

Mixing Patterns of Tree Species and their Effects on Resource Allocation and Growth in Forest Stands

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With 9 Figures and 1 Table

Abstract

The focus of this study is on differently structured mixed forest stands and their influence on resource allocation and growth patterns. Virtual mixed forest stands with different spatial structures, i.e. with a random distribution of European beech and of Norway spruce, and a mixture with groups and clusters of beech, were used for simulations over a period of 10 years. The calculations were done by using BALANCE, an individual tree based growth model which includes the simulation of the total water- and carbon flows of a forest stand. Tree growth is simulated based on physiological processes which are driven by external conditions, e.g. weather and soil conditions. The presented scenario simulations delivered realistic results for mixed spruce beech stands with random, clustered and grouped mixture. The simulations result in different resource distributions (radiation, water) within the three mixed stands which along with different leaf area index values increased biomass increment and efficiency of the random mixed stand more than of the clustered and grouped mixed stand.

Zusammenfassung

Im Mittelpunkt dieser Untersuchung stand, den Einfluss von Mischbeständen mit verschiedenen Mischungsstrukturen auf die Ressourcenverteilung im Bestand und die Wachstumsmuster zu untersuchen. Virtuelle Mischbestände in verschiedenen räumlichen Anordnungen, d.h. mit zufällig verteilten Buchen und Fichten bzw. mit Einmischungen von Buchengruppen sowie -clustern bilden die Basis für die 10-jährigen Simulationen. Die Berechnungen wurden mit dem einzelbaumbasierten Wachstumsmodell BALANCE durchgeführt, das den gesamten Wasser- und den Kohlenstoffkreislauf eines Waldbestandes abbildet. Die Berechnung des Wachstums beruht dabei auf physiologischen Prozessen, die von externen Bedingungen wie der Witterung oder den Bodenbedingungen gesteuert werden. Die Szenariosimulationen lieferten realistische Ergebnisse für Mischbestände aus Fichte und Buche mit zufälligen, gruppenweisen und geclusterten Anordnungen. Sie ergaben unterschiedliche Ressourcenverteilungen (Strahlung, Wasser) in den drei Mischungen, die zusammen mit unterschiedlichen Blattflächenindizes den Biomassezuwachs und die Effizienz des Bestandes mit zufälliger Anordnung stärker ansteigen ließen als die des gruppierten bzw. geclusterten Bestandes.

1. Introduction

In the next decades our forests must be adapted to a changing climate, which means for Central Europe higher temperatures, changed precipitation patterns and a higher number of stronger and longer lasting extreme events (*IPCC 2007*, *BENISTON et al. 2007*). Therefore, knowledge about climate effects on resource and growth allocations among trees is necessary to predict forest dynamics and to choose appropriate adaptation strategies. While allocation dynamics of tree individuals (e.g. *LANDSBERG 1986*, *NIKLAS 1994*) and growth dynamics at

the average tree level is understood quite well (e.g. OLIVER and LARSON 1996; PRETZSCH 2009), there is a lack of knowledge about growth patterns and resource allocations between the trees of a stand and their dependency on site conditions (SCHWINNING and WEINER 1998, WEINER et al. 2001, PRETZSCH et al. 2012, 2013). Because of intense interactions among individuals, the responses of individual trees cannot account for stand growth. The distribution of small and big, young and old, dominated and dominant trees within a stand as well as the species combination of a stand can alter tree interactions such as facilitation, competition or compensation. Additionally, the supply of above and below ground resources strongly depend on growth and space occupation, hence they determine the acquired amount of resources (e.g. GRAMS et al 2002, GAYLER et al. 2006, RÖTZER et al. 2009). According to MATYSSEK et al. (2005) the reaction pattern of stands are more than just the sum of individual tree responses and, thus, cannot be derived from trees grown solitarily.

Furthermore, it is still unclear to what extent mixed stands produce more or less than pure stands. PRETZSCH et al. (2010) for example found in a transect study of 23 long-term plots of Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) along an ecological gradient throughout Central Europe that dry mass growth of mixed stands varied between -46% to 138% based on the growth values of corresponding pure stands. The effects of mixture may be modified by e.g. the temporal and the spatial structure of the stands, the silvicultural treatment and the site conditions (HOLMGREN et al. 1997, KÖRNER 2006). But also the mixing pattern of forests, i.e. the formation of the single trees within the stand, can alter resource allocation and thus growth and productivity. In consideration of climate change it is questionable whether existing mixed forest stands will remain unaffected and balanced because mixing effects can also be explained by altered resource supply (e.g. VANDERMEER 1989, ROTHE and BINKLEY 2001, PRETZSCH and DIELER 2011).

To uncover such effects, i.e. resource allocation and reaction patterns of differently structured mixed forest stands, physiological growth models which include modules for resource allocation and their modification by species mixing can be proper tools. Physiological growth models simulate forest growth on the basis of generally accepted eco-physiological principles (e.g. MOHREN 1987, RUNNING and COUGHLAN 1988, SLOBODA and PFREUNDT 1989, KELLOMÄKI et al. 1993 or BOSSEL 1994). They can be used to study competition and facilitation effects of mixed forests under changing environmental conditions (e.g. RÖTZER et al. 2005, 2013). BALANCE (GROTE and PRETZSCH 2002, RÖTZER et al. 2009, 2010b) as a representative of this model type is a highly developed eco-physiological individual tree growth model adapted to simulate the growth of complex mixed species stands.

Consequently, to study the influence of different mixing patterns of tree species on resource allocation and growth patterns, scenario simulations for mixed Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) stands were done and analyzed. The objectives of this study were in detail:

- to uncover resource allocation patterns within the stands, i.e. the distribution of light and water, as well as the spatial distribution of the production area;
- to analyze the effects of the mixing structure and of the resulting resource allocations on productivity and efficiency; and
- to compare and explain the relationships of resource allocation and growth patterns both for the two species of the mixture and the entire stand along with the influence of yearly variations.

2. Model BALANCE

BALANCE, the model used for the scenario simulations, is a physiological growth model that calculates the 3-dimensional development of trees and forest stands and estimates the consequences of environmental influences. BALANCE simulates growth responses on the individual tree level and enables an estimation of the influence of competition, stand structure, species mixture, and management impacts. This is achieved by describing tree development as a response to individual environmental conditions and environmental change of conditions with individual tree development. This way, additionally to the weather conditions, CO₂ concentration, soil condition, competition between individuals, and stress factors can be regarded. The initial biomass of an individual tree is calculated from the dimensional variables tree position, tree- and crown base height, diameter, and crown radii. The increase in biomass is the result of the interaction of physiological processes which depend on the physical and chemical micro-environment that is itself influenced by the spatial structure of the stand. It is calculated based on the carbon and nitrogen that is taken up from each segment in dependence on the local energy supply and resource availability. Stress conditions as for example droughts are considered by changing the specific uptake rates below- and aboveground.

Individual carbon-, water- and nutrient balances of the tree species beech, oak, spruce, pine and Douglas fir are the fundamental processes for the growth simulations. The spatial calculation levels range from stand level and individual trees over tree components (i.e. foliage, branches, stem, fine and coarse roots) to crown and root layers, which are vertically and horizontally divided into eight crown- and root segments.

BALANCE enables the representation of asymmetric crown shapes and a spatially explicit consideration of the environment. For each layer resp. each segment micro climate and water balance are calculated by using temperature, radiation, precipitation, humidity and wind speed. While the spatial variability for light- and water availability is both calculated on a daily basis, the physiological processes assimilation, respiration, nutrient uptake, growth, senescence and allocation are calculated in 10 day time steps from the aggregated driving variables. All tissues of a segment, i.e. foliage, branches or fine and coarse roots as well as the biomass of the stem are mechanistically related to each other according to the pipe model theory (SHINOZAKI et al. 1964, CHIBA 1998).

To describe the relationships between environmental influences and growth, the development of the foliage in time and space 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 of a tree determines its assimilation and respiration rate but also affects the environmental conditions of the trees in its vicinity. In BALANCE the beginning of bud burst is modeled by using a temperature sum model (RÖTZER et al. 2004), while foliage senescence is estimated in dependence on the respiration sum (RÖTZER et al. 2010b).

Photosynthesis is calculated by using the approach of HAXELTINE and PRENTICE (1996) as a function of leaf surface, light, temperature and CO₂ concentration and is reduced by the lack of water and nutrients as well as changed by pollutants. The most prominent factor of this calculation is the radiation amount which a segment receives in a time step. To determine the radiation sum of a segment, a ‘competition-cone’ is placed over each segment and all segments within this cone are counted and weighted according to their leaf area. This calculation of the relative light consumption was derived from the competition algorithm of the

growth simulator SILVA (PRETZSCH 1992) and extended by a light extinction function of a Lambert-Beer type. 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. Consequently, light intensity of each segment is obtained based on the global radiation, the extinction coefficient of foliage and the competition factor of the segment.

Respiration is estimated according to THORNLEY and CANNELL (2000). It is separated into respiration for uptake and transport processes and compartment-specific growth respiration, as well as into respiration for maintenance purposes.

The Penman-Monteith equation (e.g. DVWK 1996), i.e. the calculation of the evapotranspiration, forms the base to estimate the water balance of each single tree. Hereby, the change in the soil water content is calculated from the daily values of precipitation, interception, percolation, and transpiration. A simple multi-layer bucket soil water model with a fixed layer width considers vertical water flows. In the horizontal extension, the model distinguishes between rooted and non-rooted fractions in each layer. The water within the rooted fractions can be used to fulfill the tree's transpiration requirements. At the end of each day the water content within the rooted and non-rooted fractions of a layer is aligned.

Via stomatal closure water balance is connected with the carbon and nitrogen cycle. The fixed carbon that is not needed for respiration is used for the distribution into the plant compartments foliage, branches, stem and roots depending on their relative sink strength (GROTE 1998). It is computed according to functional balance (MÄKELÄ 1990) and pipe model principles (SHINOZAKI et al. 1964, CHIBA 1998).

Dimensional tree growth is calculated once a year on the base of the biomass increase that has been accumulated during the year. The share that every crown resp. root segment gains is defined by its relative contribution to the net carbon and nitrogen increase. The volume expansion depends on the necessary amount of twigs and transport branches, resp. on the amount of coarse roots for the root segments. Therefore, crown development is preferred in the direction towards the best assimilation conditions during the previous year.

A detailed description of the model can be obtained in GROTE and PRETZSCH (2002), RÖTZER et al. (2005), RÖTZER et al. (2009) and RÖTZER et al. (2010b).

3. Scenario Definition

For the scenario simulations the site conditions from the 'Kranzberger Forst' were used. This site – located in southern Bavaria (Germany), about 40 km northeast of Munich (48.420° N, 11.662° E, elevation 490 m a.s.l.) – was the intensive forest research plot of the SFB 607 (MATYSSEK et al. 2010) and formed the base for the parameterization of the model BALANCE.

3.1 Climate

On average of the 10 year simulation period from 2000 to 2009 the annual air temperature was 8.3 °C, and the annual precipitation sum was 854 mm. Thus, temperature surpassed the long term average which ranges between 7–8 °C for the period 1951–1980. Precipitation, on the other hand, was on the upper limit of the long term regional average with 750–850 mm for the period 1961 to 1990 (*BayForklim* 1996).

Within the 10 year period a substantial inter-annual variability of temperature and precipitation is obvious (Fig. 1). Extremes are the year 2003, which was very hot and the driest year, and the year 2001 with a low annual mean temperature and the highest precipitation sum.

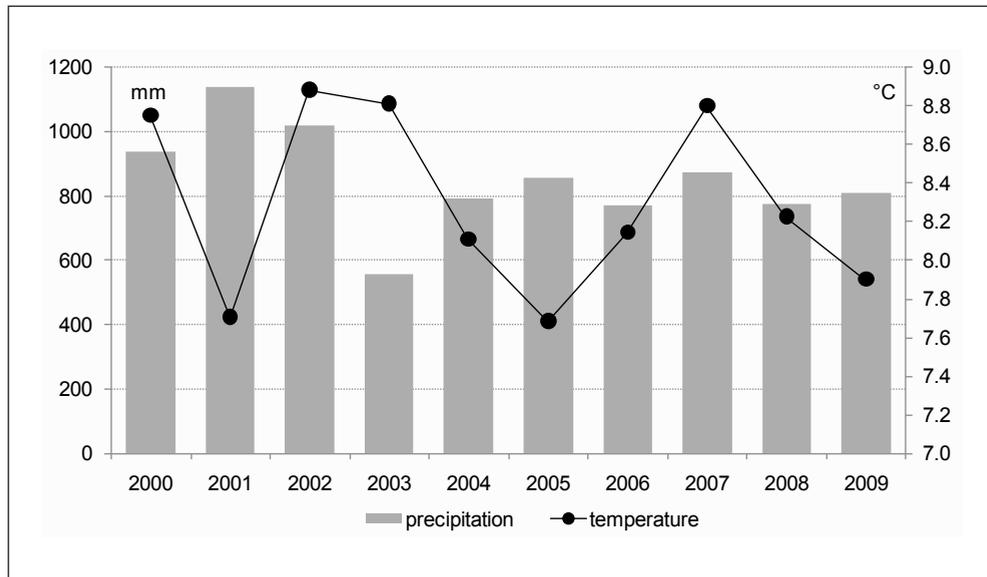


Fig. 1 Annual air temperature and precipitation sums for the simulation period from 2000 to 2009

3.2 Soil Conditions

The soil of the ‘Kranzberger Forst’ can be assigned as Luvisol, derived from loess over tertiary sediments, with good water and nutrient supply. The soil is composed of 60% silt, 20% clay and 20% sand within the upper 100 cm, while below 100 cm the quantity of sand increases to 80%. For the simulations the soil was classified in four layers (0–5 cm, 5–35 cm, 35–85 cm and 85–100 cm). Field capacity and wilting point for each soil layer were estimated with 49, 37, 37 and 37 vol% resp. 11, 8, 10 and 23 vol% based on the studies of SCHUHBÄCK (2004). The maximum rooting depth was assumed at 1.0 m.

3.3 Stand Description

Virtual mixed tree stands of adult Norway spruce (*Picea abies* (L.) Karst.), and European beech (*Fagus sylvatica*) form the base of the scenario simulations. As spatial structures a random distribution of beech and spruce trees as well as a mixture with groups and clusters of beech trees were assumed. In Figure 2 the crown maps of the three plots outline the spatial distributions.

The plot size was 30 m × 30 m for all stands. Because edge trees were not regarded in the analyses the stand area decreased to 456 m² for the random mixture *RM*, to 557 m² for the clustered mixture *CM* and to 625 m² for the group mixture *GM*. When creating the stand using

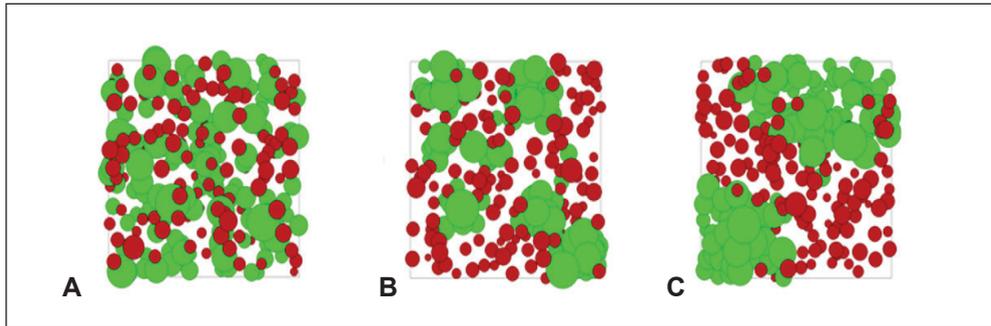


Fig. 2 Crown maps of the three virtual mixed stands: (A) random distribution, (B) cluster distribution, (C) group distribution (green circles denote beech trees, red circles spruce trees).

the STRUGEN simulator (PRETZSCH 1997) we tried to maintain similar base stand parameters for the three stands. Consequently, the initial mean diameter in breast height *dbh* of all spruce trees for the analyzed plots was 14.7 cm for *RM*, 14.9 cm for *CM* and 14.3 cm for *GM*, while mean *dbh* of the beech trees was 9.2 cm, 9.5 cm and 9.5 cm, respectively. The average initial tree height ranged between 15.2 m and 15.3 m for the spruce trees and between 15.2 m and 14.7 m for the beech trees.

4. Results

4.1 Spatial Patterns of Resources and Leaf Area Index

In order to analyze the influence of resources on the growth of tree individuals and to upscale the increments on stand level, the spatial distribution of the resources must be known. Two crucial resources for growth are light and water. Their changes in space and time are mainly determined by canopy architecture, species composition, stand density but also by the annual biomass development.

The spatial distribution of the radiation within the three differently structured mixed forest stands of beech and spruce averaged over the 10 year period can be seen in Figure 3.

On the base of the virtual stands and influenced by the environmental conditions of the years 2000 to 2009 for the annual average radiation of the random mixed stand a maximum frequency of 26 % was calculated with radiation sums of 1630 MJ m⁻². The value range, however, for this mixture was narrow (1350–1750 MJ m⁻²). On the other hand, broader ranges of radiation amounts were found for the grouped and clustered mixtures, with maximum frequencies of 19 % at 1700 MJ m⁻² for *CM*, respectively 22 % at 1570 MJ m⁻² for *GM*.

If the values of the individual trees are summed up over the analyzed stands, the mean radiation sum for the two different species as well as for the entire stand can be calculated (Fig. 4).

In all mixtures spruce trees received higher radiation sums than beech trees. In *CM* the difference was highest, while in *RM* there was no significant difference. For the entire stands the annual average radiation sum received by a tree was highest for *RM* with 1587 MJ m⁻² and lowest for *GM* with 1499 MJ m⁻².

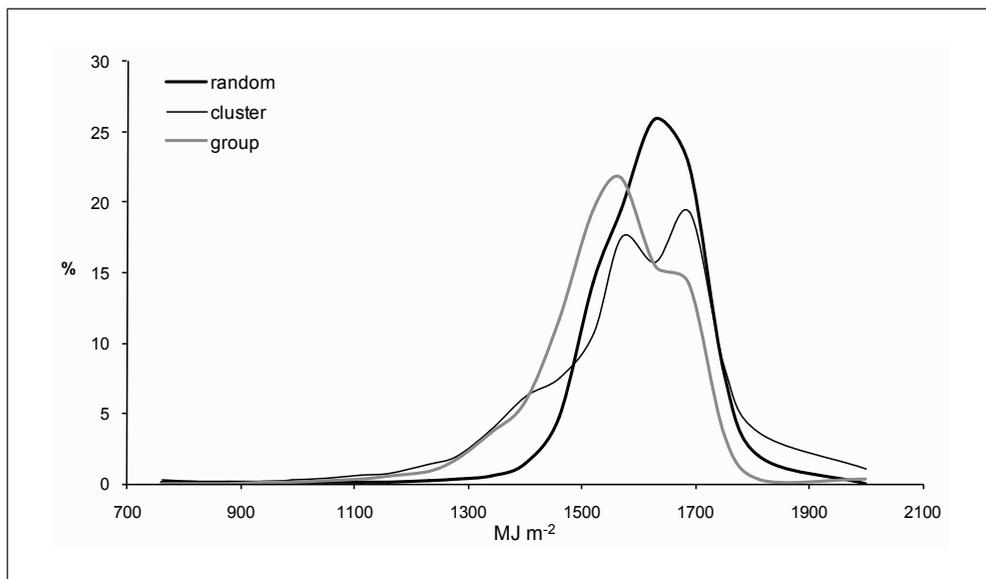


Fig. 3 Frequency distribution of the annual radiation sum a tree received in random, clustered and grouped mixtures of beech and spruce averaged over 10 years.

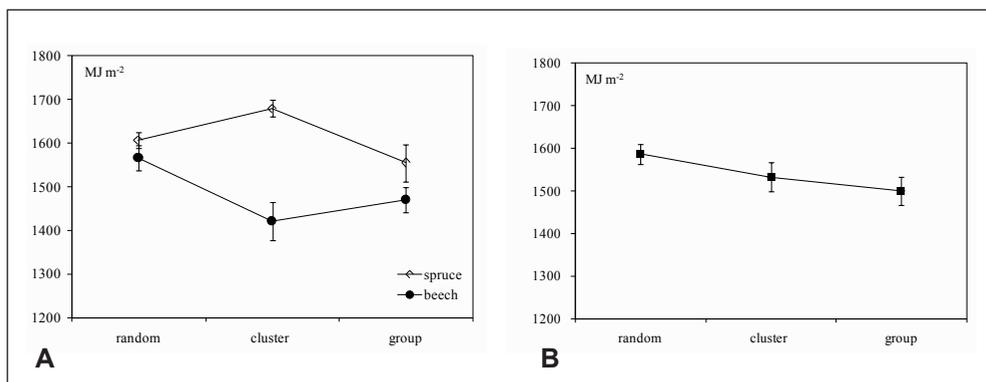


Fig. 4 Annual radiation sum received by a tree averaged over 10 years for the single species (A) and for the entire stand (B) in random, clustered and grouped mixtures.

The spatial distribution of the resource water is represented by the sum of the actual evapotranspiration in the vegetation period (May to September) eta_{VP} , which denotes the water supply of a tree very well. In Figure 5 the frequency distribution of the resource in random, clustered and grouped mixtures is given.

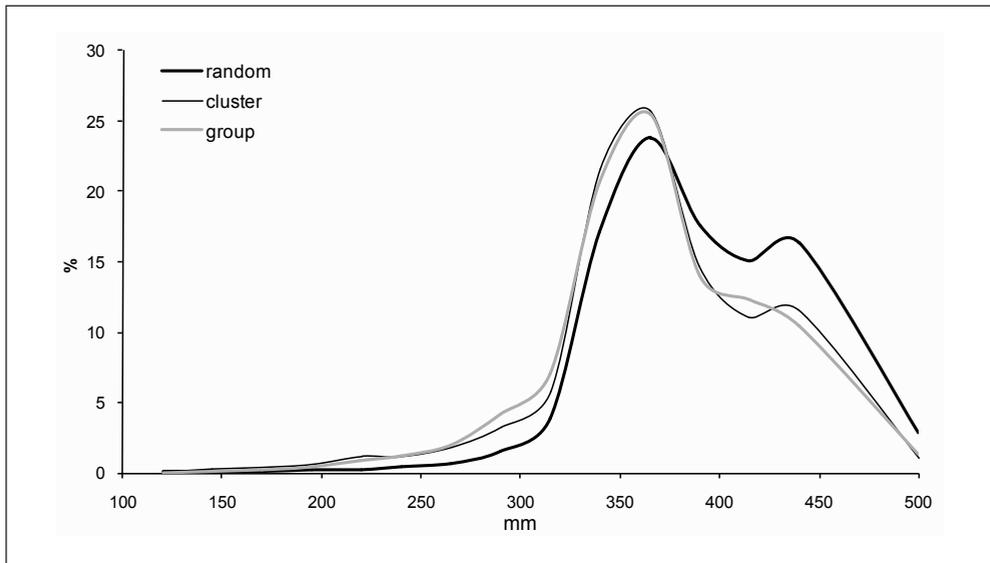


Fig. 5 Frequency distribution of the annual actual evapotranspiration in the vegetation period in random, clustered and grouped mixtures of beech and spruce averaged over 10 years.

In the random mixture the average actual evapotranspiration sum was higher than 400 mm in more than 50 % of all cases. For the grouped resp. the clustered distributions more than 60 % of all cases have et_{VP} values between 300–400 mm. If et_{VP} of the mixtures is calculated separately for the tree species (Fig. 6), the values for spruce trees were at 405 mm, the values for the beeches at 312 mm, both in the random mixture. While for the clustered mixture only a small difference between the two species can be seen (339 mm *versus* 344 mm), in the grouped mixed stand et_{VP} was higher for the beech trees (366 mm) compared to the spruce trees (304 mm).

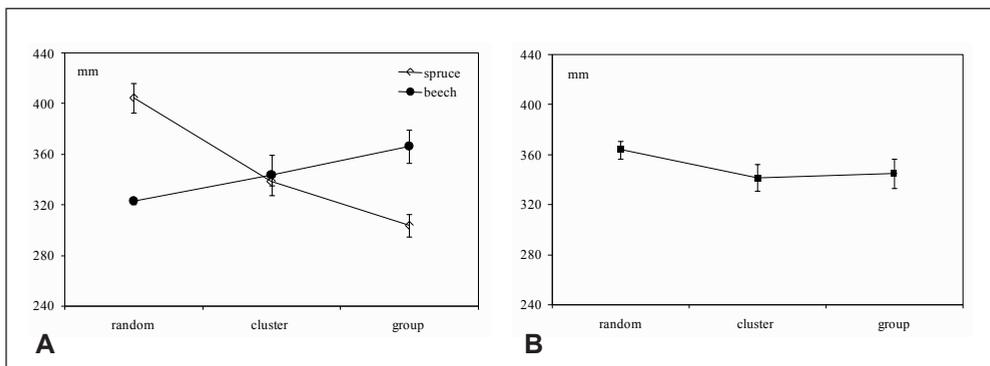


Fig. 6 Actual evapotranspiration sum in the vegetation period averaged over 10 years for the single species (A) and the entire stand (B) in random, clustered and grouped mixtures.

Summed up for the entire stands the actual evapotranspiration sum in the vegetation period reached the highest amount with 364 mm in the random mixture, but only 342 mm resp. 345 mm in the clustered resp. group mixture.

The same pattern as for the actual evapotranspiration of the three mixed stands can be found for the production area expressed by the leaf area index *LAI* (Fig. 7).

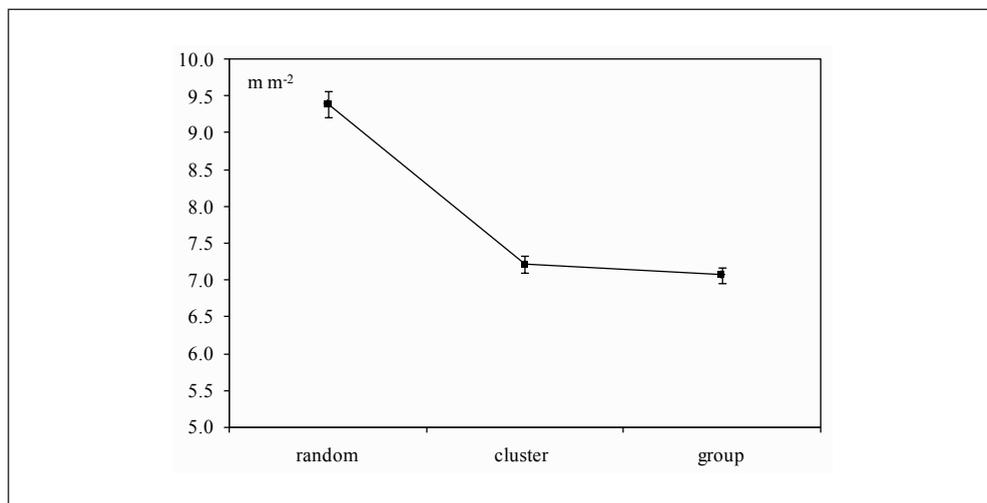


Fig. 7 Leaf area index within the period May to September (mean 2000–2009) averaged over 10 years in the random, the clustered and the grouped mixture.

Averaged over the 10 analyzed years a leaf area index of $9.4 m^2 m^{-2}$ was calculated for the random mixed stand for the vegetation period from May to September. With values of $7.2 m^2 m^{-2}$ for the clustered resp. $7.1 m^2 m^{-2}$ for grouped mixed stand the production area of the random mixed stand was significantly higher.

4.2 Growth and Efficiencies

Based on the spatial and temporal distribution of the resources and the production area within the three mixed stands, changes in their productivity could be expected, too. In Figure 8 the mean annual biomass increment both for the spruce and the beech trees in the different mixtures are presented. For all mixtures nearly no change in the biomass increment of spruce is detectable, the values vary from $7.8 t C ha^{-1} yr^{-1}$ for the clustered mixture to $8.0 t C ha^{-1} yr^{-1}$ for the group mixture. For beech trees clear but not significant differences are obvious: From $5.7 t C ha^{-1} yr^{-1}$ in *CM* over $6.0 t C ha^{-1} yr^{-1}$ in *GM* the annual biomass increment rose up to $6.2 t C ha^{-1} yr^{-1}$ in *RM*. For the entire stands this denotes mean annual increments of $6.6 t C ha^{-1} yr^{-1}$ for the clustered and grouped stand and $6.9 t C ha^{-1} yr^{-1}$ for the randomly mixed stand.

The differences of 4% between the randomly mixed stand of beech and spruce and the clustered resp. grouped mixed stands are based on the yearly variations of the biomass increments of the random mixed stand compared to clustered resp. grouped mixed stand (Fig. 9). While for the years 2000, 2001, 2002 and 2009 negative differences were calculated – i.e.

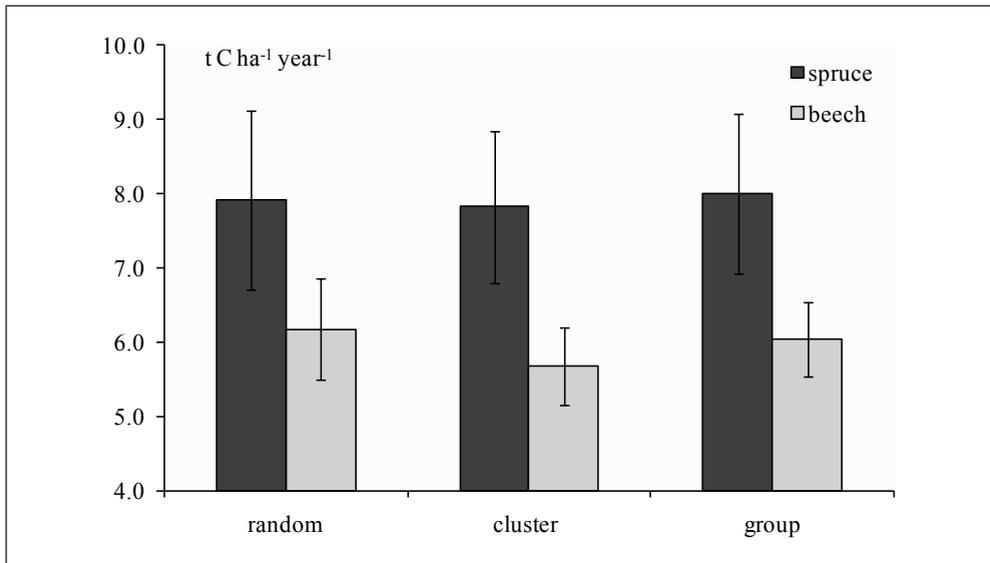


Fig. 8 Annual biomass increment of spruce and beech in random, clustered and grouped mixtures averaged over the years 2000–2009

higher growth rates for *RM* –, the period from 2003 to 2008 show higher increments for the clustered resp. grouped mixture – i.e. smaller growth rates for *RM* –. The highest differences can be seen for the years 2001 and 2003. In the year 2001, with a low mean annual temperature and the highest annual precipitation amount, the random distribution benefitted. In the dry and hot year 2003, on the other side, the clustered and grouped mixture gained.

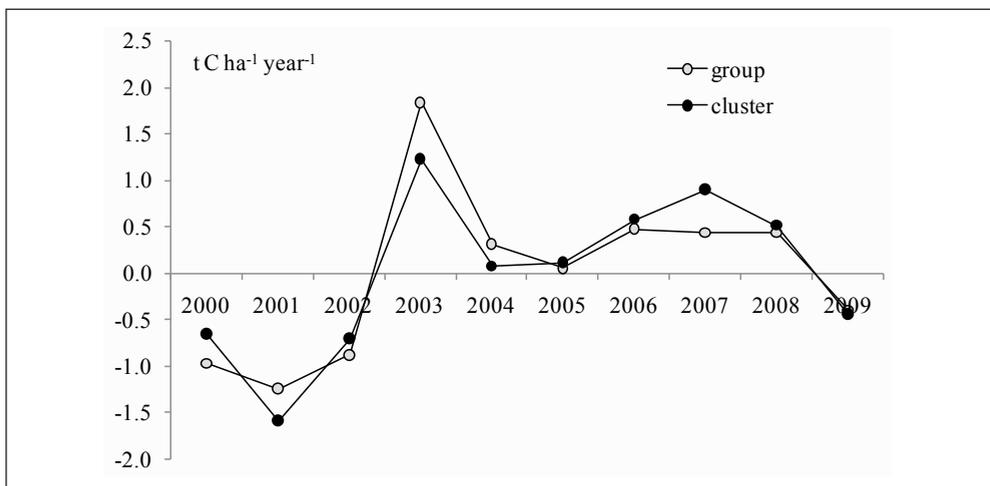


Fig. 9 Yearly differences between the annual biomass increment of the clustered resp. the grouped mixture and the random mixture for the years 2000–2009 (standardized on the annual mean)

From the net primary productivity and the actual evapotranspiration sum the water use efficiency *WUE* of spruce and beech trees in stands with random, clustered and grouped distribution can be calculated (Tab. 1). For spruce only very small differences in the efficiencies between 4.9 g kg⁻¹ (*GM*) and 5.2 g kg⁻¹ (*RM*) are obvious. Beech trees, however, were more efficient in the random mixture (3.9 g kg⁻¹) than in clustered or group mixture (3.3 g kg⁻¹ resp. 3.5 g kg⁻¹).

Tab. 1 Water use efficiencies (g kg⁻¹) of the spruce and the beech trees as well as of the entire stands for random, clustered and grouped mixtures averaged over the years 2000–2009.

mixture	random	cluster	group
spruce	5.2	5.1	4.9
beech	3.9	3.3	3.5
entire stand	4.5	4.2	4.2

For the entire stands differences of 6% resp. 7% between the clustered resp. the grouped distribution and the random distribution were found.

5. Discussion and Conclusions

In the scenario simulations considerable spatial variations of the resources within the random, the clustered and the grouped mixtures were found both for the distribution of light and water. The growth responses were different for the two species beech and spruce. On base of the entire stand the higher light and water amounts which the random mixed stand received along with higher *LAI* values resulted in higher growth rates, all compared to the clustered and group mixed stand.

BALDOCCHI et al. (1984) or ROSS et al. (1986) have already given examples of variations and changes in the radiation regime within an oak-hickory forest stand resp. in boreal forests. Crown structure and density as well as leaf properties influence the spatial distribution of radiation and result in different levels of sunny and shady areas (CANHAM 1994, LEUCHNER et al. 2012). When comparing beech and spruce LEUCHNER et al. (2012) found fundamental differences in the light regimes mainly due to the different shapes of the species: While the plane shape of the dense upper beech canopy absorbed most of the incoming radiation in the top layer, more radiation could penetrate into the spruce canopy due to larger gaps between the trees. This is especially true for high fractions of direct radiation. Thus, different structured mixed forest stands result in different radiation regimes. Because of the higher roughness the randomly mixed spruce beech stand received more radiation compared to a clustered or grouped distribution averaged over the 10 years.

On average, the actual evapotranspiration within the vegetation period – used here as an index for the spatial allocation of the resource water – was also higher in the randomly mixed stand than in the clustered respectively grouped mixed stand. Since rooting architecture varies to a great extent from tree species to tree species, different species can occupy different soil zones. While the rooting system of Norway spruce is rather shallow (e.g. LYR et al. 1992,

but see PUHE 2003), the roots of beech trees grow clearly deeper. For mixed spruce beech stands SCHMID (2002) found higher fine biomass values in mixed stands compared to the corresponding pure stands. Compared to the pure stands the fine roots of the spruce trees were enriched in the upper soil layers (SCHMID 2002), the fine roots of beech, however, in the deeper soil layers (ROTHER and BINKLEY 2001, SCHMID 2002). Other studies (HENDRIKS and BIANCHI 1995, BOLTE and VILLANUEVA 2006) support these findings that beech trees in mixture concentrate their roots in deeper soil layers, while the roots of the second species dominate the upper layer. This way, trees within a mixed stand can obtain water from different fractions of the soil (FORRESTER et al. 2010). And an increased water uptake by the trees denotes higher transpiration rates. Comparing forest stands with different mixing patterns, a higher intermingling from the group mixture over clustered mixture to randomly mixture is obvious (Fig. 2). Hence, the stratification of the roots is improved from *GM* to *RM* resulting in higher water uptake rates and higher transpiration sums of the single trees (Fig. 5 and 6).

Following ZWEIFEL et al. (2009) the complex physiological relationships between the water and the carbon cycle can be simplified in the way that more open stomata (induced by the improved water supply) provide higher carbon uptake rates and thus an increased biomass production (FORRESTER et al. 2010). This effect can also be seen for the stands with different mixing structures: while the mean annual biomass increment of the group resp. the clustered mixture was $6.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$, the increment of the randomly mixed stand was $6.9 \text{ t C ha}^{-1} \text{ yr}^{-1}$. This denotes an increase of 4%.

Elevated transpiration rates of a tree, on the other hand, can also be caused by the higher radiation amounts a tree receives. As stated above the different shapes of the tree species in a mixed forest stand allows radiation to penetrate deeper into the canopy. Since radiation is a main parameter for the evapotranspiration by providing energy for the process (e.g. DVWK 1996) the higher radiation regimes in a mixed forest stand may enhance evapotranspiration. Increasing radiation amounts of the entire stands from *GM* to *CM* to *RM* (Fig. 4) elevated the transpiration in the same direction (Fig. 6). Consequently, above as well as below ground competition is reduced and leads to higher growth rates, particularly within the beech trees. PRETZSCH et al (2010) have already found that spruce in mixture with beech reduces the degree of intra-specific competition which is obvious in pure beech stands, and thus facilitates beech growth while the growth of spruce is shortened.

Because of the better occupation of space leaf biomass – expressed as *LAI* – is increased in mixed stands compared to pure stands (FORRESTER et al. 2010), but could also be enhanced in mixed stands with higher intermingling. This could be emphasized by the results of this study, i.e. by the increased *LAI* in the randomly mixed stand compared to the group or clustered mixture (Fig. 7).

As a consequence of a higher radiation regime and higher transpiration values along with higher *LAI* values total biomass increment was enhanced in the randomly mixed stand compared to the clustered and grouped mixed stands. The simulated mean annual total biomass increment was $7.9 \text{ t C ha}^{-1} \text{ yr}^{-1}$ for the spruce trees and $6.0 \text{ t C ha}^{-1} \text{ yr}^{-1}$ for the beech trees averaged over all mixing structures. Based on the data of MUND et al. (2002) the mean annual biomass increment of 35 to 43 year old, Central European spruce stands was at $8.2 \text{ t C ha}^{-1} \text{ yr}^{-1}$. Under Central European conditions RÖTZER et al. (2010a) calculated net biomass productivities for even-aged pure stands with up to $3.1 \text{ t C ha}^{-1} \text{ yr}^{-1}$ for spruce and up to $2.9 \text{ t C ha}^{-1} \text{ yr}^{-1}$ for beech. The higher values simulated within this study fit well with the estimated mean annual biomass increments PRETZSCH et al. (2012, 2013) found in Southern Germany

with 6.4 t C ha⁻¹ yr⁻¹ for spruce in pure stands and with 7.2 t C ha⁻¹ yr⁻¹ for spruce in mixed stands, respectively 5.8 t C ha⁻¹ yr⁻¹ for beech in pure stands and with 5.9 t C ha⁻¹ yr⁻¹ for beech in mixed stands.

However, climate extremes of different years altered biomass increments to a great extent. The differences of 4% between the randomly mixed stand and the clustered resp. grouped mixed stands are based on the high year to year variability of the biomass increments (Fig. 9). It is remarkable that in the exceptionally dry and hot year 2003 the biomass increment of the clustered and grouped mixture was clearly higher than for the random mixture, while for the year 2001 with a low annual mean temperature and a high precipitation amount it was the other way round. A close intermingling of the species spruce and beech seems to be favorable under wet and cold conditions while a less close mixing copes better with dry and hot conditions.

The most efficient stand – based on the resource water – was the randomly mixed stand. Spruce trees as well as beech trees in this mixture show the highest *WUE* values with 5.2 g kg⁻¹ resp. 3.9 g kg⁻¹. CIENCIELA et al. (1994) found an average *WUE* of 4.8 g kg⁻¹ for spruces in Sweden. POLSTER (1950) and PRETZSCH (2009) estimated the water use efficiency with values of 4.3 g kg⁻¹ resp. 5.1 g kg⁻¹ for spruce and of 5.9 g kg⁻¹ resp. 4.4 g kg⁻¹ for beech. POLSTER (1950), however, used aboveground biomass and transpiration for his calculations. From the measurements of GRÜNWARD and BERNHOFER (2007) a *WUE* for the Tharandt spruce forest of 7.8 g kg⁻¹ on average can be derived, assuming net ecosystem productivity as numerator and evapotranspiration as denominator (hereby interception is estimated as 40% of precipitation). Hence, the simulated water use efficiencies for the differently structured mixed forests are in line with the cited values.

FORRESTER et al. (2010) reported about higher *WUE* in mixed Eucalyptus and Acacia plantations compared to the corresponding pure stands which suggests structural differences such as increased biomass leaf area, sapwood area and root stratification additionally to physiological adjustments. The results presented here underline these findings for mixed stands with different mixing structures.

While the water use efficiency of spruce trees in mixture increased by 6% from *GM* to *RM*, the efficiency of the beech trees increased by 18% from *CM* to *RM* (Tab. 1). This implies that the beech trees profit from a closer intermingling (= random mixture) more than the spruce trees do. Despite of lower actual evapotranspiration rates of beech in *RM* compared to *GM* and *CM* (Fig. 6), but of higher radiation amounts (Fig. 5) biomass production and in consequence *WUE* was increased clearly. For spruce, however, higher actual evapotranspiration rates of *RM* compared to *GM* and *CM* (Fig. 6) and only small changes in the biomass production lead to only small increases in the water use efficiencies.

Generally, the presented scenario simulations delivered realistic results for differently structured mixed spruce beech forests. Physiological growth models – as e.g. BALANCE – can help to analyze the effects of structured mixed forest stands on resource allocation, productivity and efficiency. It could be revealed that the changes of the resource allocations, productivities, and efficiencies found in mixed stands compared to pure stands (PRETZSCH und DIELER 2011, PRETZSCH et al. 2012, 2013 FORRESTER et al. 2010) are also obvious in stands with different mixing structures. To quantify the influence of mixing structures more scenario simulations are helpful and more empirical analyses have to be done.

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