Größensymmetrie,
Konkurrenz, Fichte, Buche

Abstract

The focus of this study is on the resource and growth distribution between trees in forest stands and the dependency of this distribution on site conditions. Growth distribution patterns of forests, empirically revealed and modeled on stand level, still lack of a causal explanation. Therefore, a physiological individual tree growth model was applied in order to explain recently published general growth distribution patterns. Our study focuses on Nor-

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way spruce (*Picea abies* (L.) H. KARST) and European beech (*Fagus sylvatica* L.). This way, simulation results of the physiologically based growth model were compared to empirically found principles of resource allocation. The results of the scenario analyses suggest that the degree of size-symmetry increases with the trees' limiting factors, light and water. Size-symmetric competition and growth was found on poor sites whilst size-asymmetric behavior is dominant on more fertile sites. Synergies made by combining empirical research and model based hypothesis testing are discussed. The study also reflects that the use of physiologically based growth models can contribute to a better understanding of stand dynamics. Consequently, biological causalities based on the analysis of model simulations can support empirical findings.

Zusammenfassung

Das Ziel dieser Studie war es, die Wachstums- und Ressourcenverteilung von Bäumen in Waldbeständen sowie die Abhängigkeit dieser Verteilung von den Standortbedingungen zu analysieren. Empirisch gefundene Muster der Zuwachsverteilung zwischen den Bäumen in Wäldern können zwar auf Bestandesebene hochgerechnet werden, es fehlen jedoch kausale Erklärungen. Mit einem physiologischen Einzelbaumwachstumsmodell wurden deshalb Szenariosimulationen durchgeführt, um die Hintergründe der Verteilungsmuster zu eruieren. Die Studie war dabei auf die Baumarten Fichte (*Picea abies* (L.) H. KARST) und Buche (*Fagus sylvatica* L.) fokussiert. Somit konnten Simulationsergebnisse auf Basis eines physiologisch basierten Modells mit empirisch gefundenen Prinzipien der Ressourcen- und Zuwachsallokation verglichen werden. Sie zeigen, dass der Grad der Größensymmetrie mit den limitierenden Faktoren des Baumwachstums wie beispielsweise Licht oder Wasser zunimmt. Größensymmetrische Konkurrenz und Zuwachsallokation ergeben sich an ressourcenarmen Standorten, während größenasymmetrisches Verhalten eher an ressourcenreichen Standorten anzutreffen ist. Die Studie zeigt, wie physiologisch basierte Wachstumsmodelle einen Beitrag leisten, das Wissen zur Bestandesdynamik von Wäldern zu vergrößern. Synergien aufgrund der Kombination von empirischer Forschung und Modellbasierten Hypothesentests werden diskutiert. Es wird gezeigt, wie Modellsimulationen empirisch gefundene Muster ursächlich erklären und so zur Aufdeckung von Gesetzmäßigkeiten beitragen können.

1 Introduction

The question whether tall dominant or small understoried trees in a stand are more affected by stress and how this size-dependent stress reaction is modified by site conditions are essential for the understanding and management of stand dynamics. This is even more relevant when considering the threat of climate change. Stress, regardless of the cause e.g. competition, drought or ozone, seems to have more of a negative impact on the growth rate of tall trees when compared to the growth of their smaller neighbors (Pretzsch and Dieler 2011). Insight into such patterns is of particular interest because tree growth and stand dynamics are increasingly affected by trends of changing growing conditions (Spiecker et al. 1996, Binkley et al. 2013) and stress events (Sandermann 2003, Jentsch et al. 2007, Matyssek et al. 2010). The effects of site fertility, disturbances and stress events on an individual tree as well as on stand growth have been the subject of many empirical analyses (Schweingruber et al. 1986, Röhle 1987, Forrester et al. 2013) and were summarized (Pretzsch 1999) and predicted by models (Bugmann et al. 1997, Pretzsch et al. 2008, Rötzer et al. 2009). The effects on an individual tree vary from growth acceleration (Pretzsch 1999) to a gradual decrease in vitality, caused by long-term deposition (Elling 1993), abrupt growth losses (Utschig 1989) and even dieback (Röhle 1987). As a result, numerous investigations have contributed to a better understanding of the effects of stress on tree or stand growth. However, how stress affects the resource and growth distributions between trees of a cohort or stand is still open for debate.

The absolute growth rate of a tree in a defined period, such as one year, plotted against plant size at the beginning of the respective period can result in different patterns of growth allocation, representing different modes of competition between trees. Fig. 1 displays a set of linear (Lines 1, 3, 4, and 5) and non-linear (Lines 2, 6) growth-size relationships (Weiner 1990). A steeper slope indicates a stronger concentration of growth rates and resources on tall trees in the stand. When all trees are provided with the same resource budget and have equal growth rates independent of their size, this is widely referred to as perfect symmetry. When the trees' resource supply and growth rate are not equal but proportional to their size, this is usually called perfect size symmetry (Weiner 1990, Schwinning and Weiner 1998). Distribution patterns where resources and growth are more or less concentrated on a subset of trees represent asymmetry. When the distribution pattern is non-proportional to size this is referred to as size asymmetry. Perfect size asymmetry, indicated by a line parallel to the y-axis (slope = ∞ ; a sub-cohort of large plants receives all growth), is rare to observe and not integrated in Fig. 1a. Note that all relationships in Fig. 1a are linear. Howe-

ver, only line 4 represents a linear and proportional increase of the absolute growth rate with increasing size, meaning that only in this case the relative growth rate is equal for all individuals.

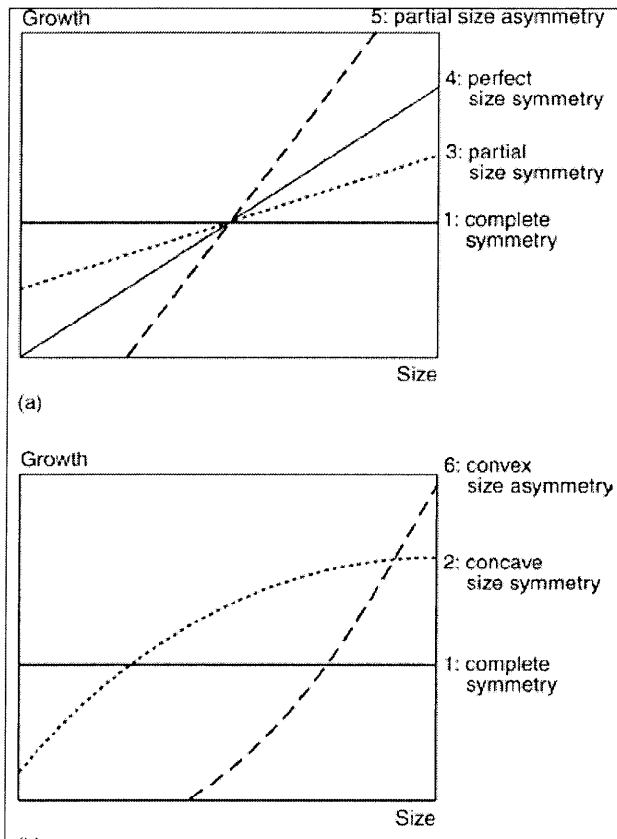


Fig. 1: Hypotheses based on the relationship between plant size and absolute growth rate. Linear (a) and nonlinear (b) relationships between size and growth: Line 1 represents the more theoretical case of perfect symmetric size-growth relationship where all plants receive the same budget of growth irrespective of size. Line 2 displays nonlinear concave size symmetry where growth increases less degressively with size. Line 3 reflects partial size symmetry where growth increases linearly with size. Line 4 represents perfect size symmetry and means that growth increases proportionally with size. Line 5 represents partial size asymmetry where growth increases linearly with size. Line 6 represents nonlinear convex size asymmetry as growth increases progressively with size.

Fig. 1: Hypothesen basierend auf den Zusammenhang zwischen Pflanzendimension und absoluter Wachstumsrate. Lineare (a) und nicht lineare (b) Zusammenhänge zwischen Dimension und Wachstum: Linie 1 stellt den mehr theoretischen Fall eines vollkommenen symmetrischen Größen-Wachstumszusammenhangs dar, in dem alle Pflanzen unabhängig von ihrer Größe das gleiche Wachstum besitzen. Linie 2 zeigt eine nicht lineare konkave Größensymmetrie, bei der das Wachstum mit zunehmender Größe degressiv ansteigt. Linie 3 gibt eine teilweise Größensymmetrie wieder, in der das Wachstum linear mit

der Größe steigt. Eine vollkommene Größensymmetrie zeigt Linie 4, d.h. dass das Wachstum proportional mit der Größe zunimmt. Linie 5 repräsentiert eine teilweise Größenasymmetrie mit linearem Anstieg des Wachstums mit der Größe, während Linie 6 eine nicht lineare konvexe Größenasymmetrie angibt, in der das Wachstum progressiv mit der Größe zunimmt.

Perfect symmetry (Fig. 1, line 1) would suggest that growth and resources, which competitors receive, are independent of their size. Tendency towards perfect symmetry (line 1) or partial size symmetry (Fig. 1a line 3) is assumed to dominate under conditions where below-ground resources (water and mineral nutrients) are limited. This is because they are mobile, diffuse quickly and are difficult to intercept by larger individuals (Kuijk et al. 2008). Partial size asymmetry or convex size asymmetry (Fig. 1a, line 5; Fig. 1b, line 6) means that larger individuals obtain a disproportionately high share of resources and growth. This type of growth-size relationship can be expected on high quality sites where light is the limiting factor and as a vector resource, is obstructed by the larger individuals (Weiner and Thomas 1986, Cannell and Grace 1993).

Under *ceteris paribus* conditions, the dominant trees on fertile sites can make more use of their advantageous position and exert a more negative effect on their neighbors' growth (Wichmann 2001, Wichmann 2002). This is reflected by steeper growth-size slopes. In contrast, when nutrients are a limiting factor the dominance of tall trees and the slope of the growth-size relationship are reduced. Pretzsch and Biber (2010), Pretzsch and Dieler (2011) and Pretzsch et al. (2012) found that low stress increases the steepness and size-asymmetry of the growth-size relationship, i.e. conditions favor the superiority of tall trees to the detriment of the smaller trees. High stress, no matter whether induced by competition, drought or ozone, distinctly reduces the superior growth rate of tall trees. The relatively clear growth reduction of tall, dominant trees in relation to small, overtopped trees in a stand in declining growing conditions appears to have an overarching reaction pattern (Fig. 2).

In order to derive the inter-individual growth-size relationships theoretical growth-size-relationships of an individual which can be expected without any stress are important (Fig. 3). In the juvenile phase of trees anabolism has the upper hand and drives growth exponentially. However, when combined with size growth, the respiration increases. The size-dependent interplay between respiration and assimilation affects the peak growth rate at medium size and a tapering off at maximum size (Assmann 1970, Zeide 1993).

Therefore, open-grown trees follow a unimodal growth-size trajectory which comprises convex (seen from below) curve sections in the juvenile

phase (1-3), concave sections in the middle age (4-6) and again convex sections in the mature phase (7-9) (Avery and Burkhart 1983, Schütz 1989). The better the site fertility, the higher the growth rates of a given plant size due to the better resource supply per plant (e.g. Campoe et al. 2013). This causes minimal change to the unimodal shape of the curve but increases its level. In contrast, on poor sites the level of the unimodal growth-size-curve lies on a much lower level due to the scarce resource supply per plant (Pretzsch and Biber 2010). Such potential growth curves can be derived from a long-term survey (real time series) or chronosequences (artificial time series) of trees grown under solitary conditions.

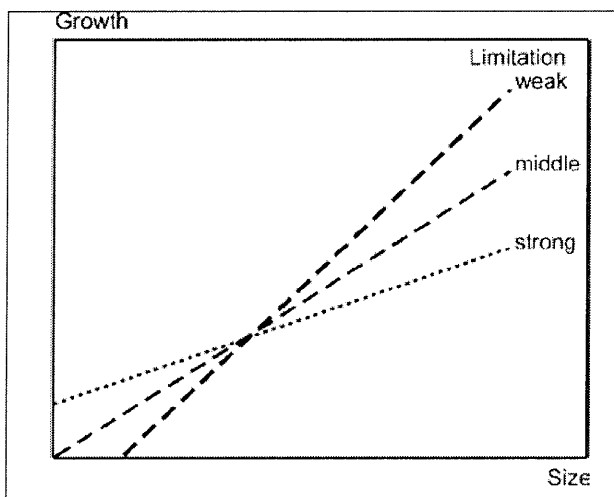


Fig. 2: A schematic representation of the effect of environmental conditions on the relationship between size and growth of trees in forest stands.

Fig. 2: Schematische Darstellung des Einflusses von Umweltbedingungen auf den Zusammenhang zwischen Baumdimension und Baumwachstum in Waldbeständen.

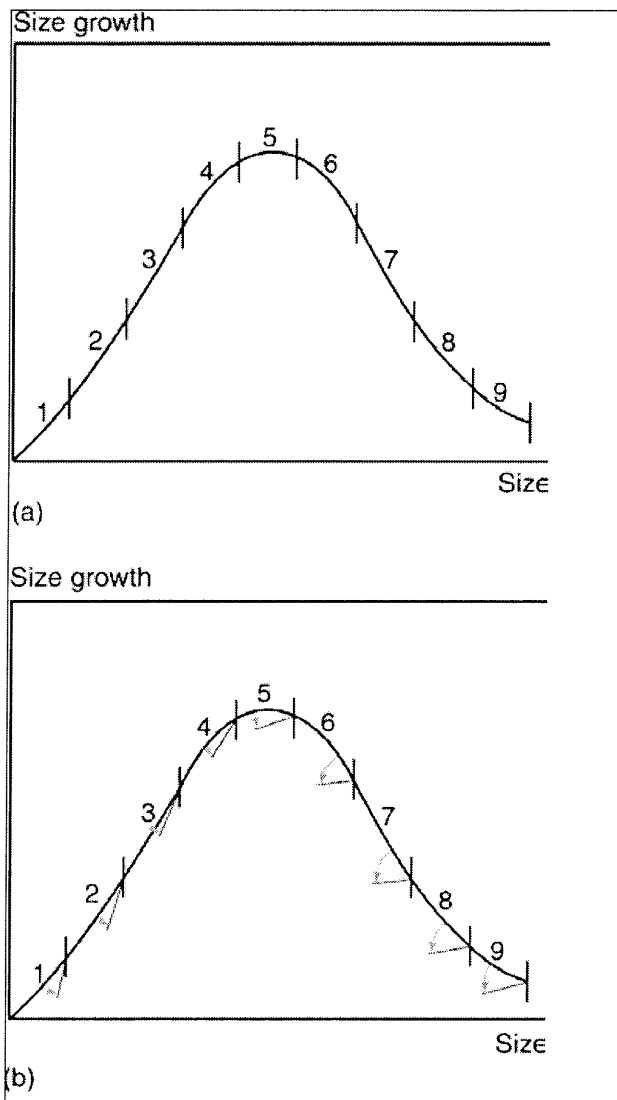


Fig. 3: Relationship between size and growth (a) without competition effect and (b) with an modification of this relationship by competition in a schematic representation. (a) Potential size-growth trajectory of an open-growing individual tree: Without competition growth is dependent on size, consisting of convex (segments 1-3 and 7-9) and concave (segments 4-6) parts. (b) Unimodal individual growth curve and linear interindividual size-growth relationships: The relationship between size and growth without competition effect (black line) and growth reduction due to competition (arrows) is represented. This growth reduction by competition results in linear size-growth relationships with steep positive slopes in early stand phase and increasingly flatter slopes with progressive stand development (segments 1-9).

Fig. 3: Schematische Darstellung des Zusammenhangs zwischen Größe und Wachstum (a) ohne Konkurrenzeffekt und (b) nach Modifizierung durch Konkurrenz. (a) Potentielle Größen-Wachstums Trajektorien eines frei stehenden Baumes: Ohne Konkurrenz ist das Wachstum von der Größe abhängig mit konvexen (Segmente 1-3 und 7-9) und

konkaven (Segmente 4-6) Anteilen. (b) Individuelle unimodale Wachstumskurve und lineare interindividuelle Größen-Wachstumsbeziehungen: Dargestellt ist der Zusammenhang zwischen Dimension und Wachstum ohne Konkurrenz (schwarze Kurve) und Wachstumsreduktion aufgrund von Konkurrenz (Pfeile). Die Wachstumsreduktion durch Konkurrenz resultiert aus linearen Größen-Wachstumsbeziehungen mit steilen positiven Anstiegen in der frühen Bestandesphase und zunehmend flacheren Anstiegen mit fortschreitender Bestandesentwicklung (Segmente 1-9).

When growing solitarily the tree size largely determines the plant's growth-size trajectory. However, within a stand individuals can fall below this trajectory, especially those trees coping with crowding or stress. As a result, trees within a stand are likely to have limited access to resources, in particular to light. In most instances, the taller a tree, the more improved access to resources, space occupation and repression effect on neighbours (Biging and Dobbertin 1995, Pretzsch 2009, Campoe et al. 2013). However, increased size can also mean higher susceptibility to wind throw (Valinger et al. 1993, Peltola 2006), drought (Condit et al. 1995, Skov et al. 2004) and attacks of bark beetles as *Ips typographus* L. and *Pityogenes chalcographus* L. (Coggins et al. 2010). In temperate forests with light as a limiting factor for individual tree growth, taller trees provide shade and thus reduce growth of their smaller neighbors. In a cohort of even-aged trees, growth of smaller trees falls behind the taller ones. Subsequently, the smaller trees fall increasingly below their potential when compared with that of their fitter neighbors. This size-dependent growth reduction is behind the phenomenon which forest scientists refer to as diameter increment-diameter line (id-d line). It is often used to describe and model the inter-individual growth-size relationship of even-aged stands in a given developmental phase or period of time (e. g. Prodan 1965, pp. 474-476). While Fig. 3a shows the potential growth-size trajectory of an individual tree, Fig. 3b shows schematically how competition can transform the unimodal curve to linear inter-individual growth-size relationships. The black curve represents the reference trajectory assumed for solitary growth without competition (see Fig. 3a) and the segments of the thin straight lines represent how interindividual competition for resources modifies the growth in a stand compared with solitary conditions.

Diameter growth plotted against diameter (or volume growth versus volume) for the trees of an even-aged cohort in a given period of time yields a straight line with a steep positive slope in early stand phases and an increasingly flatter slope with progressive stand development (Fig. 3b segments 1-9).

This study refers to this slope of the linear relationship between growth and size of a cohort in a given period of time as "slope of the inter-indi-

vidual growth-size relationship". It builds on recently published empirical findings analyzing the relationship between the growth and the size of trees in forest stands and the dependency of this growth-size-relationship on site conditions and stress (Pretzsch and Biber 2010, Pretzsch and Dieker 2011, Pretzsch et al. 2012). Based on these relationships the framework of size-asymmetry of competition -formulated by Schwinning and Weiner (1998) - was applied. These specific growth distribution patterns, empirically revealed and modeled at stand level still lack a causal explanation in this series of publications mostly because of missing information about the environmental factors at the original long-term experimental plots.

In this study empirically evident growth distribution patterns were combined with simulations of the physiological individual tree growth model BALANCE, which has been evaluated and validated extensively in the past (Rötzer et al. 2004, 2005, 2009, 2010). It is used to explain individual tree growth-size-relationship patterns found at stand level and to show how physiologically based individual tree growth models can contribute to improve the mechanistic understanding of pattern occurring at cohort and stand level. The study aims at a model application to better understand patterns and processes in ecosystems as discussed by Grimm (1999), but not on the application of a special growth model as BALANCE. For details about growth model, its reasonability, reliability, and evaluation see the works by Rötzer et al. listed in the references.

The study is focused on Norway spruce (*Picea abies* (L.) H. KARST) and European beech (*Fagus sylvatica* L.) and proves how models can be used to aid a deeper understanding of stand dynamics. It also highlights that the analysis of empirical findings at stand level can contribute to the examining of the biological plausibility of model predictions which are derived from individual plant or even organ level. The main questions are:

1. Do growth distribution patterns - uncovered at stand level - correspond with model predictions derived by the patterns from the individual level up to stand level?
2. Does scenario analysis with the use of an eco-physiological growth model show that the degree of size-symmetry and size-asymmetry of resource and growth distribution depend on the trees' limitation of light and water?
3. Can individually calculated water and light distribution be used to provide causal explanations regarding the dependencies of the growth and resource allocation between the differently sized trees in forest stands?

Finally, the benefits and the limitations of using mechanistic models for hypothesis testing in ecology, particularly with respect to patterns and processes which result from feedback reactions on varying scales were discussed.

2 Data and methods

2.1 Site description

The site 'Kranzberger Forst' provided the basic data for the scenario simulations. It is located in southern Germany, about 40 km northeast of Munich (latitude: 48.420° N, longitude: 11.662° E, elevation: 490 m a.s.l.). The soil at the 'Kranzberger Forst' consists of 60 % silt, 20 % clay and 20 % sand within the upper 100 cm, while below 100 cm the proportion of sand increases to 80 %. The soil is referred to as a Luvisol, derived from loess over tertiary sediments, which has both a good water and nutrient supply. For this study, the soil was classified in the four layers 0-5 cm, 5-35 cm, 35-85 cm and 85-100 cm, with field capacities and wilting points of 49, 37, 37 and 37 % by volume respectively 11, 8, 10 and 23 % by volume. The maximum rooting depth amounts to 1.0 m. For a detailed characterization of the soil see Schuhbäck (2004).

For the scenario simulations two virtual stands one of Norway spruce (*Picea abies* (L.) H. KARST) and one of European beech (*Fagus sylvatica* (L.) with plot sizes of 30 m x 30 m each were initialized as hypothetical examples using the STRUGEN simulator (Pretzsch 1997) (Tab. 1). The initial diameter at breast height *dbh* of the beech stand ranged from 5.4 cm up to 15.5 cm with heights between 11.6 m and 18.7 m. The corresponding values of the spruce stand are between 7.0 cm and 25.3 cm for the *dbh* respectively 9.4 m and 17.3 m for the height. In both stands a broad variety of tree sizes are represented allowing the analysis of the growth of small and tall trees within the single stands of spruce and beech.

Tab. 1: Initial characteristics of the two virtual forest stands used for the simulations.

Tab. 1: Initiale Kennwerte der zwei für die Simulationen genutzten virtuellen Waldbestände.

site		beech	spruce
n/ha		2806	2399
dbh (cm)	mean	9.3	12.5
	max	15.5	25.3
	min	5.4	7.0
height (m)	mean	15.3	13.0
	max	18.7	17.3
	min	11.6	9.4
crown length (m)	mean	7.2	4.9
	max	9.1	8.5
	min	5.2	2.7
basal area (m ² /ha)		20.1	31.8

The scenario simulations were carried out over a 10 year period. On average the annual air temperature was 8.3 °C with temperature extremes in the years 2002 with 8.9 °C and 2001 respectively 2005 with 7.7 °C (Fig. 4).

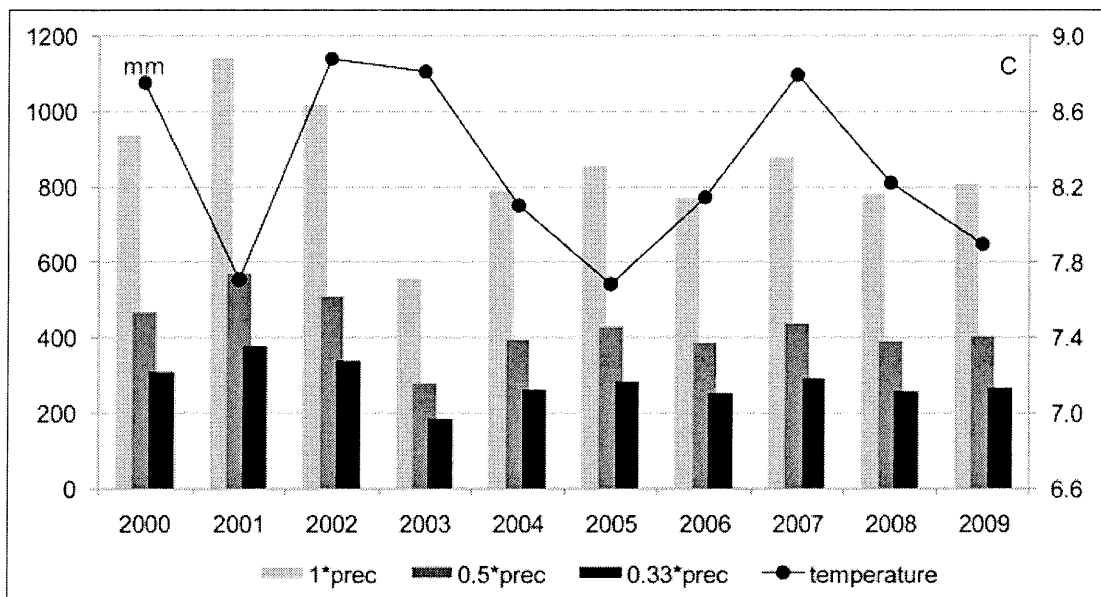


Fig. 4: Annual mean air temperature and measured precipitation sums (=1*prec) resp. changed precipitation amounts (0.5*prec and 0.33*prec) for the study site from 2000 to 2009.

*Fig. 4: Jahresmittelwerte der Lufttemperatur und der gemessenen Niederschlagssumme (=1*prec) bzw. der veränderten Niederschlagsregime (0.5*prec und 0.33*prec) am Untersuchungsstandort über die Jahre 2000 bis 2009.*

Annual precipitation sums of the years 2000 - 2009 range from 558 mm in 2003 to 1142 mm in 2001. Averaged over the entire period, yearly precipitation amounted to 854 mm ($=1 \cdot \text{prec}$). In the second scenario, precipitation was reduced by 50 % ($=0.5 \cdot \text{prec}$). Consequently, the mean precipitation sum decreased to a mean value of 427 mm. In the $0.33 \cdot \text{prec}$ scenario precipitation was reduced to 33 % based on the measured values. Thus, the average over 10 year was 282 mm.

2.2 Eco-physiological modeling

In order to simulate spatially explicit forest growth and to consider the effects of climate change, the individual and process based growth model BALANCE was used. In this chapter, only a general overview of the model can be given emphasizing processes which are fundamental to this study. A comprehensive description of the model BALANCE can be obtained from Grote and Pretzsch (2002) or from Rötzer et al. (2005, 2009, 2010).

The growth model BALANCE was applied in order to find explanations at tree level for growth-size-relationships found at stand level. Within this study we do not validate the model. Validations of the model BALANCE have already been extensively carried out for basic micro-meteorological and physiological processes like light distribution or photosynthesis (Rötzer 2006, Rötzer et al. 2010), water balance (Grote and Pretzsch 2002, Rötzer et al. 2005, 2010), annual development (Rötzer et al. 2004, 2005, 2010) and stand development (Rötzer et al. 2005). At the site Kranzberger Forst, simulated parameter values of tree segments and compartments of tree individuals and the entire stand were compared to measured values (Grote and Pretzsch 2002, Rötzer et al. 2010). Additionally, validations have also been carried out for other Central European forest stands (Rötzer et al. 2004, 2005, Liao 2011).

Model Structure

The eco-physiological growth model BALANCE is able to calculate the 3-dimensional development of trees and forest stands in dependence on their environmental conditions. Growth is simulated at the individual tree level. As tree development is calculated as a response to individual environmental conditions and environmental conditions change with individual tree development, the influence of competition, stand structure, species mixture and management impacts can be taken into account (Fig. 5).

A tree's initial biomass is calculated from the dimensional group of variables: tree position, tree and crown base height, diameter and crown radii.

Biomass increase is the result of the interaction between physiological processes which are dependent on the physical and chemical micro-environment. The latter is in turn influenced by the spatial structure of the stand. An increase in biomass is simulated on the base of the carbon and nitrogen that is taken up from each segment, dependent on the energy supply and resource availability. Stress conditions are measured by the change of the specific below and above ground uptake rates.

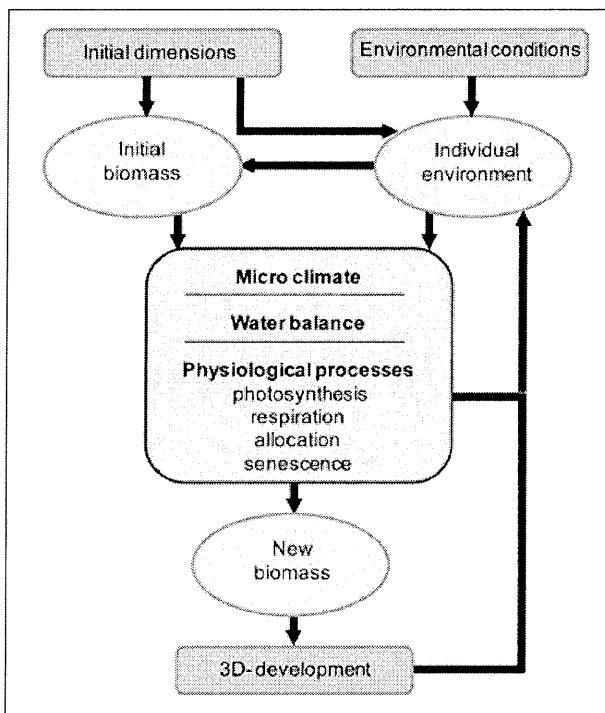


Fig. 5: The eco-physiological growth model BALANCE.

Fig. 5: Das ökophysiologische Wachstumsmodell BALANCE.

BALANCE takes the variability of crown shape into account and generates a spatially explicit representation of the environment. The calculation levels vary from stand level to individual trees, from tree compartments (i.e. foliage, branches, stem, fine and coarse roots) to crown and root layers of equal but adjustable thickness (for this study: 0.5 m). The horizontal extensions are based on the crown radii in eight directions, the relative height within the crown, and the crown length (or depth within the soil and total rooting depth). Crown and root layers are again vertically and horizontally divided into eight segments (Grote and Pretzsch 2002).

By using weather data, the microclimate and water balance are calculated for each layer respectively segment. Thus, the spatial distributions of the light and water availability are both estimated for every day within the simulation period. Based on the aggregated driving variables, all physiological processes i.e. assimilation, respiration, nutrient uptake, growth, senescence and allocation, are calculated in 10 day time steps. This way, the individual carbon, water and nutrient balances of the tree species beech, oak, spruce, pine and Douglas fir can be simulated.

Annual phenological development

The temporal and spatial development of foliage defines the relationships between environmental influences and growth i.e. with the beginning of bud burst foliage, biomass and leaf area as well as light availability and radiation absorption change. Thus, not only does the date of foliage emergence of a tree determine its assimilation and respiration rate but also alters the environmental conditions in a tree's immediate surrounding area. In BALANCE, the beginning of bud burst is modeled by using a temperature sum model (Rötzer et al. 2004), whilst foliage senescence estimations are dependent on the respiration sum (Rötzer et al. 2010).

Water Balance

Calculating evapotranspiration based on the Penman-Monteith approach (e.g. DVWK 1996) provides key information which allows the water balance simulation of a tree. Based on air temperature, radiation, air humidity and wind speed, potential evapotranspiration etp can be calculated by

$$etp = 1/L * [(s * r_{net} + \delta_{air} * c_p * vpd/r_a) / (s + p * (1 + r_c/r_a))] \quad \text{Eq. 1}$$

(L=specific vaporization heat of water in $W m^{-2}$, s=slope of the saturation curve for vapor pressure deficit in $hPa K^{-1}$, r_{net} =net radiation in $W m^{-2}$, δ_{air} =air density = $1.202 kg m^{-3}$ [$20^{\circ}C$], c_p =heat capacity of the air = $1005 J kg^{-1} K^{-1}$, vpd=vapor pressure deficit in hPa, r_a =boundary layer resistance in $m s^{-1}$, r_c =canopy resistance in $m s^{-1}$, p =psychrometer constant = $0.662 hPa K^{-1}$).

Boundary layer resistance r_a is a function of stand height and wind speed. Canopy resistance r_c is calculated based on the leaf area index and the species specific maximum conductivity for water. Actual evapotranspiration is estimated using the potential evapotranspiration and the maximum water uptake, which is derived from the water content within the soil volume that contains fine roots. Using the daily actual evapotranspiration sum along with the precipitation, the interception and the daily percolation,

the change in the soil water content can be calculated. A simple multi-layer bucket soil water model with a fixed layer width represents vertical water flows whilst horizontal flows between the rooted and non rooted fractions in each layer are examined. The water within the rooted fractions is used to fulfill the tree's transpiration requirements. At the end of each day, the soil water content within rooted and non rooted fractions is equalized. Interception is estimated for crown covered areas as a function of leaf area, species specific interception capacity and actual interception storage. Via stomatal closure the water balance of a tree is linked with the nutrient and carbon cycles.

Nutrient cycle

Nutrient uptake is the result of the minimum demand, supply and absorption capacity (Grote 1998). Initially, only the nitrogen cycle, as the most important nutrient, is taken into account. The demand is based on the difference between the actual nitrogen concentration and a given optimal concentration. The supply however, is defined by the soil characteristics of the rooted volume, the uptake capacity by the root surface and its specific absorption rate. For the purposes of this study, the soil water and nutrient status of the trees were assumed to be at their optimum at the beginning of the simulations.

Photosynthesis and respiration

Physiological processes are calculated in 10 day time steps using results from the daily environmental conditions (e.g. radiation, temperature). By using the simulation routine suggested by Haxeltine and Prentice (1996), assimilation is estimated as a function of leaf area, light, temperature and CO₂-concentration. The internal CO₂ supply depends on the stomata conductivity which is a non linear function of the soil water supply. Therefore, photosynthesis can be reduced by lack of water as well as altered by the nutrient supply and pollutants. The fixed carbon that is not needed for respiration is used for the distribution into the plant compartments foliage, branches, stem and roots depending on their relative sink strength (Grote 1998).

For photosynthesis calculations, the radiation amount which a segment receives in a time step is an essential factor. To estimate this sum a 'competition-cone' is placed over each segment and all segments within the cone are counted and weighed according to their leaf area. This calculation of the relative light consumption was derived from the competition algorithm of the growth simulator SILVA (Pretzsch 1992) and extended by a light extinction function of a Lambert-Beer type. The search cone used to estimate

competition is separately calculated for each single crown segment. Consequently, light intensity of each segment is obtained based on the global radiation, the extinction coefficient of foliage and the competition factor of the segment.

Total respiration is the sum of maintenance losses and growth respiration. Therefore, maintenance respiration is calculated separately for each segment and compartment as a function of biomass, specific respiration rate and temperature. Growth respiration however, is estimated as a constant fraction of the maximum photosynthesis (Penning de Vries et al. 1989).

Allocation and biomass increment

The carbon available for allocation (=photosynthesis – total respiration) is distributed into the different compartments according to their growth and respiration demands (Grote 1998). They are defined by the relationships between the compartments according to the functional carbon balance theory (Mäkela 1990) and the pipe model theory (Shinozaki et al. 1964, Chiba 1998). Consequently, all compartments of a segment i.e. foliage and branches or fine roots and coarse roots, as well as the amount of stem wood are mechanistically linked to each other. As a result, specific leaf area as well as leaf area density depend on the individual competition situation of the segment. Similarly to the functional balance theory, the nitrogen that is taken up is distributed across the compartments according to the estimated demand from the optimum concentrations.

Therefore, an increase in biomass is the result of the interaction between physiological processes which depend on the physical and chemical micro-environment that is itself influenced by the stand structure. It is calculated on the basis of the amount of carbon that is taken up from each segment. The proportion is dependent on the local energy supply (light, temperature) and resource availability (CO₂ concentration, nitrogen availability). Stress conditions like restricted water availability can decrease the uptake rates below and above ground.

3-dimensional tree growth (height, diameter at breast height, etc.) is calculated at the end of every year, on the basis of the increase in accumulation of biomass during that year. The increase in the proportion of biomass that every crown respectively root segment receives is defined by its relative contribution to the net carbon and nitrogen increase. The volume expansion depends on the necessary amount of twigs and transport branches, respectively on the amount of coarse roots within the root segments. Therefore, crown development is preferred in the direction towards the best assimila-

tion conditions during the previous year. If net assimilation rates are negative, the crown segment is regarded as dead. If no segments contain living biomass, the tree is assumed to be dead and removed from calculations.

2.3 Calculation of efficiencies

Based on outputs of BALANCE the water use efficiency wue as well as the light use efficiency lue can be calculated. A tree's wue is defined as the ratio between the trees' annual net primary productivity npp and the annual sum of actual evapotranspiration and lue as npp divided by the amount of radiation a tree received within a year.

3 Results

Individual tree growth in the beech and spruce stand was simulated for the 10 year period using the above described site conditions and the three different precipitation regimes. In Fig. 6 and Fig. 7, the mean annual net primary productivity for the three precipitation regimes is presented depending on tree size (=dbh). Both npp and dbh denote the averages of the simulation period.

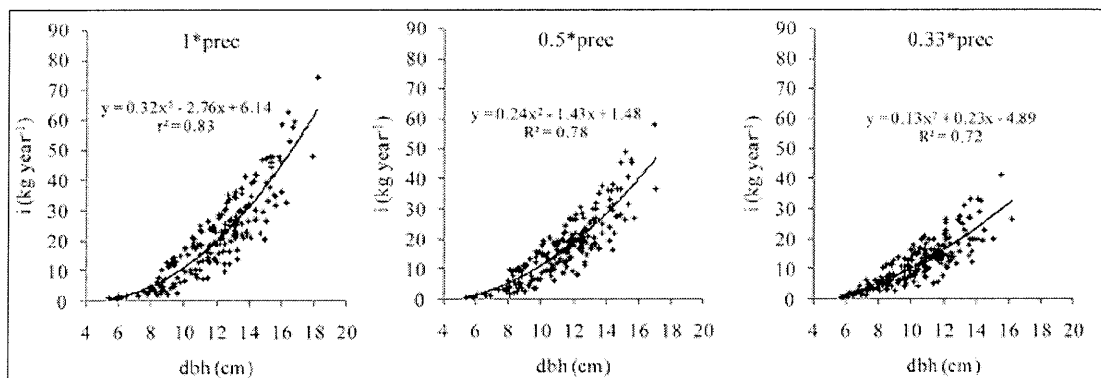


Fig. 6: NPP increment of beech dependent on tree size (dbh) under different precipitation regimes averaged over 10 years.

Fig. 6: Zunahme der NPP von Buche in Abhängigkeit der Baumgröße (dbh) unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

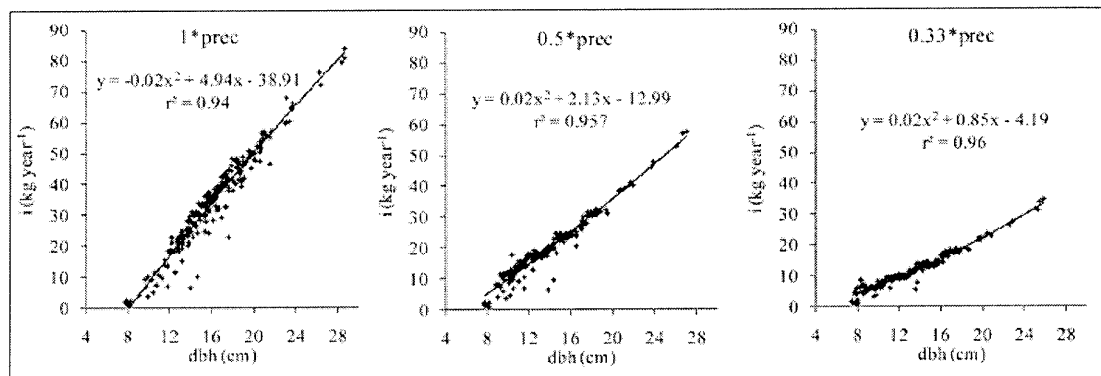


Fig. 7: *NPP* increment of spruce dependent on the tree size (*dbh*) under different precipitation regimes averaged over 10 years.

Fig. 7: Zunahme der *NPP* von Fichte in Abhängigkeit der Baumgröße (*dbh*) unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

It is evident that beech trees and in particular, spruce trees responded with decreasing *npp* increments when the water supply was limited. This was primarily based on the seasonal distribution of the plant water supply which was at its minimum in the summer months i.e. in the main growing season. Furthermore, this limitation was more pronounced in years when summer precipitation was low e.g. in the year 2003. In addition, water availability of the individual trees and with it *npp* clearly decreased between scenario 1*prec to scenario 0.33*prec.

Small beech trees react in the same way under the three different precipitation regimes i.e. there were no or only very small differences in the net primary productivity. The taller the trees the more marked was their decrease in *npp*. The slope of the growth-size relationship was steeper the more the precipitation sum increased (Fig. 6). The same pattern can be seen for the spruce trees (Fig. 7). The slope of the regression line, however, was more pronounced. Thus, a more apparent response from the spruce trees compared to the beech trees on decreasing precipitation with increasing tree size is evident.

For closer analysis the trees were classified according to their size: small trees are defined as trees with *dbh* lower than 10 cm (beech) respectively 15 cm (spruce) and big trees are defined with a *dbh* higher than 10 cm (beech) respectively 15 cm (spruce). This revealed that the average *dbh* respectively height of the big trees ranged from 13.0 cm to 11.9 cm respectively 18.6 m to 17.6 m (Tab. 2) whilst the average of the small trees was between 8.0 cm and 8.3 cm respectively between 14.3 m and 15.0 m. The respective values for

both the big and the small spruce trees decreased with decreasing precipitation.

Tab. 2: Number, diameter and height of beeches (above) and spruces (below), classified into small and big trees, under different precipitation regimes on average over a 10 year period.

Tab. 2: Anzahl, Durchmesser und Höhe von Buchen (unten) und Fichten (oben), eingeteilt in kleine und große Bäume, unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

size	parameter	1*prec		0.5*prec		0.33*prec	
		mean	sa	mean	sa	mean	sa
all trees	n	200		200		200	
	dbh (cm)	11.6	2.8	11.1	2.5	10.4	2.2
	height (m)	17.5	2.3	17.1	2.0	16.5	1.6
big trees (dbh<10 cm)	n	147		139		116	
	dbh (cm)	13.0	1.8	12.4	1.6	11.9	1.3
	height (m)	18.6	1.1	18.1	0.9	17.6	0.7
small trees (dbh<10 cm)	n	53		61		84	
	dbh (cm)	8.0	1.6	8.2	1.4	8.3	1.2
	height (m)	14.3	2.1	14.7	1.7	15.0	1.2

size	parameter	1*prec		0.5*prec		0.33*prec	
		mean	sa	mean	sa	mean	sa
all trees	n	213		213		213	
	dbh (cm)	16.0	3.8	13.9	3.6	13.0	3.5
	height (m)	16.0	1.9	14.4	1.6	13.5	1.6
big trees (dbh<15 cm)	n	128		70		52	
	dbh (cm)	18.4	2.9	17.9	2.8	17.8	2.7
	height (m)	17.1	0.9	16.1	0.8	15.6	0.8
small trees (dbh<15 cm)	n	85		143		161	
	dbh (cm)	12.5	1.9	11.9	1.9	11.5	2.1
	height (m)	14.2	1.5	13.5	1.2	12.9	1.2

The annual mean npp of big trees declined significantly when precipitation is reduced (Fig. 8). Npp of big beech trees' npp was lowered from 25.9 kg year⁻¹ to 16.3 kg year⁻¹, which is equal to a reduction of 37 % (1*prec vs.

0.33*prec). The effect of the big spruce trees was more prominent with a reduction of 58 % from 43.6 kg year⁻¹ to 18.3 kg year⁻¹.

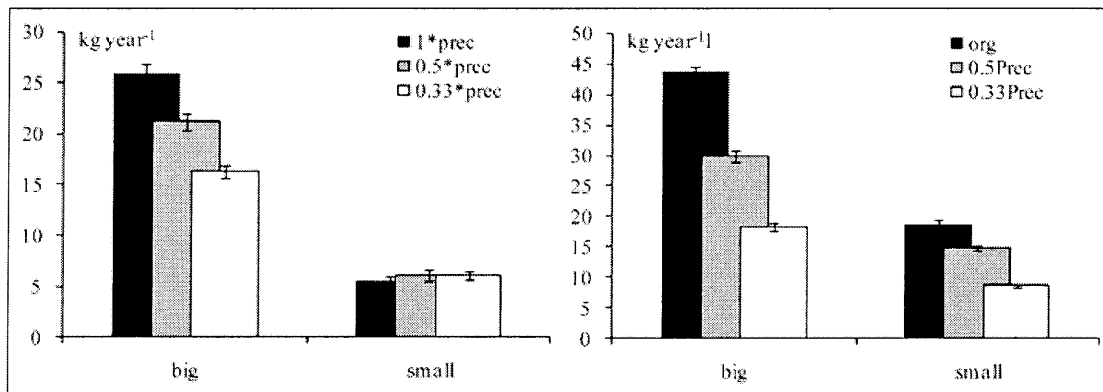


Fig. 8: *NPP* increment (mean and standard error) of beech (left) and spruce (right) for small and big trees under different precipitation regimes averaged over 10 years.

Fig. 8: Zunahme der *NPP* (Mittelwert und Standardfehler) von Buche (links) und Fichte (rechts) für kleine und große Bäume unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

No significant change of the annual mean *npp* was discernible for the small beech trees with an increase of 15 % (i.e. from 5.3 kg year⁻¹ to 6.1 kg year⁻¹). The productivity of the small spruce trees decreased by 53 % from 18.4 kg year⁻¹ to 8.7 kg year⁻¹. Consequently, the response to increasing drought is clearly stronger for big trees compared to the small trees. The reasons for the changes in the productivity can be explained by the resource supply of the different sized plants. In Fig. 9, the trees' supply with water represented by their actual evapotranspiration sum is presented.

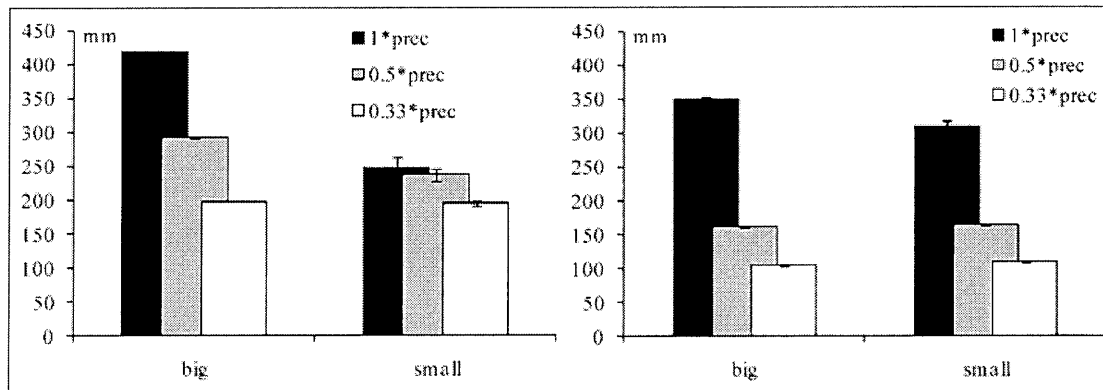


Fig. 9: Actual evapotranspiration within the growing season (mean and standard error) of beech (left) and spruce (right) for small and big trees under different precipitation regimes averaged over the 10 year period.

Fig. 9: Tatsächliche Verdunstung während der Vegetationszeit (Mittelwert und Standardfehler) von Buche (links) und Fichte (rechts) für kleine und große Bäume unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

E_{t_a} of beech clearly declined with decreasing precipitation. This relationship was much more evident for big trees. Under the 0.33*prec scenario which assumes drought stress, actual evapotranspiration for both the big and the small beech trees was approximately equal (198 mm respectively 196 mm). With regards to both big and small spruce trees, a clear decrease in the evapotranspiration values from 1*prec to 0.5*prec and 0.33*prec is evident. Whilst a clear difference of 43 mm in the actual evapotranspiration sum between the big and small trees under 1*prec (351 mm respectively 308 mm) is evident, the difference decreased to -3 mm and -5 mm for 0.5*prec and 0.33*prec denoting that the actual evapotranspiration of the small spruce trees was even higher than the e_{t_a} of the big spruces. It can therefore be concluded that for both spruce and beech trees under non stress conditions (=1*prec), big trees have higher actual evapotranspiration rates compared to small trees, whilst under strong drought stress conditions (0.33*prec), e_{t_a} of all sizes are equal or even higher for the smaller sizes.

Additionally to the below ground competition for water, the above ground competition for light is another prominent factor that influences tree growth. The 10 year average radiation regimes in the spruce as well as in the beech stand changed under the different precipitation scenarios (Fig. 10).

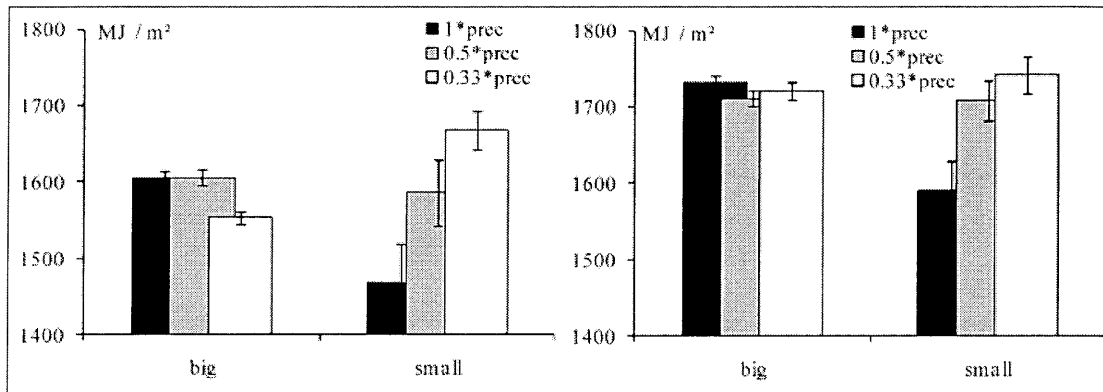


Fig. 10: Radiation amounts within the growing season (mean and standard error) of beech (left) and spruce (right) for small and big trees under different precipitation regimes averaged over the 10 year period.

Fig. 10: Strahlungssummen während der Vegetationszeit (Mittelwert und Standardfehler) von Buche (links) und Fichte (rechts) für kleine und große Bäume unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

The changes of the radiation amounts of the big trees of the spruce respectively the beech stand were only small and non significant (exception: beech under 0.33*prec). The radiation amount within the growing season ranged between 1554 MJ m⁻² and 1606 MJ m⁻² for beech and 1712 MJ m⁻² and 1733 MJ m⁻² for spruce. The radiation amount of the small trees however, clearly increased. Under 1*prec conditions, small beech trees received a radiation amount of 1468 MJ m⁻². Under drought stress conditions, it increased to 1668 MJ m⁻².

Small spruce trees perform in the same way. Under 1*prec conditions the radiation was 1590 MJ m⁻² whereas the radiation amount rose to 1741 MJ m⁻² under 0.33*prec conditions. Consequently, average radiation sums for small trees were enhanced under drought stress conditions.

4 Discussion

Growth distribution patterns, empirically revealed at stand level, still lack a causal explanation. The individual tree growth model BALANCE was applied in order to physiologically explain the general growth distribution patterns between the trees in a forest stand. Empirical observations suggest size-symmetric competition and growth on poor sites and more size-asymmetric patterns on rich sites (Fig. 1 to 3). Model simulations show that tree growth increases with size (see also Binkley et al. 2013) and that the degree

of size-symmetry increases with the trees' limitation of water and light (Fig. 6 to 10). Thus, we successfully revealed that physiologically based individual tree growth models can contribute to the understanding of stand dynamics and that empirical findings can contribute to the analysis of the biological plausibility of model behavior.

4.1 Empirical evidence

The increase in slope size reflects the resource supply and affects the structural diversity at stand level. As shown in Fig. 2, the increase in diameter or net primary productivity increases with tree size. The model simulations revealed the same results. As tree size increased, *npp* for both beech and spruce trees increased. Thus, empirically discovered growth distribution patterns at stand level correspond with predictions performed by the physiological based growth model BALANCE, bottom-up from the individual level (Fig. 6 and Fig. 7).

In the Fig. 6 and Fig. 7 (for individual trees) as well as in Fig. 8 (summarized for small and big trees) *npp* values depending on the competition for water were presented. The results of the simulations denote shallower slopes with increasing resource limitation (water) and are closely aligned with the empirical findings (Fig. 2 and Fig. 3). On sites with low precipitation sums representing poor sites, shallow slopes occurred, indicating adequate growth conditions for the small trees in the stand but less than adequate conditions for the big trees. However, on sites with high precipitation amounts representing rich sites, steep slopes indicate that dominant trees had better growing conditions whilst the small trees' conditions were unchanged. This is in agreement with the findings of Campoe et al. (2013) for an irrigated and fertilized loblolly pine plantation where the largest trees showed -compared to the smaller ones- higher growth rates, which were further intensified under conditions with better resource supply.

As water was the limiting factor, this restricted both competition and superiority of dominant trees. As a result, on poor sites with less water availability, the small sized understory trees grew proportionally to their size, whilst the growth of big sized dominant trees was limited.

4.2 Causal explanation of reaction patterns

To explain the increments between the variations in tree size in forest stands based on the resource supply, water and light consumption of small and big sized beech and spruce trees on average of the 10 year period was analyzed. A clear relationship was evident between the decreasing actu-

al evapotranspiration rates and the decreasing water supply. By reducing precipitation to 33 % big sized trees reduced their et_a to 47 % (beech) and 30 % (spruce) respectively, whilst et_a was decreased to only 79 % for small beech trees but to 36 % for small spruce trees (Fig. 9). This can explain the different reduction levels of npp , with distinct declines for big sized beech and spruce trees under drought stress, but minimal changes for small sized beech trees and small declines for the small sized spruce trees.

The mode of competition symmetry (size-asymmetry vs. size-symmetry) depends on the plant's ability to intercept resources. In other words, its ability to gain more from a directional or vector resource because the plant is closer to that resource and therefore able to use the resource before other (smaller or less plastic) neighbors use it.

The abundance of water is a crucial factor for a tree to persist and is becoming increasingly important in the context of climate change. For the future climate an increase in the number of droughts has been forecast, which are predicted to also increase in frequency and duration (Leuschner 2009, Allen et al. 2010). Whilst spruce trees are thought to react sensitively with an early stomatal closure upon increasing drought (isohydric reaction), beech trees are considered a more anisohydric species (Lyr et al. 1992). Furthermore, since root architecture varies greatly with tree species, the roots of different species occupy different soil zones. The root system of Norway spruces is rather shallow (e.g. Lyr et al. 1992, but see Puhe 2003), the beeches' roots, however, can grow much deeper (Rothe and Binkley 2001, Schmid 2002). These different strategies of above and below ground response to drought stress might change the slope of increment-size-relationship but not the mode of competition (Fig. 6 and Fig. 7). When comparing the two species analyzed in this study, the effects of drought stress on spruces were more pronounced. The npp of big sized spruces resulted in larger decreases compared to the big sized beeches. Small sized beeches, on the other hand, showed no reaction whilst the small sized spruces' npp clearly decreased (Fig. 8).

Along with the changes of the actual evapotranspiration amounts of the 10 year period, the annual npp rates adjusted to the new conditions which caused a change in the leaf biomass i.e. a lowering of the leaf area. Poorter et al. (2012) reported that whilst the root biomass fraction increases under severe drought stress, above ground biomass is reduced. This then leads to a change in light distribution within the stands (Fig. 10) which in turn, alters the npp . This feedback reaction was evident within this study and influenced the growth rates of the trees differently. Under high drought stress ($0.33 \cdot \text{prec}$), the radiation amount of the big sized beech and spruce trees

only slightly decreased to 97 % (beech), respectively to 99 % (spruce) when compared to the radiation regime with no drought stress (1*prec). Small sized beech and spruce trees however, received higher radiation amounts of 14 %, respectively of 10 %. These levels therefore aid the growth of small sized trees.

4.3 Backing of empirical results by model scenario analysis

There is mounting evidence to suggest that the competition for edaphic resources e.g. water, leads to size-symmetric growth, whilst light competition favours bigger trees according to Schwinning and Weiner (1998), Pretzsch and Biber (2010) or Pretzsch and Dieler (2011). This relationship is supported by our simulation results. Additionally, it was demonstrated that there are feedback reactions involved in a tree's competition for water and light which vary depending on the tree size. Changing one component e.g. the resource water, could alter other factors like light for which the trees compete.

Efficiencies are suitable indices which reflect the relationship between tree growth and the consumption of resources. If the efficiencies for water wue and light lue are calculated based on the npp and the et_a respectively the radiation amount (Tab. 3), an increase of wue with increasing drought stress was evident for the beech trees. The spruce trees' wue increased from 1*prec to 0.5*prec followed by a decrease from 0.5*prec to 0.33*prec. The drought stress of spruce trees under 0.33*prec was so high that npp decreased more than et_a . Under the 0.33*prec conditions, there were minimal changes in the wue for both the big and the small spruce trees compared with the 1*prec conditions. Conversely, beech trees' wue increased under 0.33*prec for 15 % (big trees) respectively 12 % (small trees). In summary, no change in the increase of the wue was present between big and small trees, when precipitation decreased.

On 10 year average, lue was reduced in all size classes of beech and spruce when drought stress increased. However, for the spruce trees lue declined independent of tree size (reduction of 33 % respectively 35 % based on the 1*prec values). For the beech trees the reduction was more evident for the big trees (58 %) compared with the small trees (79%). This matches well to the results described by Forrester et al. (2013) for *Eucalyptus nitens* or Campoe et al. (2013) for *Pinus taeda* that with increasing resource supply (fertilizing, irrigation, thinning) lue is enhanced.

Tab. 3: Water and light use efficiencies of big and small beech and spruce trees under different precipitation regimes on average over a 10 year period.

Tab. 3: Wasser- und Lichtnutzungseffizienz großer und kleiner Buchen und Fichten unter verschiedenen Niederschlagsregimen im Mittel über 10 Jahre.

efficiency	ressource supply	beech		spruce	
		big	small	big	small
wue (g C kg ⁻¹)	1*prec	8.5	6.9	7.4	6.6
	0.5*prec	9.6	7.5	8.5	7.8
	0.33*prec	9.8	7.7	7.4	6.4
lue (g C MJ ⁻¹)	1*prec	2.5	1.3	2.1	1.7
	0.5*prec	2.0	1.3	1.2	1.1
	0.33*prec	1.4	1.0	0.7	0.6

The scenario simulations of the model BALANCE produced realistic results for structured pure stands of beech and spruce. We were able to demonstrate that the use of a spatially specific, single tree based growth model which can simulate growth physiologically such as BALANCE, can help to analyze the effects of structured forest stands on competition, productivity and efficiency (Rötzer et al. 2010, Pretzsch et al. 2012). In instances where such a growth model is sensitive to climate and includes stress reaction algorithms (e.g. drought, ozone), it can be an effective tool for scenario analyses with respect to scientific hypothesis testing and practical decision support (Rötzer et al. 2005, Pretzsch et al. 2008, Rötzer et al. 2010). Potential uses include the study of effects on climate change and stress effects induced by pollutants (e.g. ozone). Additionally, growth, allocation changes and efficiencies of mixed forest stands can be compared to pure stands in order to substantiate empirical findings (e.g. Pretzsch and Dieler 2011, Forrester et al. 2010).

4.4 Implications for forest ecosystem management

The more morphologically plastic a species is, the better is their chance to utilize the resources. According to Helms (1998, p 137) crown plasticity means the extent to which a genotype varies in crown morphology in different environments. Beech for example is very plastic with regards to crown allometry and can densely close the canopy and shade the understory trees (Dieler and Pretzsch, 2013). Spruce, on the other hand, has a much lower crown plasticity and so is likely to be less able to intercept a resource. As

a result, the slope of the size-growth relationship is much steeper in the case of beech than in the case of spruce. The same can be assumed for the plasticity in the root-space: The more plastic the allometry, the better the ability of the species to hamper directional resources, thus making full use of the superior spatial position in canopy or root space. Pretzsch and Dieler (2011) ranked the Central European tree species with respect to their crown plasticity. They report that the plasticity of beech is clearly higher than that of spruce. According to this ranking, the ability for resource blocking (e.g. water) should be similar.

These assumptions are relevant to silvicultural treatment. Improved resource supply leads to a steeper slope in terms of the relationship between size and size growth. This change in slope will lead to a lower relative proportion of resources that the subdominant and understory trees can then utilize for growth. This means that the slope also reflects the structural diversity of a stand. Shallow relationships between size and size growth on poor sites indicate similar growth conditions for small and tall members of the population. Steep slopes indicate that dominant neighbors consume much more of the available resources than their smaller neighbors. Thus, the dominant trees can increase self-thinning in the understorey. Under *ceteris paribus* conditions i.e. the same stand density, age etc., structural diversity increases when resource supply becomes scarce.

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