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Modelling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate

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Abstract Tree growth and carbon dynamics are important issues especially in the context of climate change. However, we essentially lack knowledge about the effects on carbon dynamics especially in mixed stands. Thus, the objective of this study was to test the effects of climatic changes on the above and below ground carbon dynamics of a mixed stand of Norway spruce (Picea abies [L.] Karst.) and European beech (Fagus sylvatica L.) by means of scenario simulations. To account for the typical tree interactions in a mixed-species stand a spatial explicit tree growth model based on eco-physiological processes was applied. Three different climate scenarios considering altered precipitation, temperature, and radiation were calculated for an unthinned and a thinned stand. The results showed significant changes of above and belowground biomass over time, especially when temperature and radiation were increased additionally to decreased precipitation. The reduction in biomass increments of Norway spruce were more attenuated above than below ground. In contrast, the results for beech were the opposite: The belowground increments were reduced more. These results

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suggest a shift in the species contribution to above and belowground biomass under dryer and warmer conditions. Distinct effects were also found when thinned and unthinned stands were compared. A reduced stand density changed the proportions of above and below ground carbon allocation. As a main reason for the changed growth reactions the water balance of trees was identified which lead to changed biomass allocation pattern.

Keywords Biomass · Carbon · Climate change · Process modelling · Tree growth · Mixed stands

Introduction

Evidence for climate change is consolidated by the results of more and more research. The IPPC report (2007) showed the drastic consequences that global warming will have in the next decades. Precipitation and temperature will most likely change substantially in the coming years on a global scale (IPCC 2001, 2007) as well as on a regional scale (e.g. UBA 2007; KLIWA 2006). Not only mean values, but also distribution during the year will probably differ from the current climatic situation (KLIWA 2006). It also seems that the frequency of climatic extremes, such as droughts, will increase in the coming decades (Meehl et al. 2000; Jonas et al. 2005).

Considering all these aspects, the impacts of these climate changes upon our forest ecosystems are still in many ways unclear. The interest in the scientific community for the effects of global warming upon tree growth has obviously increased. There is more literature touching upon this topic than could be considered in this article. Therefore only some relevant examples are highlighted, which should document the research fields.

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Many publications deal with observed changes in forest growth. Some of them are attributed to possible effects of global change (Pretzsch 1996, 1999). Scenario simulation was soon identified as a tool necessary for assessing the possible consequences of climate change (Malanson 1993; Coops and Waring 2001; Pretzsch and Dursky 2002).

More recently the effects of climate change on tree vitality have also been considered (Rötzer et al. 2005). This topic is closely connected with the question of possible effects of environmental changes on plant-parasite and plant-herbivore interactions. Ayres and Lombardero (2000) tried to identify the impact on forest ecosystems due to global change by reviewing the available literature. They were able to reveal ecological as well as economic consequences of these interactions.

Apart from growth considerations, carbon budgeting of the forest ecosystem was also identified as a field of increased scientific effort. Boreal forests, which are most likely affected strongly by climatic changes, received increasing attention (Price and Apps 1995; Barr et al. 2002; Black et al. 2007). One probable reason for the focus on boreal forests is the greater complexity of temperate forests, which are usually dominated by a more complex species interaction.

The impact of climate change on the allocation pattern of trees is especially interesting because of their long life cycles. One essential aspect is the variation in above and below ground carbon dynamics under changed environmental conditions, which is not fully understood yet (Black et al. 2007). Even without the consideration of climatic effects, only a few empirical studies deal with a comparison of carbon or biomass allocation above and below ground with mature forest trees. The great effort required to study the below ground carbon allocation means that most empirical studies consider only juvenile trees (e.g. Oleksyn et al. 1999; Wang et al 2000) or are limited to pure stands (e.g. Skovsgaard et al. 2006). Empirical studies on mixed stands considering old trees and dealing with the interspecific effects are even more rare, and are not able to consider dynamic effects because of the destructive nature of sampling.

To contribute to the open questions addressed above, a spatially explicit process oriented tree growth model was used to simulate carbon dynamics in a mixed stand of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.). By means of scenario simulation the following questions were tested:

1. Is the total above and below ground carbon allocation of trees in mixed spruce-beech stands changed under dryer and warmer conditions?

- 2. Do species contribute in the same proportions to the total above and below ground carbon allocation under dryer and warmer conditions?
- 3. Does stand density affect carbon allocation of spruce and beech under warmer and dryer conditions?

Material and site description

The site 'Kranzberger Forst' is located in southern Bavaria (Germany), about 40 km northeast of Munich in the natural region "Tertiäres Hügelland" at about 500 m altitude. The experimental site was established in the year 1994. The main tree species are Norway spruce and European beech. There are other tree species present, however these do not contribute significantly to stand structure.

The soil of the Kranzberg Forest is a luvisol which originates from loess over tertiary sediments. The required soil input values for the model are field capacity and wilting point in the single rooting layers. The necessary values were taken from the nearby level II plot 'Freising' (Rötzer et al. 2005). For the soil with an estimated rooting depth of 100 cm an average field capacity of 34 mm/dm and a mean wilting point of 14 mm/dm were calculated. At the beginning of the simulation runs, the soil and nutrient status of the trees were set at their optimum and no nitrogen deposition was assumed.

The base simulations were done for the climate conditions of the years 2000–2005 (status quo scenario). Values of the weather were taken from the climate station 'Freising' of the Bavarian State Institute for Agriculture, which is about 2 km away from the Kranzberg forest. The simulations were based on daily temperature, precipitation, humidity, wind speed and radiation data. In Table 1 the mean annual values for the period 2000–2005 as well as for the scenario runs are listed.

Averaged over the years 2000–2005 the mean annual temperature of the Kranzberg forest was calculated at 8.7° C with a mean annual radiation sum of $1,205 \text{ J/cm}^2$ and a precipitation sum of 814 mm. Whilst the

 Table 1 Mean annual values for temperature, precipitation and radiation at the site "Kranzberger Forst" (period 2000–2005 and scenarios)

	Precipitation (mm)	Temperature (°C)	Radiation (J/cm ²)
2000-2005	814	8.7	1,205
Scenario 1	651	8.7	1,205
Scenario 2	651	11.7	1,447
Scenario 3	692	8.9	1,253

precipitation sum is almost equal to the climatological mean for this region, which ranges between 750 and 850 mm, the mean annual temperature and the radiation sum calculated for the period 2000–2005 are clearly higher than the long term means of the Kranzberg forest region which amount to 7–8°C and 1,015 J/cm² according to BayFORKLIM (1996).

In scenario 1 precipitation was reduced evenly by 20% resulting in a mean annual sum of 651 mm. In scenario 2 additionally temperature was increased by 3°C and radiation by 20% according to the results of the IPCC (2001). Because IPCC (2001) also assumes a more frequent occurrence of extreme weather events, in scenario 3 the extreme year 2003 with a very dry and hot summer was repeated every second year [for physiological effects of the year 2003 see e.g. Nikolova et al. (2008a)]. This way the weather data of the years 2001 and 2005 were replaced by the values of the year 2003, whereby the mean annual precipitation sum decreased to 692 mm. Temperature and radiation showed only a small increase to 8.9°C and to 1,253 J/cm².

For simulation an initial stand was defined, comprising of a part of the original experimental site 'Kranzberger Forst' to keep computation time in acceptable limits. The initial stand was composed of 172 spruce and 37 beech trees (Fig. 1).

Whilst all 209 trees are used for the simulations, the outer two tree rows were excluded for the analyses to eliminate edge effects. Therefore the results shown depend on 87 spruce and 32 beech trees. Table 2 shows the characteristics of the analysed stand.

Fig. 1 Tree allocation at the forest site "Kranzberger Forst"

 Table 2 Characteristics of the analysed mixed forest site

 "Kranzberger Forst"

Species	Age (years)	n	h_{mean} (m)	dbh _{mean} (cm)	ba (m²/ha)
Spruce	50	87	23.5	27.0	35.6
Beech	56	32	23.1	23.0	9.3
Total		119			44.9

n number of trees, h_{mean} mean height, dbh_{mean} mean diameter at breast height, ba basal area

A more detailed description of the site 'Kranzberger Forst' can be found in Pretzsch et al. (1998) and Wipfler et al. (2005).

For a further simulation run, stand density of the Kranzberg forest was reduced. For a thinning scenario 29 spruces and 11 beeches were removed, those having the smallest diameter at breast height, simulating a thinning from below. As a result for the stand with the reduced stand density a basal area of 38.5 m^2 /ha was calculated. The initial modelled biomass of the entire stand decreased from 71.8 tC/ha for the original stand to 64.6 tC/ha.

Model

The physiological growth model BALANCE computes the three-dimensional development of individual trees dependent on the environmental factors weather, CO₂, soil conditions, pollutants and the individual competition for light, water and nutrients. BALANCE derives explicit





Fig. 2 Spatial and temporal scheme of the model BALANCE

spatial crown shapes and rooting dimensions from the initial parameters tree height, stem diameter and from the tree coordinates. These are the basis for the initialisation of foliage-, stem-, branch-, coarse and fine root biomasses as well as for the leaf and root surfaces (Grote 2002).

The spatial calculation levels range from stand level and individual trees over single tree components (crown, stem, root) to crown and root layers, which are again vertically and horizontically divided into segments. The segments form the basis for the calculations of the physiological processes and cycles (Fig. 2).

The simulation of the processes for each segment of an individual tree is done in different time intervals. The availability of resources, i.e. the values of weather, water supply and phenology, is calculated daily. Therefore daily values of temperature, radiation, precipitation, wind and relative humidity are needed as well as daily values of the air chemistry (CO_2 , air pollutants, N-deposition). Additionally, values characterising the soil (layers, nutrient release, maximal water availability) must be available.

At the end of each month or of each decade (10 days) the daily values of the resource availability are added up. They form the basis for calculating the physiological processes and the biomass changes. These are photosynthesis, respiration and nutrient availability. Allocation of carbon and growth of the different compartments is computed in the same time interval. The above ground biomass (agb) is the sum of the biomass of the foliage (bm_{fol}), the twigs (bm_{twig}), the branches (bm_{bra}), the buds (bm_{bud}), the reserve (bm_{res}) and the stem (bm_{stem}):

$$agb = bm_{fol} + bm_{twig} + bm_{bra} + bm_{bud} + bm_{res} + bm_{stem}$$
(1)

The below ground biomass (bgb) is the sum of the fine root biomass (bm_{fr}) and the coarse root biomass (bm_{cr}) :

$$bgb = bm_{fr} + bm_{cr} \tag{2}$$

Foliage biomass is calculated based on the actual foliated volume of the segment (v_f), the foliage density (δ_f) and the specific foliage area of the segment (sfa):

$$bm_{fol} = v_f \times \delta_f / sfa \tag{3}$$

Foliage density in Eq. (3), in turn, is a function of the maximum foliage density, the maximum volume of the segment and the competition factor. The specific foliage area of the segment (sfa), on the other hand, is a function of the maximum and minimum specific foliage area and the competition factor.

Based on the foliage biomass, the twig biomass can be estimated using the species specific ratio twigs/foliage biomass (r_{twig}):

$$\mathrm{pm}_{\mathrm{twig}} = \mathrm{bm}_{\mathrm{fol}} \times r_{\mathrm{twig}}$$
 (4)

The biomass of the branches is estimated from the branch wood density (δ_{bw}) and the branch biomass volume (v_b), which is calculated from the foliage biomass and the fraction of sapwood area needed to supply the foliage biomass within the segment:

$$bm_{bra} = v_b \times \delta_{bw} \tag{5}$$

The stem biomass is calculated in an analogue way to the branch biomass:

$$bm_{stem} = v_{stem} \times \delta_w \tag{6}$$

 Bm_{stem} is the product of the volume of the stem (v_{stem}) and the wood density (δ_w). Hereby stem volume is described as function of tree height, diameter at breast height and species specific stem form.

Whilst bud biomass (bm_{bud}) is calculated from the demand of carbon required to produce the foliage for the next year, the biomass of the reserve pool (bm_{res}) , i.e. the free available carbon, is a fraction of the living woody tissue.

Fine root biomass (bm_{fr}) as a part of the below ground biomass is estimated from foliage biomass by using a species specific ratio of fine roots to foliage ($r_{\rm fr}$):

$$bm_{fr} = bm_{fol} \times r_{fr} \tag{7}$$

Coarse root biomass is—similar to the branch biomass—derived from the coarse root density (δ_{cr}) and the coarse root volume (v_{cr}), which in turn is calculated from the fine root biomass and the fraction of sapwood area needed to supply the fine root biomass within the segment:

$$bm_{cr} = v_{cr} \times \delta_{cr} \tag{8}$$

Once a year, i.e. at the end of the vegetation period, the three-dimensional structure of each tree, the development of the entire stand and the mortality are calculated.

Fig. 3 Modules and cycles of model BALANCE



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By modelling the essential parameters of the water, carbon and nitrogen balance, the growth of trees that depend on these parameters, and the consequences for the stand structure can be analysed. Within the different cycles calculated in different time intervals numerous interactions can be seen, which are indicated by arrows in the Figs. 2 and 3.

Height, diameter, stem, crown and root growth are simulated on the base of the annual net carbon gain, which is a result from the physiological processes of photosynthesis (Haxeltine and Prentice, 1996), respiration (Penning de Vries et al. 1989), distribution of carbon and nitrogen in the tree (Grote 1998) and the aging of tissues.

Respiration and photosynthesis

Respiration is the sum of maintenance and growth respiration. Photosynthesis, in our context, is calculated as a function of leaf surface, light, temperature and CO₂-concentration and is reduced by the lack of water and nutrients as well as by pollutants. The calculation of the relative light consumption was derived from the competition algorithm of the single tree simulator SILVA (Pretzsch 1992) and extended by a light extinction function of a Lambert-Beer type. In contrast to SILVA, in BALANCE the search cone for the competition estimation is not applied once for every individual tree, but separately for each single crown segment.

Phenology

In order to depict the annual development of a tree, the annual cycle of foliage development must be known. With the beginning of bud burst foliage, biomass and leaf area as well as light availability and radiation absorption change. Thus, the date of foliage emergence in a tree determines its assimilation and respiration rate and also affects the environmental conditions of the trees in its vicinity. Therefore, in BALANCE the beginning of bud burst is modelled by using a temperature sum model (Rötzer et al. 2004), and foliage senescence is estimated in dependence on the respiration sum (Rötzer 2003).

Water balance

The simulation of the water balance considers the soil conditions in different layers as well as the influence of interception and percolation based on canopy and root distributions. Rooted volume and the soil characteristics define the water and nutrient availabilities of a tree. The rooting volume is dependent on the tree size and on the competition situation and therefore the influence of the stand structure and of the species mixing is reflected again in these processes. The evapotranspiration is described as the minimum of the potential evapotranspiration (ETp) and the maximum of the evaporation (Monteith 1965). The maximum evaporation is estimated from the actual crown interception and the water supply for the tree. The relation

of actual evaporation to ETp determines the extent of water stress for the photosynthesis.

Nutrient cycle

The nutrient uptake results from the minimum of demand, supply and absorption capacity (Grote 1998). In a first step only the nitrogen cycle as the most important nutrient element is considered. The demand is determined by the difference between the actual nitrogen concentration and a given optimal concentration. The supply is defined by the soil characteristics of the rooted volume, the uptake capacity by the root surface and its specific absorption rate.

Allocation

The distribution of the net assimilates and of the nitrogen is adapted to the demand of the individual compartments (Grote 1998), which in turn are determined by the relationships between the compartments according to the "functional carbon balance"-theory (Mäkela 1990) and the "pipe-model"-theory (Valentine 1985) and by the N-content differences between the single compartments and their optimal contents.

A detailed description of the model BALANCE can be found in Grote and Pretzsch (2002) and in Rötzer et al. (2005).

Results

Figure 4 shows the above and below ground biomass of the spruce (right) and the beech trees (left) at the site 'Kranzberger Forst' for the years 2000-2005, simulated with the model BALANCE. Starting with an initial agb of 46.6 tC/ha for the 87 spruce trees in January 2000 the agb rises up to 65.1 tC/ha in December 2005. For the bgb an increase from 5.6 to 10.3 tC/ha was calculated. The 32 beech trees showed a rise of the agb from 17.9 to 25.5 tC/ha, while the bgb was 1.7 tC/ha at the beginning of



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Fig. 5 Above and below ground biomass increment of all trees for the analysed site "Kranzberger Forst" for the years 2000-2005

the simulations in 2000 and 2.1 tC/ha at the end of the simulations in 2005.

For the beech trees a steady increase of the biomass is predicted for the entire period, whereas spruce trees show a decline for the dry year 2003. The decrease was more pronounced for the below ground biomass.

This can again be seen in Fig. 5, where the increments of the above and below ground biomass summed up over all trees are shown for the years 2000-2005.

With the exception of the year 2003, the annual above ground biomass increment of the analysed stand at the Kranzberg forest varied from 3.3 to 8.1 tC/ha and the annual bgb increment was between 0.1 and 2.8 tC/ha. For the extreme dry and hot year 2003, the above ground biomass increment was simulated with only 0.3 tC/ha, whereas the below ground biomass increment was negeative, which denotes a loss of biomass of 1.1 tC/ha.

In the next step biomass dynamics of the site 'Kranzberger Forst' was estimated for three scenarios. In Figs. 6 and 7 the course of agb and bgb is illustrated for the beech and spruce trees based on the weather conditions outlined in Table 1. The values in Fig. 6 are based on the annual results of the status quo scenario, where carbon dynamics were simulated with actual empirical climate data of period 2000-2005, which were set as 100%.

Fig. 4 Simulated total above and below ground biomass of the beech (left) and the spruce (right) trees at the site "Kranzberger Forst" for the years 2000-2005



115

110

105

100

95

90

115

110

105

100

95

90

Fig. 6 Above ground (*left*) and below ground (*right*) total biomass of beech trees for the three climate scenarios at the site "Kranzberger Forst" referenced to the status quo scenario which was simulated for the years 2000–2005 (100%)





For the spruce trees of the Kranzberg forest a steady decline of the above ground biomass was found for scenario 1 compared to the status quo scenario, which lead to a reduction of 4% in the last year. The bgb had a maximum deviation of 4% in year 5, however, at the end of the simulations for scenario 1 the deviation was only 2%. The above ground biomass of scenario 2 decreased to 94% until year 5, whereas for year 6 a small increase of 1% was determined, leading to a total reduction of 5%. The bgb in scenario 2, on the other hand, showed no steady course for the single years. However, at the end of the simulation, *bgb* had a loss of 6% of the base period biomass. Agb for the "extreme" scenario 3 decreased to 95% in year 2 (an



extreme year) and afterwards increased up to 98% in year 4, followed by a decrease to 95% at the end of year 6. The bgb varies from higher values in the years 4 and 5 to lower values in the years 2, 3 and 6 for scenario 3, all compared to the base period. At the end of the simulations bgb is lowered by 9%. At the end of year 4, which was very hot and dry, the bgb from scenario 2 and 3 is about 10% higher compared to that from the base period.

The reduction of the total above and below ground biomass increment for the three scenarios referenced to the increments of the status quo scenario is illustrated in Fig. 8. In addition to the original stand, the simulations were performed for a stand with a reduced stand density.

For scenario 1 agb and bgb increment of the spruce trees of the original stand were reduced by 15 and 4% respectively, while for the spruces with the reduced stand density the reduction was only 12 and 0% compared to the base period 2000–2005. For scenario 2 we found clearly smaller reductions for the stand with the reduced stand density, both for the above (18% vs. 9%) and the below (14% vs. 4%) ground biomass increment, all compared to the status quo scenario. For scenario 3 agb and bgb increments were all reduced for over 15%. The differences between the original and the reduced density stand, however, were distinctly lower than 3%.

For the beech trees the scenario 3 simulations result in reductions of 16% for the agb increments and 15 and 14%



Fig. 8 Reduction of the total above and below ground biomass increment of the spruce and the beech trees of the original stand and the stand with the reduced stand density (sd) for the three scenarios based on the increments of the period 2000–2005

for the bgb increment, compared to the reference scenario. For scenario 2 the beech trees of the original stand show the highest decrease with 20% for the *agb* and 26% for the bgb increment. For the stand with the reduced density high values with 18% and 21% were found. For scenario 1 the lowest reductions were calculated: Whilst for the original stand agb and bgb increment were reduced by app. 8 and 12%, for the stand with the reduced density the reductions were 9 and 11%.

Discussion

Using the physiologically based model BALANCE, growth for the mixed spruce and beech stand at the site 'Kranzberger Forst' was simulated. The calculations of the above and below ground biomass for the original stand and for a stand with a reduced stand density over the period 2000– 2005 as well as for three climate scenarios can be summarised as follows:

- Scenarios: The smallest reductions of the biomass increment compared to the status quo scenario could be found for scenario 1, in which only precipitation was reduced. For scenario 2, in which additionally temperature and radiation were changed, and for the "extreme" scenario 3 agb and bgb increments (original stand) were all reduced for more than 14% compared to the status quo scenario. The highest reductions are obvious for beech in scenario 2 with up to 26% for the bgb increment. Despite a temperature change of only 0.2° C, a radiation change of only 48 J/cm² and a precipitation decrease of less than 12%, bgb and the agb increment for scenario 3 show high growth reductions. The biomass increment of spruce was shortened more for scenario 3 than for scenario 2. particularly for the bgb increment.
- Agb/bgb: In scenario 1 and 2 the reduction of the agb increment for spruce trees (original stand) was clearly higher (15 and 18%) compared to the bgb increment (4 and 14%). For beech trees in these scenarios, however, the reduction of the bgb increment was higher (agb: 8 and 20% ↔ bgb: 12 and 26%). For scenario 3 a clear differentiation between the agb and bgb increment pattern is not possible, both for beech and spruce.
- *Stand density:* If the stand density is reduced, the highest growth reductions are obvious compared to the original stand for scenario 2. For scenario 3 (extreme scenario) only small resp. no differences could be found.

One main reason for these growth reactions of the trees can certainly be found in the water balance of the trees (Nikolova et al. 2008b). In Fig. 9 the mean annual total evapotranspiration (sum of actual evapotranspiration and interception) of the original stand and of the stand with the 179

reduced stand density as well as the mean annual precipitation sum can be seen for the period 2000–2005 and for the three scenarios.

It is obvious that for the base period 2000-2005 the average precipitation sum is higher than the evapotranspiration sum. This means that on average water does not restrict growth. In scenario 2 and 3 the evapotranspiration sums are higher than the precipitation sums, which can limit growth. Because of the good soil conditions at the site 'Kranzberger Forst' with a high water storage capacity, excessive water stress could be avoided until the end of the simulated period. Over the 6 years, however, the mean soil water content for all scenarios decreases from year to year. This could result in extreme water stress for the following years related to further growth depressions. A second effect is that ground water recharge is diminished because with decreasing precipitation and increasing potential evapotranspiration run off decreases. This will further intensify water stress and growth reduction.

A good parameter showing the degree of water stress is the ratio of the actual and potential evapotranspiration eta/ etp. In Fig. 10 this ratio is illustrated for the spruce and the beech trees of the original stand and for the stand with the reduced stand density for the base period and for the three scenarios.

Lowest eta/etp values can be found for scenario 2 with 0.52 for spruce and with 0.63 for beech. Highest values were calculated for the base period with 0.71 for spruce and 0.74 for beech. Despite the fact that for scenario 3 the precipitation sum is greater than the evapotranspiration sum (Fig. 9), the biomass increment decreases clearly compared to the values of the base period (Fig. 8). Figure 10 shows the reason: the eta/etp ratio is definitely smaller than the ratio for the base period and also for scenario 1. This means that in the annual course of some



Fig. 9 Mean total evapotranspiration of the orignal mixed stand eta (org) and of the stand with the reduced stand density eta (red) and mean annual precipitation sum at the site "Kranzberger Forst" for the base period 2000–2005 and for the three scenarios



Fig. 10 Ratio of the actual and potential evapotranspiration for the spruce and beech trees of the orignal stand and of the stand with the reduced stand density at the site "Kranzberger Forst" for the base period 2000–2005 and for the three scenarios

(extreme) years the soil water content is so small that eta is reduced severely.

It is also evident from Fig. 10 that the stands with the reduced stand density (rs) have higher eta/etp ratios compared to the original stands (os), which shortens the growth reductions. The highest reduction of the biomass increment (agb from 18% for os to 9% for rs and bgb from 14% for os to 4% for rs) in scenario 2 for spruce is linked to the greatest difference in the eta/etp ratio (0.52 vs. 0.54).

The results of this study confirm that water balance of the trees is closely connected to the growth increment of the above and below ground biomass. Whether a tree invests more carbon in root growth or in foliage, branch and stem growth mainly depends upon the water supply for a tree.

To elucidate these relationships the mean annual eta/etp ratios of all simulation runs were classified in three drought classes separately for the spruce and the beech trees. Class 1 contains all ratios above 0.7 (no water stress), class 2 ranges between 0.5 and 0.7 (water stress) and class 3 includes all ratios below 0.5 (severe water stress). For all classes also the average ratios of the below and the above ground biomass increments were calculated. In Fig. 11 these ratios for spruce and beech are shown for the three drought classes.

For spruce as well as for beech trees the bgb/agb increment ratio is significantly higher for drought class 2 than for class 1. On average the bgb/agb ratio of spruce is 0.33 for drought class 1 'no water stress' and 0.64 for drought class 2 'water stress'. For beech the ratios are 0.04 for the drought class 1 and 0.13 for drought class 2, denoting that if trees are stressed by water shortage more carbon will be invested in root growth while the above ground biomass increment is reduced. These findings were supported by Polomski and Kuhn (1998), who found that trees under decreasing water supply increase the absorption surface and the branching of roots, i.e. increase root growth.



Fig. 11 Mean ratio and standard error of the below and the above ground biomass increment of beech and spruce for the three drought classes based on the eta/etp ratio (class 1: eta/etp \geq 0.7; class 2: 0.5 \leq eta/etp < 0.7; class 3: eta/etp < 0.5)

Under severe water stress (drought class 3) the bgb/agb increment ratio of beech results in significantly higher values compared to drought classes 1 and 2, indicating a higher root growth compared to the above ground biomass growth. For spruce a non significant drop of the bgb/agb increment ratio could be found for drought class 3 compared to drought class 2 indicating that under severe drought stress root growth of spruce is reduced compared to the growth of the above ground biomass (Fig. 11).

Severe water stress can lead to drastic growth reductions, in which roots as well as above ground biomass die off. This result found for spruce corresponds to Polomski and Kuhn (1998) citing Drew (1987) that droughts cause irreversible damage when water loss exceeds more than 70%. An other example of such an extreme water stress period is the summer drought in the year 2003 (see Fig. 5), where the bgb increment is negative in the simulations.

The mean bgb/agb ratios of the two tree species are 0.16 for spruce and 0.10 for beech. Compared to root/shoot ratios from literature (e.g. Bolte et al. 2004, Mund et al. 2002) we also found higher ratios for spruce than for beech, whereas the absolute values differ somewhat from the values in literature because of the different compartments defined as agb or shoot and bgb or root.

If the ratio of the initial coarse root biomass and above ground biomass for beech and spruce is calculated the values of 0.113 for spruce and 0.091 for beech are only somewhat lower than the ratios of 0.127 for spruce and 0.138 for beech that could be calculated from the data Pretzsch et al. (1998) published for the entire 'Kranzberger Forst'. The entire Kranzberg forest, however, has different basal areas of 30 m²/ha for spruce and 12 m²/ha for beech compared to the values for the stand used in this study $(35.6 \text{ m}^2/\text{ha} \text{ for spruce and } 9.3 \text{ m}^2/\text{ha} \text{ for beech; see}$ Table 2). On the other hand, the coarse root/wood ratios Fehrman et al. (2003) found for spruce (0.215) and for beech (0.090) fit well to the ratios calculated in this study with 0.179 for spruce and 0.093 for beech (based on the assumption of a wood density of 377 kg/m³ for spruce and 554 kg/m³ for beech). However, it has to be considered that ratios between below and above ground biomasses strongly depend on the plant age and on the increasing plant weight (Roloff and Römer 1989).

Conclusions

The results of the simulations for the mixed spruce-beech forest of the site 'Kranzberger Forst' showed that the model BALANCE produces realistic values for the above and the below ground biomass. Different scenarios demonstrate the reaction of biomass growth to special climate situations. We were able to show that water supply for the single trees is one of the main factors influencing growth and the allocation of carbon into the diverse compartments. For a better understanding of the reaction and the feedback of climate on the biomass growth in forest sites longer simulation runs have to be done. Furthermore the influence of the site structure (e.g. mixing ratio of tree species, stand density) must be investigated more in detail.

Regional climate scenarios (e.g. the REMO scenarios with a spatial scale of 10 km; Jacob et al. 2001) improve the simulations of the impacts of climate changes on growth. Extreme climate situations (drought events or storm disasters) and/or secondary stress effects like diseases and pests must be regarded as well (Seifert 2007). Allocation patterns of trees may additionally vary consistantly between years because of alternating cone and fruit production (Seifert and Müller-Starck 2008).

Another point of interest is the relationship of carbon allocation with the different plant compartments (roots, leafs, branches, stem) by including not only the water balance but also further environmental parameters in the analyses, such as soil temperature or soil structure for root growth as mentioned by Polomski and Kuhn (1998).

To improve the understanding of tree growth depending on environmental conditions the nutrient availability, particularly nitrogen, has to be considered in the simulations (e.g. Glynn et al. 2007). In this study for the Kranzberg Forest we assumed an optimal nitrogen supply. A further challenge for the simulation studies with the model BAs-LANCE will be to examine how nutrient availability changes in time, different for the species as well as for single trees, and how the growth of the below and the above ground biomass will change when influenced by a changed nutrient availability.

Closely connected with the nutrient availability but also with the water uptake are the rooting depth and the rooting systems of the species and the single trees. To analyse these influences is one of the next tasks of the simulations that have already been started for the Kranzberg Forest and other forest stands in Germany.

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References

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286

- Barr AG, Griffis TJ, Black TA, Lee X, Staebler RM, Fuentes JD, Chen Z, Morgenstern K (2002) Comparing the carbon budgets of boreal and temperate deciduous forest stands. Can J For Res 32:813–822
- Black TA, Hogg EH, Griffis TJ, Morgenstern K, Klujn N, Theede A, Nesic Z (2007) Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. Glob Change Biol 13:561–576
- BayFORKLIM (1996) Klimaatlas von Bayern. Buchhandlung Kanzler, München
- Bolte A, Rahmann T, Kuhr M, Pogoda P, Murach D, von Gadow K (2004) Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). Plant Soil 264:1–11
- Coops C, Waring RH (2001) Assessing forest growth across southwestern Oregon under a range of current and future global change scenarios using a processmodel, 3-PGN. Glob Change Biol 7:15–29
- Fehrman L, Kuhr M, von Gadow K (2003) Zur Analyse der Grobwurzelsysteme großer Waldbäume an Fichte [*Picea abies* (L.) Karst.] und Buche [*Fagus sylvatica* L.]. Forstarchiv 74:96– 102
- Drew MC (1987) Function of root tissues in nutrient and water transport. In: Gregory PJ, Lake JV, Rose DA (eds) Root development and function. Cambridge University Press, Cambridge, pp 71–101
- Glynn C, Herms DA, Orians CM, Hansen RC, Larsson S (2007) Testing the growth-differentiation balance hypothesis: dynamic responses of willows to nutrient availability. New Phytol. doi: 10.1111/j.1469-8137.2007.02203.x
- Grote R (1998) Integrating dynamic morphological properties into forest growth modelling. II. Allocation and mortality. For Ecol Manage 1111(2/3):193–210
- Grote R (2002) Foliage and branch biomass estimation of coniferous and deciduous tree species. Silva Fenn 36(4):779–788
- Grote R, Pretzsch H (2002) A model for individual tree development based on physiological processes. Plant Biol 4:167–180
- Haxeltine A, Prentice IC (1996) A general model for the light use efficiency of primary production by terrestrial ecosystems. Funct Ecol 10:551–561
- CC IP (2001) Land, use, land use change and forestry. In: Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ, Docken DJ (eds) IPCC special report. Cambridge University Press, Cambridge, p 337
- IPCC (2007) IPCC WGI Fourth assessment report to climate change: The physical science basis; summary for policymakers. IPCC Secretariat, Geneva, Switzerland, p 18
- Jacob D, Andrae U, Elgered G, Fortelius C, Graham LP, Jackson SD, Karstens U, Koepken C, Lindau R, Podzun R, Rockel B, Rubel F, Sass HB, Smith RND, Van den Hurk BJJM, Yang X (2001) A comprehensive model intercomparison study investigating the water budget during the BALTEX-PIDCAP period. Meteorol Atmos Phys 77(1–4):19–43
- KLIWA (2006) Regionale Klimaszenarien für Süddeutschland. KLIWA-Berichte 9, p 102
- Jonas M, Staeger T, Schönwiese CD (2005) Berechnung der Wahrscheinlichkeiten für das Eintreten von Extremereignissen durch Klimaänderungen–Schwerpunkt Deutschland -. UBA-Bericht 201 41 254, Dessau, p 252
- Malanson GP (1993) Comment on modelling ecological response to climatic change. Clim Change 23:95–109
- Mäkela A (1990) Modelling structural-functional relationships in whole-tree growth: Resource allocation. In: Dixon RK, Meldahl RS, Ruark GA, Warren WG (eds) Process modelling of forest growth responses to environmental stress. Timber Press, Portland, pp 81–95

- Meehl GA, David TK, Easterling R, Changnon S, Pielke R Jr, Changnon D, Evans J, Groisman P, Knutson TR, Kunkel KE, Mearns LO, Parmesan C, Pulwarty R, Root I, Richard T, Sylves T, Whetton P, Zwiers F (2000) An Introduction to Trends in Extreme Weather and Climate Events: Observations, Socioeconomic Impacts, Terrestrial Ecological Impacts, and Model Projections. Bull Am Meteorol Soc 81(3):413–416
- Monteith JL (1965) Evaporation and environment. In: Fogg GE (ed) The state and movement of water in living organisms, Sym Soc Exp Biol, vol 19. Academic Press, New York, pp 205–234
- Mund M, Kummetz E, Hein M, Bauer GA, Schulze ED (2002) Growth and carbon stocks of a spruce forest chronosequence in central Europe. For Ecol Manage 171:275–296
- Nikolova P, Raspe S, Andersen CP, Mainiero R, Blaschke H, Matyssek R, H\u00e4berle KH (2008a) Effects of the extreme drought in 2003 on soil respiration in mixed forest. Eur J For Res. doi: 10.1007/s10342-008-0218-6
- Nikolova P, Blaschke H, Matyssek R, Pretzsch H, Seifert T (2008b) Combined application of computer tomography and light microscopy for analysis of conductive xylem area in coarse roots of European beech and Norway spruce. Eur J For Res. doi: 10.1007/s10342-008-0211-0
- Oleksyn J, Reich PB, Chalupka W, Joelker GT (1999) Differential above- and below-ground biomass accumulation of European *Pinus sylvestris* populations in a 12-year-old provenance experiment. Scand J For Res 14(1):7–17
- Penning de Vries FWT, Jansen DM, ten Berge HFM, Bakema A (1989) Simulation of ecophysiological processes of growth in several annual crops. Simulation Monographs 29. PUDOC, Wageningen, The Netherlands
- Polomski J, Kuhn N (1998) Wurzelsysteme. Eidgenössische Forschungsanstalt f
 ür Wald, Schnee und Landschaft, Birmensdorf (eds) Haupt, Bern, Stuttgart, Wien, p 290
- Pretzsch H (1992) Modellierung der Kronenkonkurrenz von Fichte und Buche in Rein- und Mischbeständen. Allgem Forst- u Jagdztg 163(11/12):203–213
- Pretzsch H (1996) Growth trends of forests in southern Germany. In: Spiecker H, Miellkäinen K, Köhl M, Skovsgard JP (eds) Growth trends in European forests: studies from 12 countries. Springer, Berlin, pp 107–131
- Pretzsch H (1999) Changes in forest growth. Forstw Cbl 118(4):228– 250
- Pretzsch H, Kahn M, Grote R (1998) Die Fichten-Buchen-Mischbestände des Sonderforschungsbereiches Wachstum oder Parasitenabwehr? im Kranzberger Forst Forstw Cbl 117:241–257

- Pretzsch H, Dursky J (2002) Growth reaction of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus silvatica* L.) to possible climatic changes in Germany. A sensitivity study. Forstw Cbl 121:145–154
- Price DT, Apps MJ (1995) The boreal forest transect case study: global change effects on ecosystem processes and carbon dynamics in boreal Canada. Water Air Soil Pollut 82:203–214
- Roloff A, Römer HP (1989) Beziehungen zwischen Krone und Wurzel bei der Rotbuche (*Fagus sylvatica* L.). Allgem Forst- u Jagdztg 160(9/10):200–205
- Rötzer T (2003) Modellierung der Baumkronenentwicklung mittels eines ökophysiologi-schen Prozessmodells. Bundesministerium für Verbraucherschutz, Ernährung und Land-wirtschaft Ref. 533, Bonn:73-42
- Rötzer T, Grote R, Pretzsch H (2004) The timing of bud burst and its effect on tree growth. Int J Biometeorol 48:109–118
- Rötzer T, Grote R, Pretzsch H (2005) Effects of environmental changes on the vitality of forest stands. Eur J For Res 124:349– 362
- Seifert T (2007) Simulating the extent of decay caused by *Hetero-basidion annosum s.l.* in stems of Norway spruce. For Ecol Manag. doi:10.1016/j.foreco.2007.02.036
- Seifert T, Müller-Starck G (2008) Impacts of fructification on biomass production and correlated genetic effects in Norway spruce (*Picea abies* [L.] Karst.). Eur J For Res. doi: 10.1007/s10342-008-0211-0
- Skovsgaard JP, Stupa I, Vesterdal L (2006) Distribution of biomass and carbon in even-aged stands of Norway spruce (*Picea abies* (L.) Karst.): A case study on spacing and thinning effects in northern Denmark. Scand J For Res 21:470–488
- UBA (2007) Neue Ergebnisse zu regionalen Klimaänderungen. Hintergrundpapier Neue Ergebnisse zu regionalen Klimaänderungen http://www.umweltbundesamt.de/uba-info-presse/ hintergrund/Regionale-Klimaaenderungen.pdf, Umweltbundesamt Dessau, p 27
- Valentine HT (1985) Tree-growth models: derivations employing the pipe-model theory. J Theor Biol 117:579–585
- Wang JR, Letchford T, Comeau P, Kimmins JP (2000) Above- and below-ground biomass and nutrient distribution of a paper birch and subalpine mixed-species stand in the Sub-Boreal Spruce zone of British Columbia. For Ecol manag 130:17–26
- Wipfler P, Seifert T, Heerdt C, Werner H, Pretzsch H (2005) Growth of adult Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) Under free ozone fumigation. Plant Biol 7(6):611–618