

Chapter 18

Effects of Stress and Defence Allocation on Tree Growth: Simulation Results at the Individual and Stand Level

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18.1 Introduction

The long life span of trees implies that they are more or less frequently confronted with different biotic and abiotic stress situations during their lives. However, biotic stress such as attacks by herbivores or pathogens and abiotic stress such as frost or drought could strongly vary in frequency, intensity, duration, time of occurrence as well as in the involved tissues. This urged trees to develop flexible defence mechanisms during their evolution ensuring a high probability of survival to regenerate successfully. Based on an analysis of existing literature on plant response to herbivory, McNaughton (1983) concludes that "...the yield of the tissue affected and other tissues is not affected in proportion to the amount of tissues damaged by the herbivore", referring also to Lee and Bazzaz (1980) and Neilsen (1981). McNaughton presents a set of alternative patterns about the effect

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of herbivory; at low herbivory levels growth reactions of individual plants range from immediate decline to a certain compensation. At moderate herbivory even a positive effect and overcompensation can be the result. These described patterns are in line with the phases of stress response defined by Larcher (2003).

Under the conditions of limited resources, a tree has the “choice” either to invest in growth to stay competitive against its neighbours, or to adapt to biotic and abiotic stress to keep the gained resources (see Chap. 1). Koricheva (2002) classified the costs involved in the context of herbivory in three major groups, which are also applicable to other pathogens and stress situations: allocation costs, ecological costs and opportunity costs. Allocation costs define the internal trade-offs between growth, defence and reproduction within the individual plant (Chew and Rodman 1979; Rhoades 1979; Bazzaz et al. 1987; Simms 1992; Seifert and Müller-Starck 2009), while ecological costs are external trade-offs caused by defence investments in other than defence or growth-related properties, such as increased susceptibility against other pathogens or abiotic stress. Other ecological costs are negative effects of the induced defence on pollinators, predators and parasitoids (Simms 1992; Rausher 1996). Opportunity costs are costs incurred through an investment in defence instead of investing in growth. In this sense these are costs of resources to defend against herbivores and pathogens, based on what could have been earned if the resources had been used for growth. Based on published results of Coley et al. (1985), Gulmon and Mooney (1986), and Koricheva (2002) and first simulation studies of Seifert (2007) with an empirical growth model, it could be assumed that opportunity costs have a substantial influence on the consequences of an allocation strategy of a tree and may be even more important than the actual diversion of resources. Opportunity costs involve similarly tree and stand level, and imply a decline of competitiveness of the subject tree compared to neighbouring trees. This effect is caused by the fact that the subject tree cannot use the invested products of the assimilation for growth since they were allocated to defence. This can lead to a feedback cycle that consistently increases the loss of competitiveness over time (Fig. 18.1).

It is obvious that an adapted defence strategy is only one determinant of the allocation strategy that ensures a tree’s long-term survival. Growth and space occupation strongly determine the access to above- and below-ground resources, and thus define the absolute amount of resources that can be acquired (e.g. Grams et al 2002; Gayler et al. 2006; Rötzer et al. 2009). The consequence is that social position and tree size in relation to the competing trees are highly correlated with tree growth (e.g. Seifert 2007; Seifert and Müller-Starck 2009). As a result a tree has to adjust its allocation in a way that it allows sufficient defence without losing competitiveness regarding space occupation and resource acquisition. “Allocation” can be defined as biomass partitioning, in the sense of translation of resources to structural components of a plant (e.g. Niklas and Enquist 2002). Defence-related allocations are only partly structural; they involve chemical compounds in a non-structural sense.

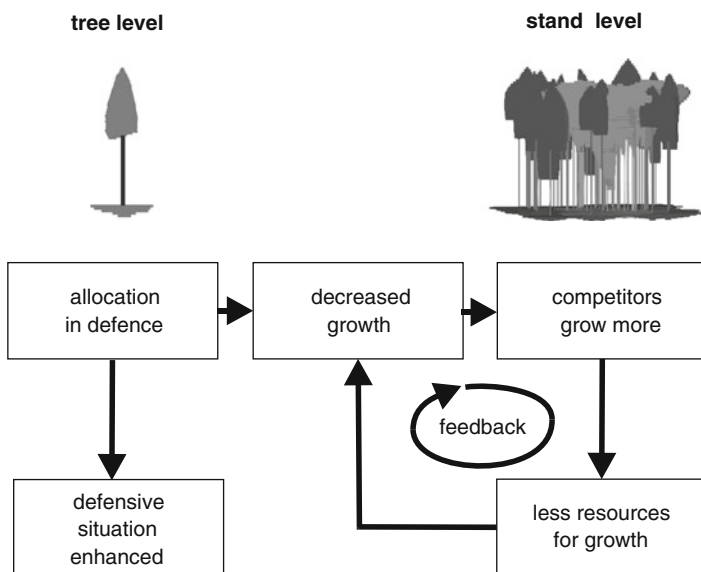


Fig. 18.1 Concept of opportunity costs of a tree as a consequence of defence allocation

During the past years allocation patterns of trees have gained increasing scientific attention. Particularly the trade-off questions of growth and defence, subject to the resource availability of the tree, have been analysed (e.g. Häberle et al. 2009; Chap. 1). Several competing hypotheses have been presented and were highly discussed (Hamilton et al. 2001; Stamp 2003). Most of the empirical and theoretical work is focussed on the allocation pattern within the individual plant. With regards to forest trees, it seems especially rewarding to extend the focus in order to have a closer look at the effects of stress-induced allocation patterns in a competitive environment. This opens up a way to evaluate the long-term success of certain allocation strategies. This approach includes the examination of the effects at the tree and at the stand level alike, to take into consideration that forests are highly complex spatially and temporally determined systems.

There is strong evidence for a feedback of the resource availability on the allocation pattern in defence- or growth-related metabolism (Coley et al. 1985; Herms and Mattson 1992; see also Chap. 17). This interdependence of defence- and growth-related allocation can lead to trade-off situations where the tree grows less in favour of strengthening its defence. The correlation between environmental stimuli and internal allocation processes are still not understood well enough.

Further lack of knowledge becomes evident if the focus of interest is moved from the individual tree to the stand level. Due to the intense interaction of the individuals, the stand cannot be explained from reaction of solitary trees. For example if a certain proportion of trees in a stand has decreased growth in

consequence of herbivore attack, or an allocation shift from growth to defence metabolism, one could assume that other trees, which are not affected, will take the opportunity and try to occupy the space. These compensation effects are dependent on the spatial pattern of trees and are especially regarded to be attenuated in mixed species stands, which contribute to their resilience and economic feasibility (e.g. Knoke and Seifert 2008).

From the above stated it can be concluded that stressor–plant interactions are inevitably linked with plant–plant interaction patterns. A rigorous examination of those dependencies is necessary to understand trade-off reactions of the individual. As a result of an extensive meta-analysis on costs of plants confronted with stress as, e.g. herbivores, Koricheva (2002) pointed out that most of the compiled studies were aimed at the internal trade-offs of the individual plant and excluded the interaction with the biotic environment.

To overcome the problems described above an alternative way was followed to evaluate the effects of biotic and abiotic stress on the growth, defence and allocation patterns by resorting to a growth model-based approach. Provided the tree–tree interaction and the resource competition are reproduced plausibly in the model, scenario analysis can give most desired stress scenarios for various types of tree stands with defined spatial stand structures.

In the following a simulation study is presented to analyse the effects of biotic and abiotic stress on growth, allocation and defence at tree and stand level. The scenario simulations were based on the eco-physiological individual-tree growth model BALANCE and include three scenarios with pure and mixed stands. The objectives were to investigate

1. The magnitude of opportunity costs
2. The effects of different intensities and frequencies of defoliation stress and
3. The effects of drought stress.

18.2 The Eco-Physiological Growth Model BALANCE

Growth models—particularly eco-physiological growth models—have been proven suitable tools for analysing the effects of environmental changes on the growth of entire forest stands, individual trees or even specific tree compartments such as roots or stems, as they integrate a wide range of system knowledge (Pretzsch et al. 2008; Fontes et al. 2010). They simulate forest growth on the basis of generally accepted eco-physiological principles (see Chap. 15). Well-known physiological models were developed by Running and Coughlan (1988), Kellomäki et al. (1993), Mohren and van de Veen (1995), Landsberg and Waring (1997), Bossel (1996), and Bartelink (2000).

Apart from the evaluation and understanding of a tree’s internal resource allocation and related “decisions” on regulation, these kinds of models can also

be used as versatile tools for revealing the effects of defence allocation on the long-term growth and competitive success of trees.

Dedicated spatial and eco-physiologically based tree-growth models, such as the newly developed model BALANCE (Grote and Pretzsch 2002; Rötzer et al. 2005, 2010), allow for scenarios confronting different forest stands with biotic and abiotic stress. The competitive capacity of a tree can be quantified, i.e. the amount of resources which has to be allocated to defence instead of to growth. Eco-physiologically based models give answers about the consequences and implications of these trade-offs. BALANCE is a functional–structural model, which accounts for the influence of competition, stand structure, species mixture, and management impacts on individual tree growth. Tree development is calculated depending on the explicitly spatial environmental conditions of each tree. In turn, each tree is influencing its microenvironment in terms of, e.g. shading or water consumption.

The three-dimensional development of the individual trees in a forest stand is estimated based on the annual increase of biomass. The simulation of the carbon, water and nutrient balances of the individual trees form the core processes of the model. Each tree of a forest stand is divided into crown and root layers, which are in turn subdivided into eight crown- and eight root sectors. For each layer or each sector respectively, the micro-climatic conditions and the water balance are computed daily. Assimilation, respiration, nutrient uptake, growth, senescence and allocation are calculated in 10-day periods from the aggregated weather and water balance variables. This way, the approach takes into account the physiological responses to weather conditions, CO₂ concentration, water and nitrogen availability, as well as biotic and abiotic stress. The seasonal development of foliage is explicitly modelled to include light availability and radiation absorption changes depending on leaf biomass (see also Chap. 8). The beginning of bud burst is predicted based on temperature sums (Rötzer et al. 2004), while foliage senescence is estimated depending on the respiration sum (Rötzer et al. 2010). The individual tree approach of BALANCE facilitates the simulation of pure and mixed stands of various age structures and patterns of species mixtures.

For the initialisation of BALANCE, tree position, stem diameter, crown dimensions and stem height for every tree are required as well as a basic description of the soil (field capacity, wilting point, nutrient status, rooting depth). Daily meteorological values of temperature, radiation, wind speed, humidity and precipitation are used as driving forces of the simulations. Additionally, CO₂ concentration of the air and N-deposition data can be considered. Output is obtained from daily up to annual values in a spatial resolution of individual tree compartments and can be aggregated to tree and stand values. Apart from growth data such as diameter, height or carbon content, data describing stand micro-climate and water balance can also be obtained.

Growth model evaluation was an integral part of the development of BALANCE. The basic processes, i.e. micro-climate within the stand, water balance, photosynthesis and phenology, have been evaluated for the site “Kranzberger Forst” (Rötzer et al. 2010). Further on, numerous validation studies for different sites in Central Europe, for different tree species and different climate regimes have proven that

BALANCE is suitable for growth simulations and analyses after adapting the model to the site (Grote 2002; Grote and Pretzsch 2002; Rötzer et al. 2004, 2005, 2010).

18.3 Scenario Definition

To elucidate the reactions and feedback reactions of growth, defence and competition different scenarios simulating biotic stress are presented: Defined investment proportions for the defence against a pathogen, specific loss of biomass to herbivores, and abiotic drought stress. Both biotic and abiotic stresses were varied with respect to intensity, duration, frequency and time of occurrence. Within the simulations not only individual trees, but also entire stands, different stand structures, i.e. species mixtures and their spatial formations were considered. Each scenario required defining an initial stand with a certain structure. These stands were then confronted with defined biotic and abiotic stress scenarios over the simulation period of 14 years.

18.3.1 Initial Stand Structure

Virtual tree stands (30 m × 30 m) of different mixing ratios and spatial structures of adult Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) were created based on the structure generator “STRUGEN” (Pretzsch 1997). The mixing structure varied to represent mixture in groups and clusters of beech and a random individual tree mixture (Fig. 18.2).

18.3.2 General Site Conditions

The site conditions used for the scenario simulations were based on data of the SFB 607 site “Kranzberger Forst”, located in Southern Germany (48.420°N, 11.662°E, elevation 490 m a.s.l.). For the simulation period of 1994–2007 the mean annual air temperature was 8.1°C, the mean annual radiation 1,096 J/cm and the mean annual precipitation sum 842 mm. Thus, temperature as well as precipitation were at the upper limit of the long-term regional averages (BayFORKLIM 1996), which ranged between 7 and 8°C (period 1951–1980) resp. between 750 and 850 mm (period 1961–1990). Radiation, on the other hand, was somewhat higher than the long-term mean with 1,015 J/cm for the period 1976–1989 (BayFORKLIM 1996). The growing season extended from mid April through the end of October. The soil of the study site—a Luvisol—is described in more detail in Chap. 9. For the calculation of the water balance, we distinguish four soil layers with a maximum rooting depth of 1.2 m.

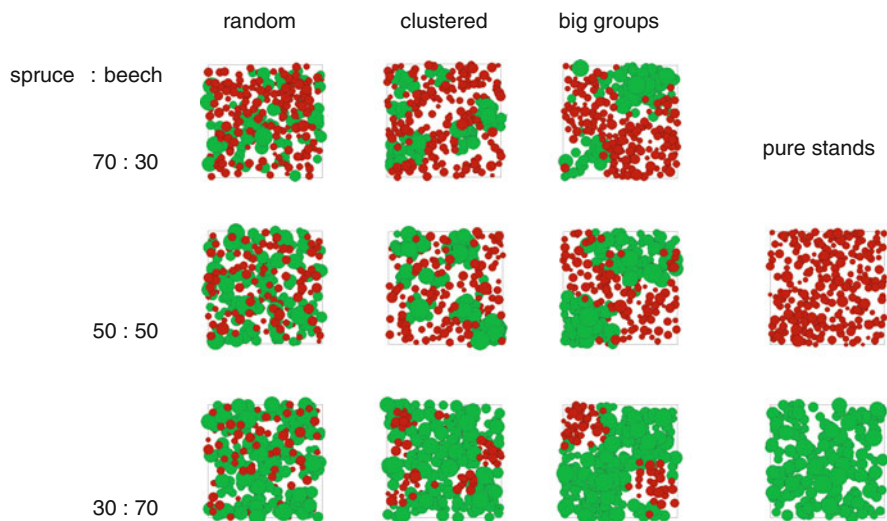


Fig. 18.2 Initial stands for the scenario simulation. The stands differ in the proportion of spruce and beech in the crown projection and the degree of clustering of the tree species (*green circles* represent beech, *red circles* spruce trees)

18.3.3 Stress Scenarios

Regardless whether biotic or abiotic, stressors can occur and lead to disturbances in the growth of individual trees and forest stands. Growth rates may change competition of trees or allocation patterns to a great extent according to the stress intensity, the duration of the stress (short, long or even continuous) the stress frequency (received as a single or repeated pulse), and the phase of stress occurrence (early or late within the growing period) (Fig. 18.3).

For the simulation studies three stress scenarios were defined that varied according to the intensity, duration and frequency of the stress (Table 18.1):

Scenario I (opportunity costs) was set up to investigate opportunity costs of beech in a mixed stand. A constant defence investment rate was deducted from the available net resources for all beech trees while spruce trees were not subjected to defence investments.

In *Scenario II (consequences of defoliation)*, different rates of defoliation were simulated for a pure beech stand. Defoliation was simulated by a proportional removal of leaf biomass equally over all crown parts. A partial replacement of leaves by proleptic sprouting as found in beech was not simulated. Four levels of defoliation intensity were compared with the control. These were combined with three different frequencies of the years of leaf loss in a 10-year period. In the last 5 years no defoliations were simulated.

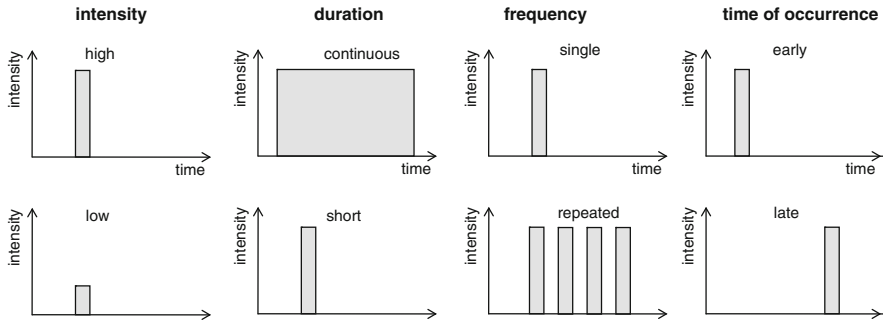


Fig. 18.3 Contrasting levels of stress patterns (intensity, duration, frequency and time of occurrence)

In *Scenario III (effects of drought stress)* years with different intensities of drought periods as well as years with optimal growth conditions were chosen to analyse the effects of water deficit on the growth of individual trees and entire pure and mixed stands. The influence of drought stress on allocation patterns was studied.

18.4 Analysis Methods

The response variables to characterise stress effects were production rates of leaf biomass, fine root biomass, free C-pool (reserve), total structural biomass (above- and below-ground), tree diameter and net primary production. Additionally, allometric relationships were calculated to look for changes in the partitioning. Pretzsch (2009) proposed a set of different ways for empirical diagnosis of growth disturbances of forest trees. Two main methods were applied to analyse the simulation results: a pairwise comparison of affected and unaffected trees and a comparison of the average response with variation on the plot with a control plot.

The first method is the method of choice if the initial stand is homogenous. Compared to empirical studies, the advantage of simulation studies is that the determination of equal pairs of trees is simple since initially identical trees can be simulated *ceteris paribus* with different treatments (Seifert 2007; Pretzsch 2009).

In the case that stand structure is used as an independent variable, the initial stand structure is different. That favours the second method with the average and variance of trees affected and unaffected by stress of a plot to be contrasted with the values of the control plot.

In most cases relative changes of the stress scenarios to the control were chosen to analyse the patterns because the main focus of the simulation study was to reveal the reaction rather than providing absolute magnitudes. The main response variables were the allocation patterns of the trees, and tree growth, both analysed on the individual tree and stand level.

Table 18.1 Stress scenarios that vary in intensity, frequency, duration and time of occurrence of the stress

Scenario	Initial stands	Intensity	Frequency	Duration	Time of occurrence (month)	Number of simulation runs	
<i>Scenario I</i>							
"Opportunity costs"	Pure beech	0, 10, 20, 30, 40, 50 % for defence investment	Single	Continuous	–	6	
	All (only beech was stressed)	0, 10, 20, 30, 40, 50 % for defence investment	Single	Continuous	–	60	
<i>Scenario II</i>							
"Consequences of defoliation at tree level"	Pure beech	% Defoliation	Repetition	Year			
		0	0×	–	–	1	
		25, 50, 75, 99	1×	1	Pulse	5	4
		25, 50, 75, 99	3×	1, 6, 11	Pulse	5	4
		25, 50, 75, 99	4×	1, 4, 7, 10	Pulse	5	4
<i>Scenario III</i>							
"Drought stress and stand structure"	All	No drought and selected "drought" years	–	–	–	11	

18.5 Effects of Stress on Growth and Allocation Pattern

18.5.1 Scenario I: Biotic Stress on Stand Level

In the first scenario, a response to a species-specific pathogen was simulated for a mixed stand. The beech trees in the stand were subjected to a constant defence investment while the competing spruce trees were not. For each beech tree the available free carbon pool was reduced by 10–50% to simulate different defence rates. The objectives of the scenario simulation were the quantification of opportunity costs and the investigation of the structural stand variables that influence the opportunity costs. Additionally, a closer look was taken at adaptive changes of structural allometric relationships as a consequence of defence allocations.

In Scenario I, it was assumed that a tree incurred opportunity costs if the predicted growth losses were higher than indicated by the specified defence investment. For example in case of incurred opportunity costs a tree with a defence investment of 30% of the available net resources should lose more than 30% of its growth, compared to the control tree, which was not subjected to that investment. Over time compound interest effects have to be considered.

18.5.1.1 Quantification of Opportunity Costs

Economic theory can be employed to analyse investment patterns in plants (Bloom et al. 1985). An adequate response variable to assess possible opportunity costs is the total biomass of the tree and its changes because it is unaffected by shifts in the partitioning between the tree compartments. A cross-sectional analysis of all Scenario I simulations revealed a significant drop in biomass production after 14 years of simulation (Fig. 18.4). The results indicate an effect beyond the relative reduction of net resources. At 10% defence rate beech trees showed a decrease in total biomass of 16.1% on average compared to the control. At 50% defence rate, 67.4% of the biomass was lost. These results strongly suggest the presence of compound interest effects caused by losses of competitiveness in space occupation and resource acquisition of trees investing in defence instead of growth, which leads to opportunity costs.

The spruce trees profit from the decreased growth of the beech trees, but from a beech defence investment rate of 30% upwards, spruce trees were not able to compensate for the decreased growth of beech trees any more. However, we have to take into account the “compound interest effect”. A quantification of the annual costs instead of the accumulated costs over the 14 years is therefore necessary to investigate the presence of opportunity costs. In the simulated early growth phase trees grow with nearly constant increment rates. Thus in approximation the well-known concept of the compound interest rate can be adapted from economics (Eq. 18.1)

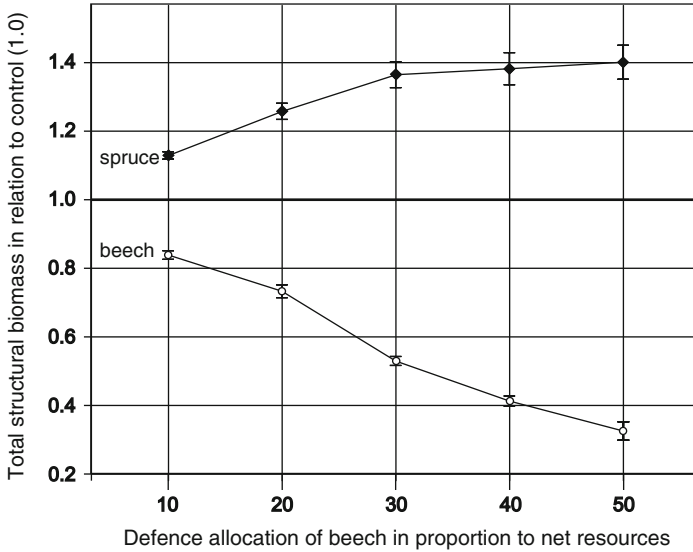


Fig. 18.4 Predicted deviation of total structural biomass of beech and spruce in a simulated mixed stand in relation to the control (1.0 line): Beech trees are subjected to different defence investment proportions (*lower line with circles*). They are compared to the reaction of the non-investing spruce trees in the same stand (*upper line with diamonds*)

$$i = (\text{FV}/\text{PV})^{1/n} - 1, \quad (18.1)$$

where i is the compound interest rate, PV is the present value, FV the future value, and n the time in years.

Translated to biological terms PV is the tree biomass at the beginning and FV the biomass at the end of the simulation period which will be denoted by x and y resp. further on. The compound interest rate i represents the annual biomass increment. In our case two effects influence biomass increment: the given defence investment d , and c , the true opportunity costs that are incurred by the loss in competition. It is important to note that the opportunity costs c are incurred additionally to the defence investment d . In order to obtain c Eq. 18.1 has to be extended (Eq. 18.2)

$$y_d = x \cdot (1 + i \cdot (1 - d) \cdot (1 - c))^n, \quad (18.2)$$

where y_d is the final biomass with defence investments considered according to the simulation; x is the initial biomass, i can be obtained from the control simulation without defence investment (Eq. 18.3) and d is the given defence investment percentage divided by 100; n represents the simulation period (14 years)

$$y_c = x \cdot (1 + i)^n, \quad (18.3)$$

where y_c is the final biomass of the control simulation, without defence investment.

Table 18.2 Opportunity costs expressed as competition-based growth reductions c in relation to direct defence investments d (given in the first column)

Defence investment	%	10	20	30	40	50
Opportunity costs	Mean	1.40	1.35	1.87	2.63	3.08
95% Confidence interval	Lower	1.25	1.23	1.79	2.39	2.98
	Upper	1.57	1.51	1.97	3.03	3.18

By obtaining i from Eq. 18.3 and inserting it in Eq. 18.2, Eq. 18.2 can be solved for c (Eq. 18.4)

$$c = 1 - \frac{\sqrt[n]{\frac{y_d}{x}} - 1}{i \cdot 1 - c}. \quad (18.4)$$

The results are presented in Table 18.2, where the opportunity costs (competition effects c) are calculated in proportion to the defence investments d .

The scenario results suggest that the relative importance of opportunity costs compared to allocation costs increase in a nonlinear fashion with increasing defence rates, ranging from 1.5 at 10% defence investment to more than 3.0 at 50% defence investment. This means that opportunity costs caused by competition effects were always higher than the direct defence investments.

18.5.1.2 Influence of Stand Structure on the Opportunity Costs

A particularly relevant question in mixed stands is how stand structure and inter-specific competition influence the opportunity costs, because this determines the long-term competitiveness of a tree species. It also gives an indication for practical forestry on how stand composition impacts growth, in situations where one species is stressed in a mixed stand. An analysis of the simulation results of Scenario I was carried out based on multiple linear regression. The objective was to determine the influence of the beech proportion and the spatial distribution of beech (mixing pattern) within the stand on biomass growth. As a response variable, the biomass at the end of the simulation period in relation to the control was selected (Eq. 18.5)

$$\text{Biomass}_{\text{proportion}} = a + b \cdot \text{defence}_{\text{proportion}} + c \cdot \text{beech}_{\text{proportion}} + d \cdot \text{mixing pattern}, \quad (18.5)$$

where a , b , c and d are fitted regression parameters.

Again beech was the tree species subjected to different degrees of defence allocation.

The results in Table 18.3 indicate for beech that the deviation of biomass from the control is significantly influenced by the proportion of beech in the stand.

Table 18.3 Multiple linear regression analysis of simulation results in Scenario I: Influence of proportionally invested resources in defence (Defence proportion), beech proportion in the stand and spatial species distribution (Cluster) on the total biomass in relation to the control

Species	Model parameter	Unstandardised coefficients		Standardised coefficients		Sig.
		<i>B</i>	Std. error	Beta	<i>t</i>	
Spruce	<i>a</i> (Constant)	1.276	0.037		34.787	0.000
	<i>b</i> Defence proportion	0.007	0.001	0.280	11.623	0.000
	<i>c</i> Beech proportion	0.000	0.001	0.017	0.716	0.474
	<i>d</i> Cluster	-0.099	0.010	-0.236	-9.786	0.000
Beech	<i>a</i> (Constant)	0.826	0.019		42.427	0.000
	<i>b</i> Defence proportion	-0.014	0.000	-0.733	-46.953	0.000
	<i>c</i> Beech proportion	0.002	0.000	0.213	10.916	0.000
	<i>d</i> Cluster	0.008	0.004	0.037	1.891	0.059

The spatial distribution of the mixture (random, cluster, group) is only significant at the 0.1 level. An increased beech proportion leads to less severe growth reductions, because the interactions with spruce trees were decreased. For spruce, which was not subjected to defence investments, the beech proportion in the mixture was non-significant while the distribution of species had a highly significant influence. Spruce trees seem to profit from a random individual tree mixture much more and are able to gain competitiveness over the beech in our scenario. The bigger the beech groups, the less attenuated the advantage of spruce.

18.5.1.3 Changed Allometric Relations as a Result of Defence and Different Stand Structures

It is important to consider the cause of the changes at the individual tree level. Changes in structural partitioning become obvious if the allometric relationships of the trees are changed. Based on the results of Scenario I, allometric functions were calculated that relate the diameter at breast height (dbh) to the total tree biomass. Based on a double logarithmic function: $\ln(\text{biomass}) = a + b \cdot \ln(\text{dbh})$ the influence of the beech proportion and the way the trees are mixed spatially (mixing pattern) on the allometric slope parameter *b* were assessed for each of the stands in Scenario I. The database for the analysis was again the situation at the end of the 14 years simulation period.

The regression fits of the simulation results with a second-degree polynomial suggest that beech trees subjected to defence allocation react to increasing inter-specific competition with a changed allometry. The slope parameter showed a correlation to the beech proportion (Fig. 18.5, left). In the stand with the 70:30 spruce/beech proportion, the allometric relation had the lowest slope parameters indicating the lowest biomass per dbh. The biomass per stem diameter in beech is reduced with increasing amount of spruce in the stand. Interestingly, the allometric

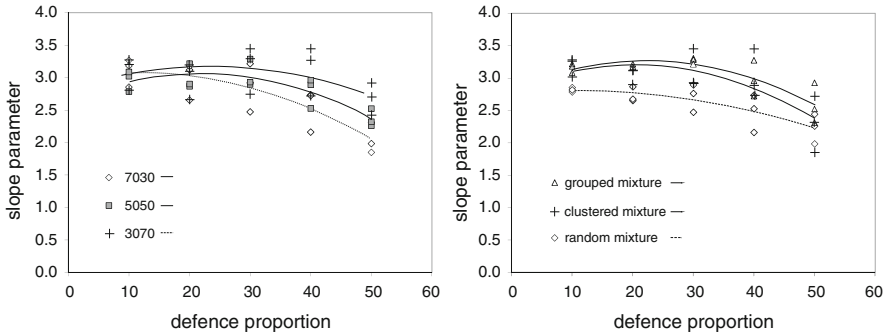


Fig. 18.5 Influence of species' mixing ratios (*left*) and spatial mixing structure (*right*) on the allometric relationship of beech between dbh and total biomass (the first two digits in the species code indicate the proportion of spruce, the second two the proportion of beech; e.g. 7030 codes for 70 % spruce and 30 % beech)

slope values peak according to the proportion of net resources that are allocated to defence. At 70:30 spruce/beech proportion the peak is around 15% defence proportion, 50:50 proportion led to a peak at around 20% and with 30:70 spruce/beech proportion in the stand the peak was around 25%. The influence of the interspecific mixture of the two species is similar (Fig. 18.5, right). The more intensively the individual trees of the two species intermingle spatially, the more the allometry is changed and the biomass per dbh of beech is reduced. The statements made on the nonlinearity of the correlation and the maximum of the slope parameter at the examination of the beech proportion are equally valid for the clustering structure as for the independent variable.

18.5.1.4 Scenario I: Discussion

Our results suggest that opportunity costs in their compound interest effect are a relevant factor for trees, confirming results obtained by Koricheva (2002) and Seifert (2007). The observed pattern suggests that competition-related opportunity costs have a bigger effect on annual biomass increment than the defence investments themselves. Moreover, opportunity costs increased over-proportionally with increasing defence investments. In the mixed scenario decreased increments of the defence investing beech trees were compensated for by the non-investing spruce trees, if defence investments of beech did not exceed 20–30%. The proportion and type of mixture of affected trees in a stand influenced growth losses and compensation, and were reflected in changed allometric relationships between stem diameter at breast height and biomass of the affected species. The allometric changes indicate an adaptation of the allometric pattern of beech according to defence investment and the amount of beech in the stand with an interaction between both variables. Spruce trees were strong competitors for resources because they were not subjected to a defence allocation in this scenario. With an increasing proportion of spruce trees in the stand, the maximum biomass per diameter of beech trees is

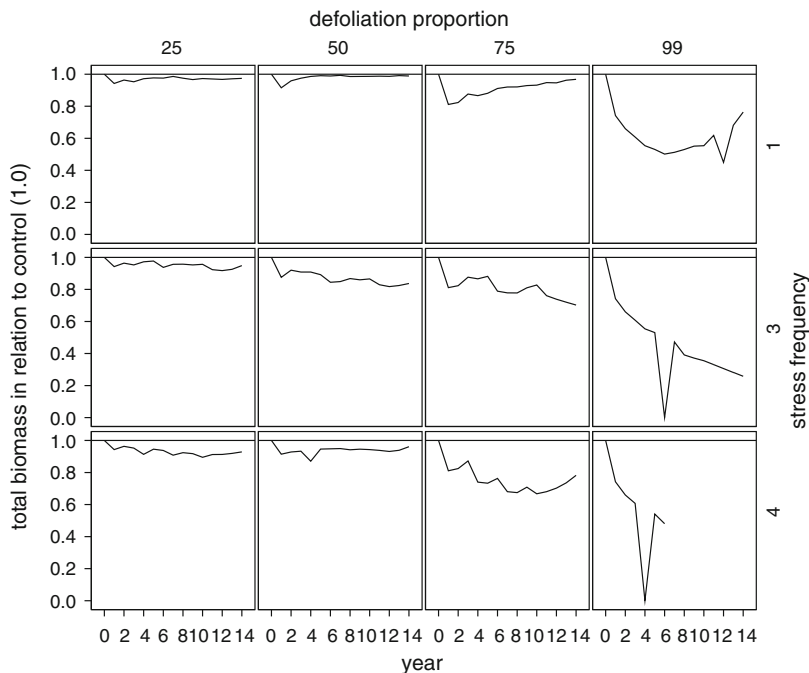


Fig. 18.6 Effects of proportion of defoliated leaves and the frequency of the defoliation on the total biomass in relation to the control

reached at increasingly smaller defence rates. This reaction pattern shown in the simulations is supported by the fact that intensive intermingling of the species resulted in decreased biomass per dbh of the beech trees.

18.5.2 Scenario II: Biotic Stress on Tree Level

18.5.2.1 Influence of Defoliation Patterns

The second scenario aims at investigating the influence of different defoliation patterns on tree growth and partitioning at the individual tree level. Using the total biomass in relation to the control as a response variable, the simulation results show that low intensities of defoliation like 25 and 50% at low frequencies (only once in the simulation period) led to a recovery but no overcompensation of biomass (Fig. 18.6). Also three consecutive defoliations with 25% leaf loss were followed by a near complete recovery. Higher defoliation rates, especially in combination with higher frequencies, resulted in a decline in total biomass compared to the control which only recovered gradually after defoliation was stopped, or otherwise lead to a permanent decline (Fig. 18.6.).

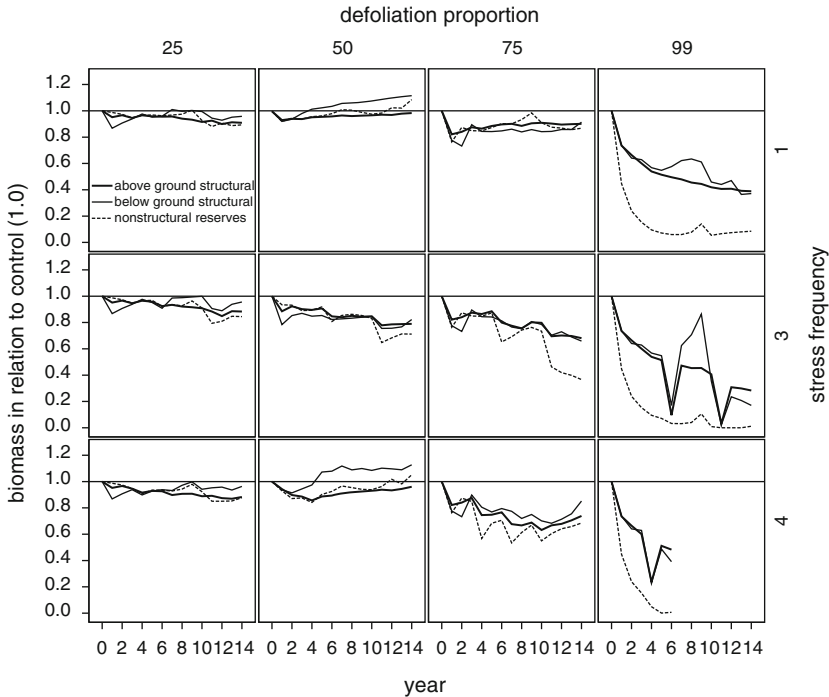


Fig. 18.7 Effects of proportion of defoliated leaves and the frequency of the defoliation on the above-ground biomass (*bold line*), below-ground biomass (*thin line*) and reserves (*dotted line*) in relation to the control

A closer look at the pattern of above-ground, below-ground, and reserve allocation reveals that the simulation results propose a more complex reaction (Fig. 18.7). While defoliation at any intensity and frequency was detrimental to the predicted relative above-ground biomass, below-ground biomass and free C-pool showed a distinctive overcompensation (values greater 1.0) at certain combinations of defoliation intensities and frequencies, as a result of internal interactions of the model.

18.5.2.2 Scenario II: Discussion

The results obtained in Scenario II would favour McNaughton's second hypothesis (McNaughton 1983) that suggests compensation to a certain extent, but not overcompensation at low levels of herbivory. Decreases in diameter and volume increments were often described as proportional to the needle losses in conifers (Craighead 1940; Bruce 1956; Chalupa 1965) while other authors negate proportionality in a strict sense (Fournier et al. 2010). Brubaker (1978) stated that no significant decrease in ring width occurred if more than 50% of needles were

remaining, which can be seen as an argument for a nonlinear relationship, where small needle losses do not lead to proportional diameter growth losses and with increasing defoliation the growth losses increase progressively. A similar reaction pattern was apparent in our simulation results for beech. Our findings confirm the empirical results of Krause and Raffa (1996), who compared the growth and recovery rates of 10-year-old deciduous and evergreen conifers after defoliation. They found a quick recovery for deciduous *Larix decidua* in contrast to evergreen *Pinus resinosa* trees. Pines with 66% defoliation rates never recovered with regards to above-ground biomass. They attributed the differences partially to the plastic architectural response of *Larix* but also to the differences of nutrient and carbon distribution in evergreen and deciduous conifers. Beech may be more comparable with *Larix* as it is also a deciduous tree. There is ample evidence from defoliation studies that leaf and needle losses are nonlinearly related to diameter growth and above-ground biomass (Kulman 1971).

The overcompensation of below-ground biomass, predicted by BALANCE, requires some interpretation. BALANCE does not allow for efficiency changes in the chemical pathways of photosynthesis itself, but is sensitive to changed leaf areas, modified root–shoot ratios and higher light and water availability. However, the observed effects suggest a complex interaction on the eco-physiological levels covered by the model, which includes extrinsic and also intrinsic mechanisms to a certain extent as discussed by McNaughton (1983).

18.5.3 Scenario III: Abiotic Stress (Drought)

In the Scenario III simulations, the influence of abiotic stress on growth and competition of individual trees and entire forest stands was analysed. Abiotic stress that changes tree and stand growth includes, for example, storms, drought or heat. In this study, we concentrate on the influence of drought. The analysis provides answers to the questions: (1) What is the influence of drought stress on biomass growth? (2) Does drought stress change the allocation patterns of trees (free C-pool, above and below-ground biomass)? and (3) Do stand structure and interspecific competition influence the growth of individual trees resp. entire stands in drought periods?

18.5.3.1 Quantification of Drought Stress

To assess drought quantitatively and qualitatively for the single years of the period from 1999 to 2007, several drought indicators were analysed. As a first indicator a meteorologically based index, i.e. the number of days with precipitation sums lower than 0.1 mm within the summer months June to August (n_{NIE0}), was used. In Fig. 18.8a, the annual deviations of n_{NIE0} from the mean of the years 1999–2007 are given. The year with the highest positive deviation, i.e. the year with the most days without precipitation, was 2003. Other dry years were 2002 and 2006, while

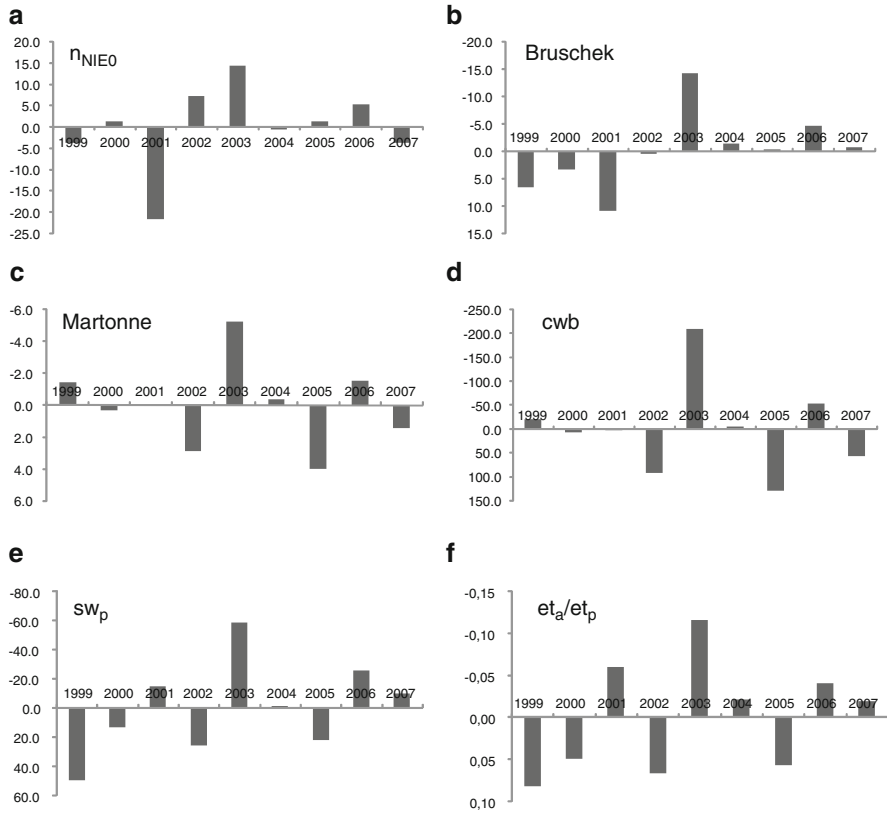


Fig. 18.8 Anomalies of different drought indices (**a** = n_{NIEO} , **b** = Bruscek, **c** = Martonne, **d** = cw_b , **e** = sw_p , **f** = et_a/et_p) for the years 1999–2007 from the average of 1999–2007 for the site Kranzberger Forst

2001 was the year with the lowest number of n_{NIEO} . If, however, other climate parameters that influence the water balance of a site are additionally taken into account, the ranking of years with drought is changing. The drought indices of Bruscek or De Martonne consider temperature as well as precipitation. While the Bruscek index is based on the annual precipitation sum and the number of summer days, i.e. the number of days with temperatures above 25°C (Bruscek 1994), the De Martonne index is calculated from the precipitation sum and the temperature of the summer months June, July and August (De Martonne 1926). Both indicators show the highest drought stress in 2003 and a lighter drought stress in 2006, followed by the years 2004 (Bruscek) and 1999 (De Martonne) (Fig. 18.8b, c).

A more sophisticated index is the climatological water balance cw_b , calculated from the difference between precipitation sum and potential evapotranspiration. Based on the values for the summer months, the order of the drought stress intensity is again 2003 followed by 2006 and 1999 (Fig. 18.8d).

By using the plant available soil water sw_p as an indicator for drought, site conditions other than the meteorological conditions are also considered (Fig. 18.8e). The annual anomalies of the summer month June to August against the average were highest for the year 2003 and 2006. If the ratio of actual to potential evapotranspiration et_a/et_p is used 2003 indicated the strongest drought (Fig. 18.8f). Hereby the water balance parameters sw_p , et_a and et_p were simulated with BALANCE for the beech stand using the above-mentioned site and weather conditions. In contrast to the above drought indices, positive anomalies based on sw_p and the et_a/et_p ratio were also found for the years 2001 and 2007. This is because the favourable growth conditions in these 2 years increased growth and in consequence also actual transpiration, which lowered et_a/et_p ratios and sw_p values.

Based on these results the year 2001 was selected as a year with sufficient water availability, the year 2006 as a year with a moderate drought and the year 2003 with a severe drought in order to analyse the influence of drought on tree growth and competition.

18.5.3.2 Influence on Individual Tree and Stand Level

To compare total biomass development of single years, simulated total biomasses of 10-day periods were related to the initial biomass of each year. Figure 18.9 presents the results for the pure beech stand.

Starting in May biomass development of the year 2001 increased stronger than the mean values of the period 1999–2007. Already in the spring months growth rates were smaller compared to the average for the moderate dry year 2006. In the severe dry year 2003 beech tree growth in spring was somewhat higher than on average. However, in the mid of June growth rates dropped severely. At the end of the dry years 2006 and 2003, there was no detectable increase in the stand biomass compared to the initial biomass.

Compared to the average biomass increment (1999–2007) the biomass increment of the beech stand was increased by 1.8% in the year 2001 while it was clearly lower in the drought years with 4.5% (2006) respectively 4.9% (2003). Spruce, on the other hand, was more affected by the year 2003 with a decrease of 7.1% compared to the mean growth rate. In 2006, biomass growth was lowered by 1.5%. In 2001, a year with good growing conditions, the growth rates of spruce were 4.1% higher compared to the average.

An essential factor of the production of forest stands is the condition of each tree, i.e. its individual light regime, nutrient status and water supply. Figure 18.10 illustrates that at the individual tree level the influence of droughts on the growth rates of trees varied strongly. In dependence on the tree size, denoted as dbh, net primary productivity (npp) increased clearly with tree size.

As can be seen from Fig. 18.10, particularly in the year 2001 with good growth conditions individual trees developed huge differences in npp. Small-sized trees

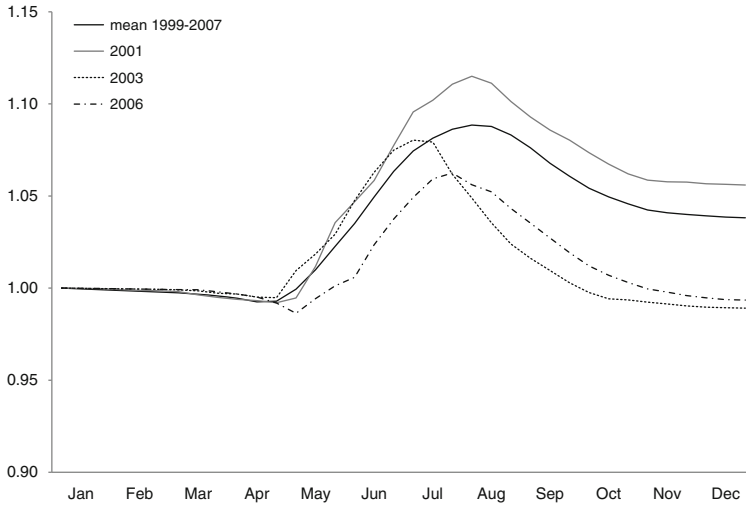


Fig. 18.9 Relative total biomass development of a pure beech stand at the site Kranzberger Forst for single years and on average

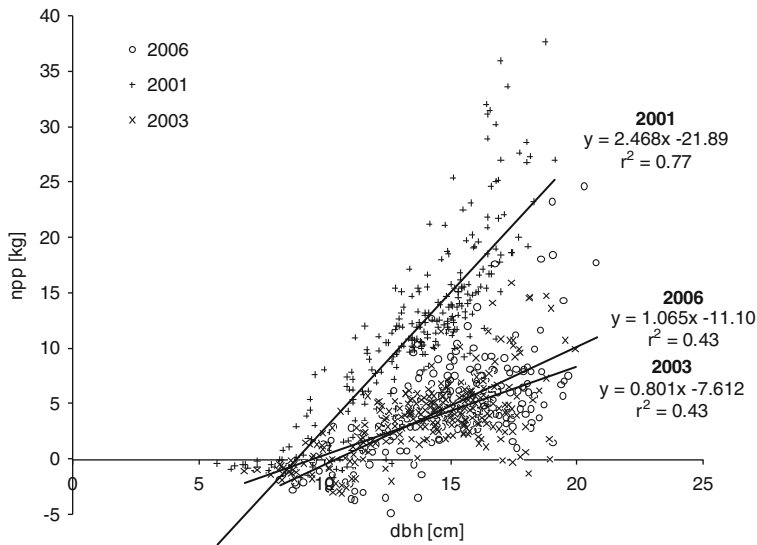


Fig. 18.10 Net primary productivity of individual beech trees at the site Kranzberger Forst for the years 2001, 2003 and 2006 in dependence on their sizes (dbh); lines denote the linear regressions of the 3 years

had npp values smaller than 5 kg, big-sized trees, on the other hand, had rates above 15 kg. In years with drought, the slope of the regression line clearly dropped. While small trees still grew with the same increment rates as calculated for 2001, big trees reduced their growth rates severely (Fig. 18.10).

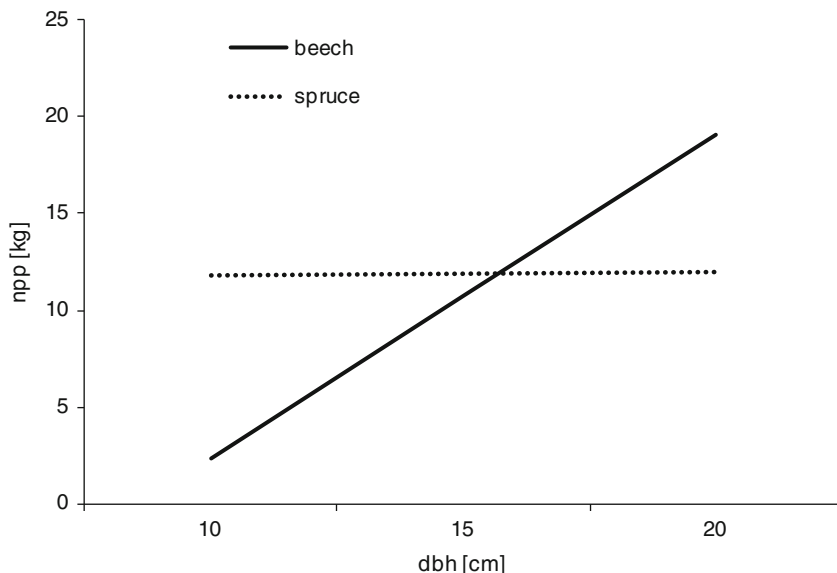


Fig. 18.11 Regression line of the npp differences between the year with favourable growing conditions (2001) and the drought year 2003 for beech and spruce trees at the site Kranzberger Forst depending on tree size (dbh)

To elucidate the loss of npp based on tree size in a drought year compared to a year with favourable growing conditions, the differences of the linear regression lines of the years 2001 and 2003 were calculated (Fig. 18.11). While the spruce trees of the Kranzberger Forst lost approximately 12 kg per tree in all size classes, small-sized beech trees of about 10 cm in dbh decreased npp in 2003 by 2.5 kg per tree compared to 2001. The npp of big beech trees with a dbh of 20 cm, on the other hand, decreased by 19 kg per tree.

18.5.3.3 Influence on Individual Tree and Stand Level: Discussion

Higher growth rates of spruce compared to beech in years with suitable growing conditions are well known (e.g. Pretzsch 2009). This is reflected in our simulation results since the growth of spruce is reduced more than the growth of beech in intensive drought years. These findings confirm the results reported by Beierkuhnlein and Foken (2008). Additionally, Pichler and Oberhuber (2007) found for the year 2003 a 30% reduction of the radial tree growth for spruce compared to the reference period (1998–2002). The annual energy flux measurements of Grünwald and Bernhofer (2007) for the spruce forest Tharandt show a distinctive lower net ecosystem productivity of 395 g C/m in 2003 compared to 2001 with 559 g C/m. Based on the long-term mean for the years

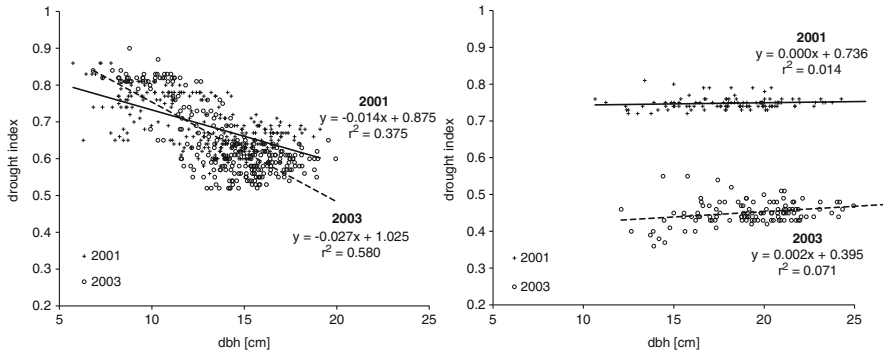


Fig. 18.12 Drought index e_a/e_p of beech (*left*) and spruce (*right*) at the site Kranzberger Forst for 2001 and 2003; *lines* denote the linear regressions for the single years

1996–2005 this is a 30% reduction in 2003, but no reduction in 2001. An increase of the above-ground biomass with tree size is also reported by Ogaya and Penuelas (2007) for a holm oak forest using initial above-ground biomass as a representative for tree size.

The growth patterns for different sized trees under stress and no stress conditions can also be seen in the studies shown in Chap.14, where size–growth relationships in forest stands are analysed, amongst others under drought events. Pichler and Oberhuber (2007) found at a dry mesic site for dominant spruces the strongest growth reductions in the year 2003 compared to the 1998–2002 period. The results of Ogaya and Penuelas (2007) were similar to our results: The above-ground biomass increment was clearly lower under drought conditions averaged over all species; the slope of the regression line for the above-ground biomass increment based on tree size was higher for non-drought conditions compared to the drought conditions averaged over the species. The response of the single tree species, however, was quite different (high for *Arbutus unedo* and *Quercus ilex*, low for *Phillyrea latifolia*).

The simulation results for npp based on tree size in drought years (Fig. 18.11) were in accordance with findings of Peterken and Mountford (1996) that 30-year-old beeches (small trees) were largely unaffected by droughts, while the growth of 75- to 105-year-old beeches (big trees) declined or ceased. Further on, Dohrenbusch et al. (2002) reported that spruces of the dominant social classes reacted more on low water supply than suppressed trees.

A reason for the different growth patterns of beech and spruce depending on tree size is related to their water supply. The e_a/e_p ratio can serve as an indicator for the water supply of a tree (Fig. 18.12). For beech trees a clear decrease of the e_a/e_p ratio with increasing tree size (dbh) for the year 2003 and 2001 is evident, which means that big trees have higher water deficits.

Spruce trees, however, showed no correlation of the drought index to tree size. For the year 2001 the ratio oscillated around a value of 0.75, which denotes good

water supply for all size classes. In 2003 the e_{t_a}/e_{t_p} ratios ranged between 0.36 and 0.44, which indicates severe drought stress for all size classes. For beech trees such low ratios were only found for big trees in the year 2003. The 2003 drought stress for all tree sizes of spruce caused low npp values in 2003, while in 2001 the high e_{t_a}/e_{t_p} ratios for all tree sizes (indicating no water stress) caused equally high npp values. This implies that drought stress changed growth rates of the individual trees, of the entire stands, but also of the tree species to a different extent. Longer stress periods can therefore change stand structure and stand growth (e.g. Peterken and Mountford 1996; Dohrenbusch et al. 2002; Ogaya and Penuelas 2007). The assumption of Dohrenbusch et al. (2002) that a worsening of the environmental conditions, for example drought, mainly affects the dominant trees of a stand compared to the dominated was confirmed for beech, but not for spruce. It seems that the 2003 drought intensity was so strong that all tree sizes of the spruces were similarly influenced.

18.5.3.4 Effects on Allocation Patterns

Up to now, the influence of abiotic stress is shown on individual tree and on stand level. But there is also evidence (e.g. Polomski and Kuhn 1998; Frank 2007; Pichler and Oberhuber 2007; Rötzer et al. 2009) that stress such as droughts change the allocation pattern of plants. In two examples, BALANCE simulations demonstrate allocation changes of a beech stand.

Figure 18.13 presents the relative annual development of the free C-pool averaged over the years 1999–2007 as well as for the single years 2001, 2003 and 2006. In 2001, a year with good growing conditions, from mid May onwards the free C-pool increased more than the long-term mean. In the moderately dry year 2006 with the beginning of May, the free C-pool increased slower than on average.

In the dry year 2003, the development of the free C-pool nearly matched the average values in the first months. Since the beginning of July, however, the free C-pool had clearly dropped. At the end of the year 2003, the C-pool was 19% lower than at the end of the year 2001.

Fine root biomass was also clearly influenced by drought stress. Figure 18.14 depicts the development of the fine root growth again for the long-term mean and the three chosen years. Higher growth rates for the fine roots than on average can be found in all years. In the course and at the end of the year, the highest amount of fine root biomass was available in the severe dry year of 2003. However, there was only a small difference in the fine root growth rate at the end of the year 2003 compared to 2001, a year with favourable growing conditions.

If the fine root to leaf biomass ratio of the beech trees of the single years were combined with a drought stress indicator like the e_{t_a}/e_{t_p} ratio, a close relationship ($r^2 = 0.59$) is obvious (Fig. 18.15). Increasing drought stress, i.e. decreasing e_{t_a}/e_{t_p} values, stimulated fine root to leaf biomass ratio positively.

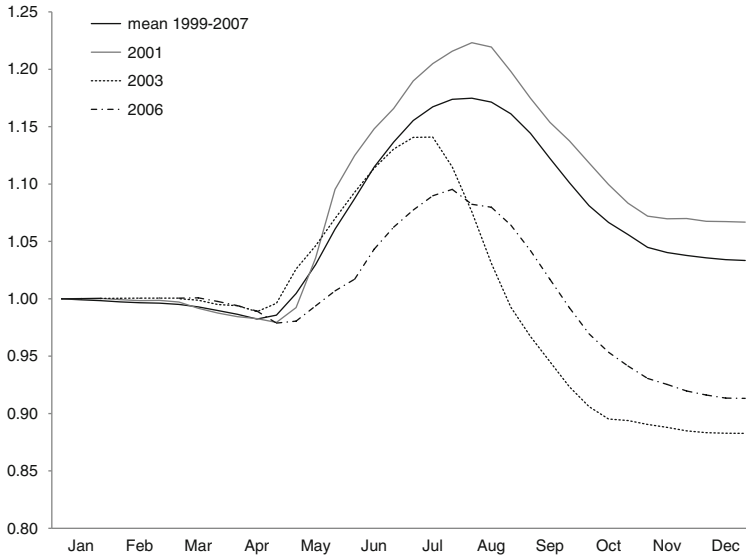


Fig. 18.13 Relative course of the free C-pool of beech at the site Kranzberger Forst

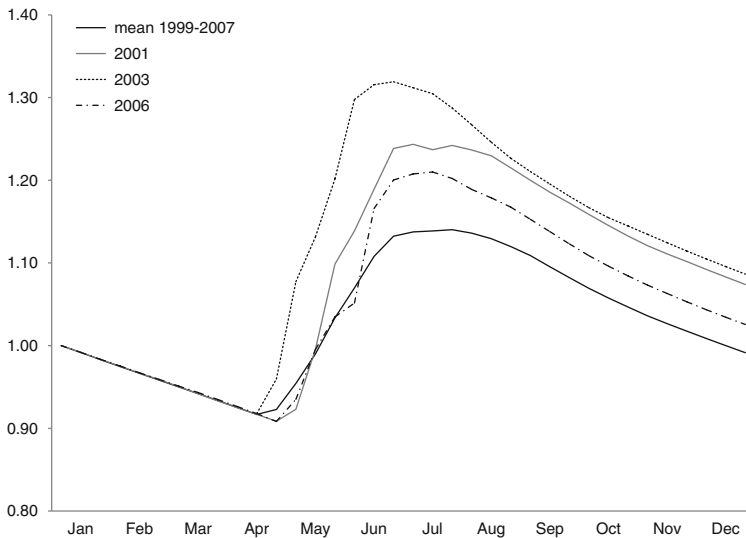


Fig. 18.14 Relative course of the fine root growth of beech at the site Kranzberger Forst

18.5.3.5 Effects on Allocation Patterns: Discussion

Nikolova et al. (2009) found for the mixed beech/spruce stand in the Kranzberger Forst similar levels of fine root production and fine root recovery for beech in the year 2003 compared to 2002. For spruce, on the other hand, these values were

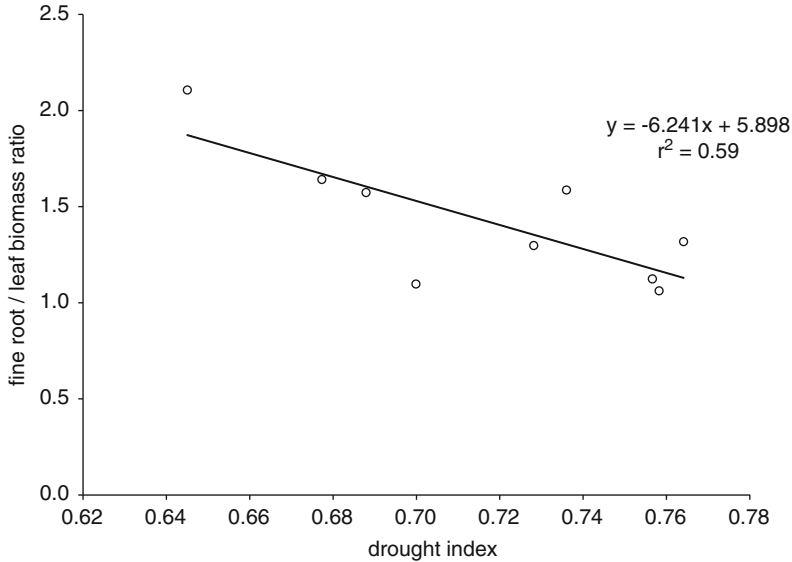


Fig. 18.15 Simulated fine root/leaf biomass ratio and drought index e_{t_d}/e_{t_p} of the vegetation period for beech

significantly lower in 2003. Regarding that both years 2001 and 2002 show quite low drought indices (Fig. 18.8b–f), the results for beech of Nikolova et al. (2009) are consistent with the simulation results. Konopka et al. (2007) found that fine root biomass of Japanese cedar decreased by drought treatment. They refer to Eissenstat (1997), who stated that “plant root responses to drought are diverse, ranging from shedding of roots to the stimulation of root production”. Konopka et al. (2007) further argued that these strategies are modified by the intensity and duration of a drought. This is in accordance with our results (Fig. 18.14), and with the conclusion of Mainiero and Kazda (2006) who found no evidence that fine root formation of beech counter-balances short-term soil water shortages.

Leuschner et al. (2001) stated that fine root growth is more vulnerable to soil water shortage than leaf expansion and photosynthesis, causing (inter-annual) shifts in the carbon allocation patterns of trees. This suggestion is confirmed by the simulation results as shown in the Figs. 18.13 and 18.14 for the free C-pool and the fine root biomass. Despite the fact that fine root biomass greatly varies among tree species, forest type and climate (e.g. Vogt et al. 1996; Noguchi et al. 2007), there are also significant year to year changes. Our results (Figs. 18.9, 18.13 and 18.14) support these findings.

Increased root growth as observed in the simulations in response to drought (Fig. 18.15) was reported by several authors (e.g., Cienciala et al. 1994; Leuschner et al. 2001; Frank 2007). This is in conformity with the plant allocation theory. This theory states that above- and below-ground biomass is allocated in order to

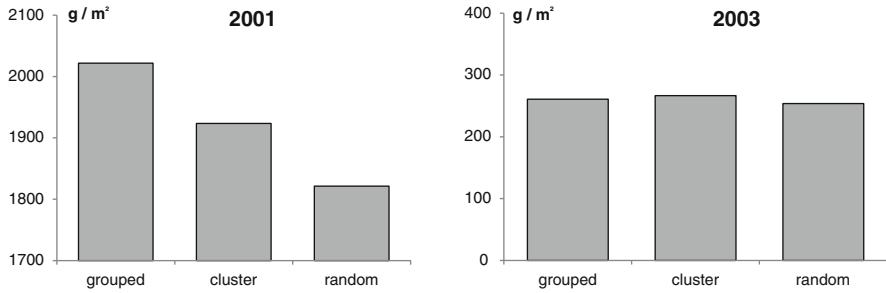


Fig. 18.16 Net primary production of the entire stand for different mixing structures (average of mixing ratios) in the year 2001 with good growing conditions (*left*) and in the dry year 2003 (*right*) at the site Kranzberger Forst

minimise resource limitation resp. to maximise resource capture (e.g. Chapin 1980). Vivin and Guehl (1997), however, report that the root to shoot biomass ratio of *Quercus robur* seedlings decreased by drought, which contradicts the theory that under limiting water supply increased root growth would be advantageous for the acquisition of water (Tyree and Alexander 1993).

In dry periods more carbon was invested in root growth of beeches compared to leaf growth (Fig. 18.15) indicating that more fine root biomass is formed in the trees' search for resources (water). These changes in the carbon allocation from above- to below-ground guarantee the water supply during drought (Cermak et al. 1993; Leuschner et al. 2001). Noguchi et al. (2007) found that the ratio of fine root biomass to total biomass of different tree species clearly increased in drought periods pointing out a biomass allocation to the fine roots.

18.5.3.6 Influence of Stand Structure

Other factors that influence growth of forest stands in drought periods are stand structure and interspecific competition. Based on three different mixing ratios (spruce to beech 30:70, 50:50 and 30:70) and three different mixing structures (random, clustered, grouped), the growth of mixed stands was simulated. Figure 18.16 shows the net primary production of the mixed stands for the three mixing proportions averaged over the mixing ratios for the year 2001 and 2003.

Again, distinctively smaller net primary production values in the drought year 2003 compared to the 2001 values were evident. In 2003 only about 14% of the npp of 2001 was gained by the different forest stands. When the effects of the different mixing structures on npp were compared, decreasing values were obvious in 2001, starting with a grouped mixing structure over a clustered structure to randomly distributed beeches and spruces. The low npp of the randomly structured stand was due to the low npp of spruce that cannot be compensated by the higher npp values of beech in the randomly structured stand. In 2003, all three mixing structures produced nearly the same (250–270 g/m). Hereby, the spruces had the highest

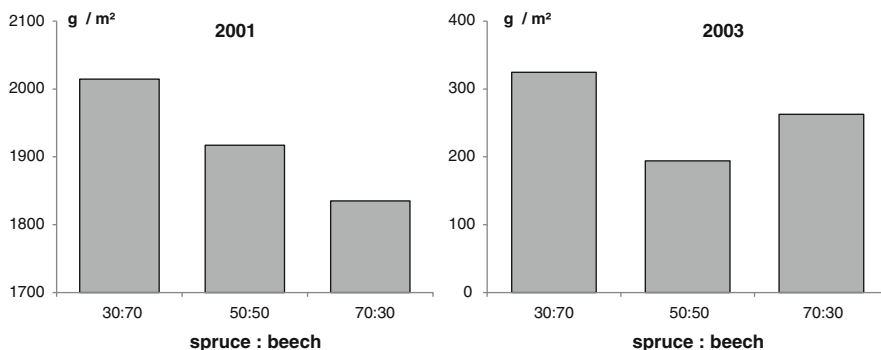


Fig. 18.17 Net primary production of the entire stand for different mixing ratios (average of mixing structures) in the year 2001 with good growing conditions (*left*) and in the dry year 2003 (*right*) at the site Kranzberger Forst

npp reductions (in relation to the 2001 values), particularly the grouped mixing structure. Because there was also a clear drop in the npp of the beech trees in all mixing structures, npp of the year 2003 fell to a low level showing no differences between the mixing structures.

If the mixing ratios were analysed (Fig. 18.17), in the year 2001 with good growing conditions the stand with a spruce beech ratio of 30:70 had the highest npp, followed by the 50:50 ratio and the 70:30 ratio. The differences between the mixing ratios, however, were small, less than 9% based on the maximum. In the dry year 2003 the lowest npp was found for the 50:50 mixture, which was 40% less compared to the 30:70 mixture and 26% less compared to the 70:30 mixture. Generally, npp rates were clearly lower in 2003 than in 2001.

Based on npp and on the e_{ta} for the different mixed forest stands the water use efficiencies (wue), i.e. the dry matter production per kg of water used for evapotranspiration, were calculated for the years 2001 and 2003 (Fig. 18.18).

The lower the proportion of beeches in the stand the lower is the wue. For the different mixing structures, the efficiencies of the year 2001 ranged from 6.1 g/kg H₂O for grouped mixtures to 4.3 g/kg H₂O for randomly distributed trees. The sharp decline in wue from pure beech to pure spruce stands for the year 2001 could not be found for the dry year 2003. Although wue of pure beech was relatively high with 2.5 g/kg H₂O, the efficiencies of all mixing ratios and mixing structures and of the pure spruce stand varied between 0.2 and 1.0 g/kg H₂O.

18.5.3.7 Influence of Stand Structure: Discussion

Stand structure can influence the growth of mixed beech–spruce stands to a great extent (see Chap. 13). Productivity and efficiency of a stand was changed by the mixing structure (random, cluster, group) and mixing proportion, as well as by drought stress. The simulations revealed comparatively small efficiency differences between the mixing ratios respectively the mixing structures in years with drought

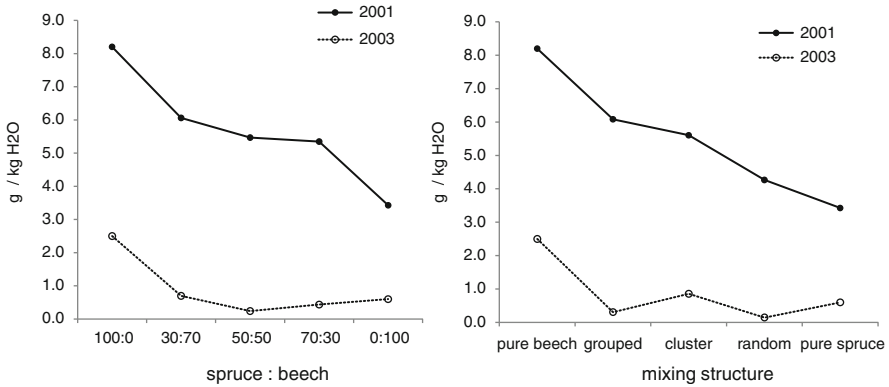


Fig. 18.18 Water use efficiency of mixed beech–spruce stands for different mixing ratios (*left*, averaged over all mixing structures) and different mixing structures (*right*, averaged over all mixing ratios) for the years 2001 and 2003 at the site Kranzberger Forst

stress but distinct differences in years with good water supply. This result was consistent for pure stands as well as for stands with different mixing structures of beech and spruce. It can be deduced that the wue of a tree species is reduced under drought stress. The mixing structure of a forest stand altered the water use efficiency. The efficiency differences are more pronounced under favourable growing conditions than under drought influence. The findings of Guehl et al. (1995), Barr et al. (2007) and Menon et al. (2007) underline this assumption of lower water use efficiencies under stress.

18.6 Conclusions

The scenario simulations with the eco-physiologically based, individual tree growth model BALANCE proved feasible for analysing the influence of environmental changes on growth, productivity and efficiency of forest stands. The simulation results were plausible and in accordance with empirical studies. From the simulations, the following conclusions can be drawn:

Defoliation of beech led to a decline of total biomass growth as expected. The intensity and the frequency of the defoliation stress determined whether trees recovered fully, partially to a lower biomass level, or died.

Even without changing physiological parameters like photosynthetic efficiency explicitly in BALANCE, intrinsic changes of allocation patterns led to an over-compensation of the growth of certain tree compartments under low defoliation rates. The recovery time between the defoliation events was more important than the number of defoliations.

Opportunity costs were incurred by beech trees in mixed stands that invested in defence of a species-specific pathogen, which did not attack their interspecific competitors. Competition effects between investing and non-investing trees caused

losses that ranged from 1.5 to 3.1 of the direct defence investments. The competing non-affected spruce trees were able to increase their total biomass at the cost of the beech trees, to 140% when compared to the control, but were only able to compensate for the losses of beech if the defence investments of beech did not exceed 20–30%. This showed the limits of the buffering capacity in mixed stands.

Additionally to the defence rate of beech, stand structure influenced the growth of beech and spruce significantly. The simulation results revealed a differential pattern considering the two species. Spruce significantly profited from an individual tree mixture but could not compensate for the growth of beech in clustered and grouped situations. In contrast, beech reacted more to the absolute proportion of spruce in the stand than to the distribution of the spruce trees.

The simulation results suggest that the allometry between dbh and above-ground biomass was changed nonlinearly. The factors influencing allometry were the proportion of net resources invested in defence, the proportion of a tree species at the total crown area of a stand, and the degree of clustering of the tree species. The findings suggest a higher biomass to dbh ratio for beech at higher proportions of beech in the stand. The more beech was spatially intermingled with spruce the lower the biomass to dbh ratio of beech trees.

Compared to dominated, small trees, productivity of dominant big trees was influenced more by decreasing resource availability (e.g. water). Under severe drought stress as for example for the year 2003, however, for spruce a nearly constant loss of productivity for all size classes was obvious.

Drought stress clearly changed the allocation patterns of trees. Total biomass growth was decreased particularly for spruce under intensified drought. While in years with favourable growing conditions, the free C-pool of the trees increased, more severe drought caused increasing losses of the free C-pool. Fine root biomass of beech, on the other hand, increased with increasing drought. This is in conformity with the plant allocation theory, that above and below-ground allocation is adjusted to minimise resource constraints resp. maximise resource acquisition.

Stand structure characterised by the kind of mixing and/or tree species composition was shown to change productivity and efficiency of a forest stand.

Overall, climate sensitive, physiologically based growth models like BALANCE are useful tools for analysing influences of environmental changes on productivity and efficiency. They can help to map out adaption strategies to avoid negative consequences of environmental changes. Furthermore, such models can provide interesting hypotheses for subsequent empirical or experimental testing and can thus support theory building.

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