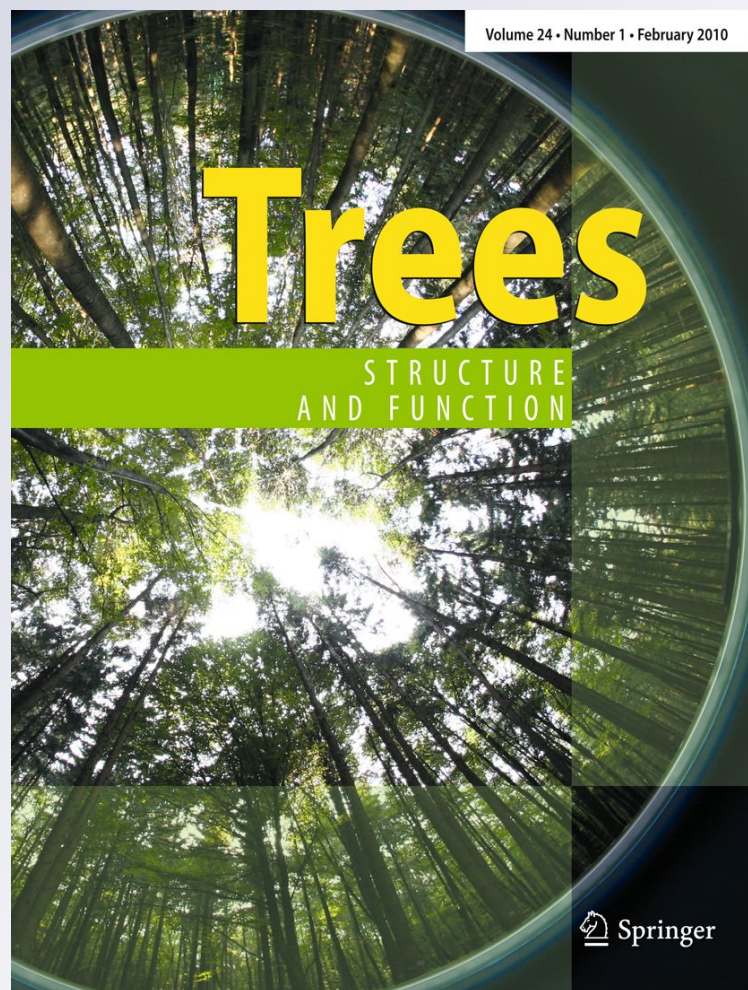*Climate effects on productivity and resource-use efficiency of Norway spruce (Picea abies [L.] Karst.) and European beech (Fagus sylvatica [L.]) in stands with different spatial mixing patterns*

H. Pretzsch, J. Dieler, T. Seifert & T. Rötzer

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Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in stands with different spatial mixing patterns

H. Pretzsch · J. Dieler · T. Seifert · T. Rötzer

Abstract Species mixing is widely held to stabilize productivity, increase resilience and contribute to risk minimization in forest stands in need of special as a result of longevity. However, research on the effects of mixing on productivity and resource consumption so far yielded fairly incoherent results rather than general findings. We focused on the effects of the spatial mixing pattern and the annual climate conditions on the mixing effect, which to date have seldom been considered as modifiers of mixing effects. Nine years of intensive survey of four pure stands of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) and two mixed plots with different mixing pattern showed: (1) mixing hardly changed annual net primary productivity at stand level when Norway spruce and European beech are cultivated group-wise but increased by 37 % on account of a higher efficiency of water and light use in individual tree-wise mixture. (2) Favourable climatic conditions increased the superiority of mixed versus pure stands productivity, while, in particular, water stress cancelled the benefit of mixing considerably. (3) An interaction between the spatial pattern and variable climatic conditions was revealed. Both improved light and water use were found in favourable years in close inter-specific intermingling. However, in unfavourable years the spatial pattern played a less pronounced role in terms of productivity.

Introduction

Species diversity has the potential to enhance a wide range of forest ecosystem functions and services, especially stand productivity (Hector and Bagchi 2007; Hector et al. 1999; Hooper et al. 2005; Pretzsch 2005a). Previous mixed stand research was mainly done to enhance yield potential in agriculture and forestry. The main question was how to achieve positive mixing reactions in terms of productivity by mixing species with complementary ecological niches (Vandermeer 1989). More recent research considers a whole range of mixing reaction patterns—from mutualistic to antagonistic reactions. It stresses that the observed mixing effects in terms of productivity depend on how complementary the ecological niches (fundamental and realized niches) of the mixed species are and under which environmental conditions (local site conditions) the species are mixed (Forrester et al. 2010; Pretzsch 2005a). The local environment contributes significantly to the kind of growth reaction in mixed stands compared to pure stands (Pretzsch et al. 2010). Studies of mixed stands, in particular along ecological gradients, have the potential to reveal whether mixtures over- or under-yield pure stands. In particular, they are able to address under which site conditions and why mixing pays off or not in terms of productivity.

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A growing number of studies provide evidence that species mixing can result in considerable gains in growth on poor sites, but also severe losses in productivity on fertile sites (Callaway and Walker 1997). However, the finding that only a relatively small number of mixing effects can be statistically explained by commonly used site variables (e.g. site index) suggests that other factors, such as genetic diversity, local or temporal environmental conditions, or spatial mixing pattern are all important modifiers of the feedback between growing stock and environment (Vandermeer 1989, p. 11).

The mixing of Norway spruce (*Picea abies* [L.] H. Karst.) and European beech (*Fagus sylvatica* L.) is the most widespread in Central Europe and has been exhaustively analyzed in regional studies (Assmann 1961; Burger 1941; Kennel 1965; Mettin 1985; Petri 1966; Wiedemann 1942). However, these regional studies did not conclude whether mixed stands are more productive than pure stands. A transect study included 23 long-term plots along an ecological gradient from nutrient-poor and dry to nutrient-rich and moist sites throughout Central Europe to investigate a potential site-based modulation of mixing effects on yield (Pretzsch et al. 2010). The results of this transect study provided evidence that, depending on site conditions, dry mass productivity in mixed stands can range between −46 and +138 % of the growth that would have normally been achieved if the tree species had been grown in pure stands. According to these results, mixing reactions appear to be triggered by two separate mechanisms. On poor sites, where significant over-yielding is found to have occurred quite commonly, facilitation by beech might offset nutrient-related growth limitations in spruce (Rothe 1997; Rothe et al. 2002b). In contrast, the less frequently observed over-yielding of mixed stands on rich sites appears to be based on an admixture effect, with spruce reducing the severe degree of intra-specific competition common in pure beech stands. Interaction models such as the one derived from the transect study (Pretzsch et al. 2010), or more restricted data sets (Rothe 1997), explain little more than 30–40 % of the variance of any productivity losses or gains; probably because they only included mixing portion (volume portions) and site conditions (site index) as modifiers.

From studies in other ecosystems, we know how severely spatial pattern (Pretzsch 1995; Pukkala 1989) and annual climatic conditions (Rötzer et al. 2009; Wichmann 2001) can influence stand growth. Since previous mixed stand research has rarely considered these co-variables as far as we could ascertain, the focus of this study was to investigate the relevance of these co-variables. We compared mixed stands of spruce and beech with pure stands with respect to productivity (gross primary production, GPP; net primary production, NPP; net biomass growth, WP; net stem volume growth, VP) and resource-use efficiencies for water, WUE, and light, LUE, to test the following hypotheses:

1. Productivity and resource-use efficiencies are changed by different spatial mixing patterns (group-wise mixture vs. tree-wise mixture).
2. Favourable climatic conditions (annual average of temperature, precipitation and evapotranspiration) enhance productivity and efficiency advantages of mixed stands compared to pure stands.
3. Spatial mixing patterns and climate conditions (e.g. effect of extreme events in group-wise mixture, respectively, tree-wise mixture) modify the mixing effects.

As study objects, we applied two triplets (pure spruce, pure beech and mixed spruce/beech) of middle-aged stands on fertile sites, with one of the mixed stands representing group-wise mixture and the other tree-wise mixture. The plots have been closely monitored since 1999 (Matyssek et al. 2010) yielding annual records of volume growth, biomass growth as well as climate data. Because of the extensive instrumental equipment (scaffolding, crane) and time intensive monitoring (permanent measurement tapes, dendrometers) of the stands, each variant (pure spruce, pure beech and mixed spruce/beech) was replicated only once as in many other extensive ecosystem studies. However, the covered site conditions were representative and in practice relevant for large forest areas in southern Germany.

Materials and methods

Study area

The two mixed spruce–beech stands of age series FRE 813, in detail plot FRE 813/1 and plot FRE 813/6 (cf. Pretzsch and Schütze 2009), are located between 11°39′41″E and 11°40′01″E, and between 48°24′45″N and 48°25′09″N in the ecological region 12.8 "Tertiäres Hügelland, Oberbayerisches Tertiärhügelland" in Bavaria near Freising, 35 km northeast of Munich at about 480–515 m above sea level.

Based on data from the "Weihenstephan" climate station of the German Weather Service, which is located about 2 km from the forest plots, the mean annual temperature (T) was 8.3 °C for the study period 1999–2005; the mean annual radiation (RAD) was 1,080 J cm^{-2}; and the mean annual precipitation sum (P) was 867 mm (Table 1). When compared to long-term averages (BayFORKLIM 1996), the T, P and RAD in the study period

Table 1 Annual and average values of temperature, *T*, radiation, RAD, and precipitation, *P*, at the weather station Weihenstephan

	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean	Long-term average	Period
Temperature (°C)	8.1	8.8	7.7	8.9	8.8	8.1	7.7	8.1	8.8	8.3	7.0–8.0	1951–1980
Radiation (J cm^{-2})	1,130	1,094	1,044	1,064	1,195	1,057	1,029	1,040	1,065	1,080	1,085–1,135	1976–1989
Precipitation (mm)	849	938	1,142	1,020	558	792	857	772	880	867	750–850	1961–1990

exceeded the average records of previous decades (Table 1).

Table 1 provides evidence of a considerable inter-annual variability in *T*, *P* and RAD. To highlight the extremes, 2003 was one of the hottest and driest years with the highest RAD within the study period, in contrast to 2001, which was the coldest year with the highest *P* and a low RAD.

The predominant soil on the site is a luvisol originating from loess over tertiary sediments (eutric cambisols according to FAO classification). Soil texture above 100 cm depth consists of 60 % silt, 20 % clay and 20 % sand; below 100 cm the quantity of sand increases to 80 % at the expense of clay and silt. To calculate the water balance, the soil was classified into four layers (0–5, 5–35, 35–85 and 85–100 cm). Field capacity and wilting point for each soil layer were determined to be 49, 37, 37 and 37 vol%, respectively, and 11, 8, 10 and 23 vol% according to the studies of Schuhbäck (2004). Because of the absence of measured soil values for plot FRE 813/6, the same soil characteristics were used for both plot FRE 813/6 and plot FRE 813/1. The base saturation in the forest floor is about 90 %. In the upper mineral soil (10 cm depth) it is 10 %, and increases again to 90 % in the depth from 50 to 100 cm. The C/N-ratio was 25 in the humus layer with decreases from 18 in the upper mineral soil to 3 at a depth of 140 cm. The potential natural vegetation would be a *Galio-odorati-Fagetum association* dominated by European beech (Walentowski et al. 2004).

Both of the plots included sections of pure stands of Norway spruce and European beech and stand sections in which both species were mixed. For the evaluation of hypotheses (1)–(3), the research plots were divided into six subplots consisting of four pure and two mixed stands of Norway spruce and European beech. In plot FRE 813/1, which is commonly known as 'Kranzberger Forst' (Pretzsch et al. 1998), the mixing pattern of species was grouped, whereas in plot FRE 813/6 the distribution pattern was random. In plot FRE 813/1, all areas with a potential influence of the Kranzberg Ozone Fumigation Experiment (Matyssek et al. 2010) were excluded. The average stand age of plot FRE 813/1 was higher than that of plot FRE 813/6. In 2007, the age of the spruce and beech trees on plot FRE 813/1 was determined as 56 and 66 years, whereas on plot FRE 813/6 the age of spruce and beech

trees was 50 and 58 years. The characteristics and growing conditions throughout the analyzed period are separately summarized for each subplot in Table 2. The fact that the subplots of each plot show analogue tree sizes and site conditions ensured comparison of the analyses. Both stands were characterized by maximum density and self-thinning conditions because they had not been harvested for at least 10–20 years before the establishment in 1994.

At the date of plot establishment in autumn 1994, the precise positions of all trees were determined by total station (LEICA TC500). Diameter at breast height (*d*) and corresponding increments were recorded annually on plot FRE 813/1 by permanent diameter tapes at breast height (1.3 m). These tapes manufactured by UMS, Germany, were equipped with a vernier scale, allowing diameter records at an accuracy of 1 mm. On plot FRE 813/6, every tree was cored at breast height to reconstruct the annual diameters from 1998 to 2007. Data on tree height (*h*) and height of the crown base (hcb), defined as the base height of the first foliated branch, were obtained from hypsometer measurements (HAGLÖF VERTEX) in 1999, 2005 and 2007 on a representative collective of trees, comprising about a third of the whole stand. This data were used to fit height–diameter as well as crown base curves to estimate the height of all trees for each year, species and plot. The interpolation of tree height between successive measurements was based on diameter increment, so that tree height could be obtained for each year. Individual tree mortality was recorded at annual intervals.

Methods

Scaling from tree to stand level

A set of measurements was applied to each individual tree to establish productivity. The area of each subplot allowed scaling from individual tree to stand level by the aggregation of individual variables. Annual productivity at the tree level was derived from the difference between two successive years, i.e. increment (*i*) of size (*x*) in year (*n*) was calculated as $ix_n = x_n - x_{n-1}$. In turn, annual stand productivity resulted from $\sum_{k=1}^{m} ix_k$ with ix_k is the increment *i* of size *x* of tree *k*, and *m* is the number of individuals per area.

Table 2 Growth and yield characteristics of FRE 813/1 and 813/6

Plot	Subplot	Mixture type	Species	Growth and yield characteristics for the first–last survey				h_q (m)	Mixing proportion (ha ha^{-1})
				Plot area (m^2)	Age (years)	N (trees ha^{-1})	d (cm)		
813/1	Pure stand		N. spruce	673	48–57	877–757	26.7–31.8	25.7–28.6	1–1
			E. beech	312	55–64	1,374–1,054	22.0–25.1	24.3–27.8	1–1
	Mixed stand	Group wise	N. spruce	448	48–57	419–269	27.1–33.7	24.9–29.1	0.45–0.47
			E. beech		55–64	449–329	26.0–28.9	23.0–27.5	0.55–0.53
813/6	Pure stand		N. spruce	150	41–50	1,033–1,067	20.1–25.1	18.2–24.4	1–1
			E. beech	345	49–58	870–812	14.4–18.3	15.1–19.8	1–1
	Mixed stand	Tree wise	N. spruce	480	41–50	625–375	19.3—29.0	17.8–25.6	0.46–0.48
			E. beech		49–58	854–708	13.7–18.1	15.5–19.0	0.54–0.52

The data in each column refer to the first and last survey (1998H–2007H)

Measuring productivity

In order to calculate the effects on different scales and for different purposes, the following four productivity indicators were applied. While stem volume productivity is highly relevant for decision-making in forest practice, weight productivity as well as net and gross primary productivity contribute to analyzing and understanding mixing effects in forest science. By reporting and comparing both response variables, we go beyond available studies which mostly focus on variables with relevance for either the merchantable effects of mixing (e.g. Knoke et al. 2005; von Lüpke and Spellmann 1997; Petri 1966) or production ecology effects (e.g. Forrester et al. 2010; Richards et al. 2010; Scherer-Lorenzen et al. 2005).

The *stem volume productivity* (VP) represents the increment in the volume of stem wood. Individual tree volume (v) was calculated using the form functions according to Franz et al. (1973) to calculate v based on d and h. All stem volume data refer to cubic metres merchantable wood over bark.

$$\text{VP} = v_n - v_{n-1} \ \left(\text{m}^3\text{ha}^{-1}\text{year}^{-1}\right) \qquad (1)$$

The *weight productivity* (WP) is defined as the aboveground biomass production, which consists of changes in stem, branch and leaf biomass between two successive measurements. For the estimation of aboveground tree biomass, w_{above}, we applied allometric functions according to Pretzsch (2005b). In order to consider biomass partitioning in different tree compartments, the trees' biomass was determined separately for stem, branches and leaves with diameter (d) as the independent variable. The allometric functions for Norway spruce were as follows: $w_{stem} = -3.839 \times d^{2.861}$ ($n = 51$, $d_{range} = 7.0$–56.8, $R^2 = 0.97$), $w_{branch} = -2.427 \times d^{1.763}$ ($n = 215$, $d_{range} = 3.8$–98.2, $R^2 = 0.83$), $w_{leaf} = -3.118 \times d^{1.840}$ ($n = 235$,

$d_{range} = 7.0$–98.2, $R^2 = 0.86$); for European beech: $w_{stem} = -2.856 \times d^{2.678}$ ($n = 80$, $d_{range} = 3.0$–67.0, $R^2 = 0.98$), $w_{branch} = -1.588 \times \text{d}^{1.778}$ ($n = 90$, $d_{range} = 6.5$–67.0, $R^2 = 0.87$), $w_{leaf} = -5.479 \times d^{2.181}$ ($n = 61$, $d_{range} = 6.5$–67.0, $R^2 = 0.88$).

$$\text{WP} = w_{above_n} - w_{above_{n-1}} \ \left(\text{t ha}^{-1}\text{year}^{-1}\right) \qquad (2)$$

Net primary productivity (NPP) quantifies the annual organic production and the turnover. NPP is equal to the plants' photosynthesis minus respiration. According to Eq. 3, NPP refers to changes in stem and branch biomass (cf. WP) as well as the belowground biomass production of fine and coarse roots, altogether called net growth. The belowground part of NPP was calculated according to the production of fine and medium (roots <5 mm) as well as coarse roots (stump + roots >5 mm). While coarse root biomass was calculated based on d, fine roots were estimated as a constant fraction of w_{leaf} (Rötzer et al. 2010a). The loss of individual trees and tree organs, which die over a given growing season, is expressed by the term losses consisting of the total above- and belowground biomass in terms of natural tree mortality. The leaf fall of beech is expressed as w_{leaf}, whereas that of spruce is 1/6 of w_{leaf}. The latter is based on empirical measurements at Kranzberger Forst where six needle ages have been found on spruce. Biomass production by seeds and fruits are not considered for NPP and GPP because of a lack of data. Obviously, a substantial part of the production might be used for reproduction; Seifert and Müller-Starck (2009) report about a cone crop of spruce of up to 707 kg ha^{-1} year^{-1}. However, only little is known about masting effects on NPP (Mund et al. 2010).

$$\text{NPP} = \text{net growth} + \text{losses} \ \left(\text{t ha}^{-1}\text{year}^{-1}\right) \qquad (3)$$

Gross primary productivity, GPP, refers to the total biomass production including respiration, thus addressing

the entire photosynthetic capacity. In the absence of sufficient respiration measurements, we calculated respiration by applying the physiological growth model BALANCE (Rötzer et al. 2009, 2010b, 2012). Within BALANCE, respiration is calculated as a function of biomass, specific respiration rate and temperature (Grote and Pretzsch 2002). It is estimated for each individual compartment (roots, stem and branches) according to its growth and respiration demands. To stay as close as possible to measured values, the annual ratios between respiration and GPP, $resp_{\%}$, from BALANCE were used. This way GPP can be calculated as

$$\text{GPP} = \frac{\text{NPP}}{(1 - resp_{\%}/100)} \ (\text{t ha}^{-1}\text{year}^{-1}) \tag{4}$$

Comparison of the mean growth in the 9-year period 1999–2007 of spruce and beech in pure and mixed stands is relevant for decision-making in practice. The subsequent back tracing of such differences to the annual performance contributes to understanding the species-specific contributions to the mixture. We selected NPP for analysing the annual behaviour because similar results were gained for GPP and NPP and it can be compared more easily to other published studies. Volume growth alone, which neglects wood density and contribution of wood <7.00 cm, is less indicative for the reaction pattern at the tree and stand level.

Estimation of mixing effects

For the close study of any mixing effects, we applied the productivity indicators (p) such as VP, WP, NPP and GPP for both the pure stands for spruce, p_{sp}, and beech, p_{be}, as well as for the mixed spruce/beech stands $p_{sp,be}$. In order to differentiate between the contribution of spruce and beech to $p_{sp,be}$ that of spruce is specified as $pp_{sp,(be)}$ and $p_{sp,(be)}$, which corresponds with the productivity per hectare, and that of beech as $pp_{(sp),be}$ and $p_{(sp),be}$.

Assmann (1961, p. 352) stresses that the most appropriate estimation of mixing portions is via the species crown projection areas. However, he showed that a weighting of the species basal areas by their specific wood density results in plausible mixing portions, which scale with crown projection areas. A basic wood density R of Norway spruce versus European beech of 390:560 kg m^{-3} yields a ratio of 1:1.44 or $\cong 0.70$:1.0. When applied, the weighted basal area of Norway spruce is reduced by 0.68. Keller (1995) criticized the adjustment with the untransformed specific wood density R. He argued that R represents a density in relation to volume, but that the basal area should be corrected by relating density to area, i.e. $\sqrt[3]{R^2}$. This adjustment is based on the assumption that tree size

follows geometrical scaling relations which yields $v \propto d^3$, $ba \propto d^2$ and finally $ba \propto v^{2/3}$. Since $v \propto w$, BA of Norway spruce was weighted by $\sqrt[3]{R_{sp}^2}$ and that of European beech by $\sqrt[3]{R_{be}^2}$, whereby average basic wood densities of 390 kg m^{-3} for Norway spruce and 560 kg m^{-3} for European beech were used according to Trendelenburg and Mayer-Wegelin (1955).

In consequence, the mixing proportion (m), as defined by Pretzsch (2009, p. 355), was calculated based on the basal area (BA) of all standing trees and adjusted with the specific wood density (Eq. 5 refers to the exemplary calculation for spruce). The proportion of spruce in the mixture is notated as m_{sp} and that of beech as m_{be}, respectively.

$$m_{sp} = \frac{\text{BA}_{sp}\sqrt[3]{R_{sp}^2}}{\text{BA}_{sp}\sqrt[3]{R_{sp}^2} + \text{BA}_{be}\sqrt[3]{R_{be}^2}} \tag{5}$$

By applying Eq. 5, the expected productivity of an imaginary mixed stand, $\hat{p}_{sp,be} = p_{sp}\,m_{sp} + p_{be}\,m_{be}$, can be calculated. Both species would have the same productivity as neighbouring pure stands of identical area. If the observed productivity in the mixed stand, $p_{sp,be}$, is higher than the expected productivity $\hat{p}_{sp,be}$, i.e. $p_{sp,be} > p_{sp}\,m_{sp} + p_{be}\,m_{be}$, it suggests an over-yielding. Over- or under-yielding can be quantified by a mixing effect ratio, $me_{sp,be} = p_{sp,be} : \hat{p}_{sp,be}$, which amounts to 1.0 if the mixed stand grows like neighbouring pure stands of the same area. However, values above or below 1 indicate and quantify over- and under-yielding, respectively. For instance, $me_{sp,be} = 1.5$ means over-yielding by 50 %. The ratios $me_{sp,(be)} = p_{sp,(be)} : p_{sp}$ and $me_{(sp),be} = p_{(sp),be} : p_{be}$ set each species' production per hectare in mixed stands in relation to its production per hectare in the neighbouring monoculture. Thus, these values allow the determination to what extent a species contributes to the effect of over- or under-yielding in mixed stands. Further details and a theoretical background on this adaptation of the relative yield concept developed for herbaceous stands by Harper (1977) and Vandermeer (1989) were presented specifically for forest stands by Pretzsch (2009) and Pretzsch and Schütze (2009).

Resource-use efficiencies

Efficiency, in general, can be defined as the amount of production per unit of resource consumption. For this study, growth efficiencies were calculated for the resources light and water. The estimation of water-use efficiency (WUE) which is the amount of biomass production or carbon uptake per amount of water used, was based on varying parameters (Jørgensen and Schelde 2001). To

calculate WUE, different productivity measures (p) and the actual evapotranspiration (et_{act}) were applied:

$$WUE = \frac{p}{et_{act}} \ (g \ kg^{-1}) \qquad (6)$$

Light-use efficiency (LUE) was also calculated for the productivity measures; resource is the sum of the annual global radiation (RAD):

$$LUE = \frac{p}{RAD} \ (kg \ GJ^{-1}) \qquad (7)$$

While RAD was directly calculated from the meteorological data, et_{act} had to be modelled with BALANCE. In this growth model, a water balance module is included, which simulates the entire water balance, i.e. soil water content, stand precipitation, interception, run-off and both potential and actual evapotranspiration. Evapotranspiration is described according to Penman–Monteith (e.g. DVWK 1996). The model includes air temperature, radiation, air humidity and wind speed. et_{act} is derived from the potential evapotranspiration and the maximum water uptake, which in turn is calculated from the water content within the rooted soil volume (Rötzer et al. 2009). Validations of the growth model BALANCE and particularly of the water balance module have been performed and published for several German forest sites (e.g. Rötzer et al. 2005, 2010b). Especially, for FRE 813 and neighbouring sites the simulated water balance parameters soil water content and interception reflected the corresponding measurements sufficiently well (Rötzer et al. 2005, 2010b).

Results

Effect of spatial mixing pattern

The two sites FRE 813/1 and FRE 813/6 consisted of three plots with pure Norway spruce, pure European beech and a mixture of Norway spruce and European beech each. Both trials had similar site conditions but considerably different spatial distribution of both species in their mixture. The dominant height at age 100 (SI_{100}) (a surrogate for site conditions) was in the range of $h_o = 34.2$–39.2 m for Norway spruce and $h_o = 29.2$–35.8 m for European beech [assessed on the basis of the yield table by Assmann and Franz (1965) and Schober (1975), respectively]. The comparatively high SI_{100} values, particularly for beech, were indicative of the plots' good to excellent growing conditions. This is substantiated by the VP of 27.9–30.9 $m^3 \ ha^{-1} \ year^{-1}$ in the pure Norway spruce stand and 11.0–25.1 $m^3 \ ha^{-1} \ year^{-1}$ in European beech stand, which represents the upper or even exceeded the highest level of the yield tables (Table 3). The two plots FRE 813/1 and FRE 813/6 differed in their growth phases because the trees on plot 813/6 were a few years younger. Whereas trees from plot FRE 813/6 represented the upturn phase of the current annual growth, trees from plot FRE 813/1 were close to the growth curve's culmination phase. This ontogenetic difference affected the results. Because of the younger age, trees from plot FRE 813/6 contained less merchantable wood (diameter >7 cm), which affected stem volume productivity negatively. The solution was to define subplots in each plot and compare species in pure versus mixed subplots, which were of the same age and thus shared the same ontogenetic stages. In this way any age effect was eliminated before any over- or under-yielding of mixed compared with pure stands was analyzed. Thus, when analysing mixing effects, we could compare FRE 813/1 and FRE 813/6 directly.

Plot FRE 813/1 represented a group-wise mixture with spruce surrounded by European beech, whereas plot FRE 813/6 represented an intensive tree-wise mixture where both species are closely interlocked. The mixing structure was underlined by Pielou's Index of Segregation which amounted to 1.00 for 813/1 and -0.07 for 813/6 (cf. Pielou 1961). Pielou's index quantifies whether species are spatially associated, $S = -1$; unsegregated, $S = 0$; or segregated, $S = 1$.

The effect of mixing patterns on productivity and resource-use efficiency was as follows: on plot FRE 813/1, NPP amounted to 21.1 t $ha^{-1} \ year^{-1}$ for Norway spruce and 22.9 t $ha^{-1} \ year^{-1}$ for European beech in the pure stands (Table 3). The hectare-related NPP in the mixture was 25.0 and 19.2 t $ha^{-1} \ year^{-1}$, respectively, showing that spruce benefited from group-wise mixture with an increase of 19 % in NPP, while the NPP of beech decreased by 16 %. According to the mean mixing proportions of $m_{sp} = 0.46$ and $m_{be} = 0.54$ (Table 2) and the species-specific mixing effects, the total mixed stand NPP compared to the expected NPP of imaginary pure stands of the same species and area amounted to 21.9:22.1 t ha^{-1}-$year^{-1}$ or $me_{sp,be}^{NPP} = 0.99$ and was more or less balanced.

The NPP-related efficiencies WUE and LUE showed the same pattern (Tables 4, 5). In the case of spruce, both relative values were increased resulting in $me_{sp}^{LUE_{NPP}} = 1.19$ and $me_{sp}^{WUE_{NPP}} = 1.15$, while those of beech decreased with $me_{be}^{LUE_{NPP}} = 0.84$ or remained unchanged ($me_{be}^{WUE_{NPP}} = 1.00$). The resource-use efficiencies observed in the mixed stand amounted to $LUE_{NPP} = 0.56$ kg GJ^{-1} and $WUE_{NPP} = 6.7$ g kg^{-1}, respectively, reflecting disappearing differences at stand level ($me_{sp,be}^{LUE_{NPP}} = 1.00$; $me_{sp,be}^{WUE_{NPP}} = 1.05$).

The tree-wise mixture on plot FRE 813/6 showed a contrasting pattern compared to the group-wise mixture

Table 3 Mean periodic (±SE) volume productivity, VP, weight productivity, WP, net primary productivity, NPP, and gross primary productivity, GPP, on the plots FRE 813/1 and 813/6

Plot (1)	p (2)	Unit (3)	Pure stands p_{sp} (4)	p_{be} (5)	$\hat{p}_{sp,be}$ (6)	Mixed stand $pp_{sp,(be)}$ (7)	$pp_{(sp),be}$ (8)	$p_{sp,be}$ (9)	$p_{sp,(be)}$ (10)	$p_{(sp),be}$ (11)
813/1 (group-wise mixture)	VP	m³ ha⁻¹ year⁻¹	27.94 (±2.01)	25.09 (±1.48)	26.40 (±1.63)	15.22 (±1.48)	15.80 (±2.41)	31.01 (±3.36) / *1.17*	33.02 (±3.32) / *1.18*	29.38 (±4.42) / *1.17*
	WP	t ha⁻¹ year⁻¹	12.84 (±1.28)	11.54 (±0.66)	12.13 (±0.91)	6.56 (±0.66)	6.41 (±0.33)	12.98 (±0.88) / *1.08*	14.24 (±1.47) / *1.11*	11.92 (±0.59) / *1.03*
	NPP	t ha⁻¹ year⁻¹	21.12 (±1.28)	22.89 (±0.73)	22.06 (±1.03)	11.55 (±0.73)	10.32 (±0.36)	21.87 (±1.00) / *0.99*	25.04 (±1.68) / *1.19*	19.20 (±0.64) / *0.84*
	GPP	t ha⁻¹ year⁻¹	43.90 (±2.07)	38.38 (±2.07)	40.94 (±1.46)	23.87 (±1.37)	17.81 (±0.60)	41.68 (±1.44) / *1.02*	51.69 (±3.11) / *1.18*	33.19 (±1.27) / *0.86*
813/6 (tree-wise mixture)	VP	m3 ha⁻¹ year⁻¹	30.89 (±1.46)	10.99 (±0.68)	20.43 (±1.01)	14.28 (±0.86)	9.26 (±0.56)	23.54 (±1.35) / *1.15*	30.16 (±1.92) / *0.98*	17.62 (±1.07) / *1.60*
	WP	t ha⁻¹ year⁻¹	10.71 (±0.48)	7.32 (±0.48)	8.93 (±0.45)	6.47 (±0.42)	6.16 (±0.39)	12.64 (±0.78) / *1.41*	13.67 (±0.93) / *1.28*	11.73 (±0.74) / *1.60*
	NPP	t ha⁻¹ year⁻¹	17.63 (±0.60)	11.38 (±0.57)	14.34 (±0.57)	9.99 (±0.50)	9.66 (±0.45)	19.64 (±0.90) / *1.37*	21.08 (±1.12) / *1.20*	18.39 (±0.89) / *1.62*
	GPP	t ha⁻¹ year⁻¹	33.00 (±1.03)	18.92 (±0.89)	25.60 (±0.94)	17.19 (±0.75)	14.68 (±0.54)	31.88 (±1.15) / *1.25*	36.29 (±1.69) / *1.10*	27.97 (±1.12) / *1.48*

Productivity differentiates between mixed and pure stands as well as between species

The productivity of the pure Norway spruce stands is denoted as p_{sp}, the European beech stand as p_{be}. In the mixed stand, the productivity of Norway spruce is notated as $pp_{sp,(be)}$, European beech as $pp_{(sp),be}$ and per hectare $p_{sp,(be)}$ ($=pp_{sp,(be)} \times m_{sp}$) and $p_{(sp),be}$, respectively. The total mixed stand productivity $p_{sp,be}$ is represented by the sum of $pp_{sp,(be)}$ and $pp_{(sp),be}$. From this follows that $p_{sp,be}$ is the expected productivity of the pure stands assuming mixing proportions of the neighbouring mixed stand species (cf. Table 2)

The italic values within the columns 9–11 refer to the ratios for the comparison of stand level production of pure stands versus mixed stand of Norway spruce and European beech. Column 9 calculates the productivity $p_{sp,be}$ of the total mixed stand (column 9) divided by the productivity $\hat{p}_{sp,be}$ expected for the pure stand (column 6). Column 10 is the quotient of $p_{sp,(be)}$ and p_{sp} (column 10:column 4) and column 11 of $p_{(sp),be}$ and p_{be} (column 11:column 5)

Table 4 Average (1999–2007) water-use efficiencies, WUE, for VP, WP, NPP and GPP on the plots FRE 813/1 and 813/6 for the pure spruce and beech stands, respectively, the mixed spruce–beech stand

| Plot	Efficiency measure		Pure stands			Mixed stands		
	Eff	Unit	p_{sp}	p_{be}	$\hat{p}_{sp,be}$	$p_{sp(be)}$	$p_{(sp),be}$	$p_{sp,be}$
1	2	3	4	5	6	7	8	9
813/1 (group-wise mixture)	WUE_{VP}	$cm^3\ kg^{-1}$	6.6 (±0.6)	8.2 (±0.6)	7.5 (±0.5)	7.5 (±0.8) *1.14*	11.6 (±2.0) *1.41*	9.7 (±1.3) *1.30*
	WUE_{WP}	$g\ kg^{-1}$	3.02 (±0.32)	3.80 (±0.26)	3.44 (±0.28)	3.24 (±0.35) *1.07*	4.70 (±0.33) *1.24*	4.02 (±0.29) *1.17*
	WUE_{NPP}	$g\ kg^{-1}$	4.96 (±0.37)	7.53 (±.37)	6.34 (±0.35)	5.68 (±0.41) *1.15*	7.55 (±0.43) *1.00*	6.68 (±0.36) *1.05*
	WUE_{GPP}	$g\ kg^{-1}$	10.28 (±0.48)	12.61 (±.57)	11.54 (±.48)	11.75 (±0.80) *1.14*	12.96 (±0.04) *1.03*	12.38 (±0.43) *1.07*
813/6 (tree-wise mixture)	WUE_{VP}	$cm^3\ kg^{-1}$	7.4 (±0.3)	4.1 (±0.3)	5.7 (±0.3)	6.9 (±0.5) *0.93*	7.1 (±0.5) *1.72*	7.0 (±0.4) *1.24*
	WUE_{WP}	$g\ kg^{-1}$	2.56 (±0.08)	2.76 (±0.19)	2.66 (±0.16)	3.13 (±0.23) *1.22*	4.74 (±0.34) *1.72*	3.97 (±0.27) *1.49*
	WUE_{NPP}	$g\ kg^{-1}$	4.21 (±0.09)	4.27 (±0.24)	4.24 (±0.02)	4.82 (±0.29) *1.14*	7.41 (±0.42) *1.74*	6.18 (±0.32) *1.46*
	WUE_{GPP}	$g\ kg^{-1}$	7.90 (±0.19)	7.08 (±0.31)	7.46 (±0.23)	8.30 (±0.45) *1.05*	11.24 (±0.49) *1.59*	9.83 (±0.38) *1.32*

Table 5 Average (1999–2007) light-use efficiencies, LUE, for VP, WP, NPP and GPP on the plots FRE 813/1 and FRE 813/6 for the pure spruce and beech stands, respectively, the mixed spruce–beech stand

Plot	Efficiency measure		Pure stands			Mixed stands		
	Eff	Unit	p_{sp}	p_{be}	$\hat{p}_{sp,be}$	$p_{sp(be)}$	$p_{(sp),be}$	$p_{sp,be}$
1	2	3	4	5	6	7	8	9
813/1 (group-wise mixture)	LUE_{VP}	$cm^3\ GJ^{-1}$	710 (±53)	639 (±42)	671 (±44)	840 (±87) *1.18*	752 (±119) *1.18*	792 (±91) *1.18*
	LUE_{LP}	$kg\ GJ^{-1}$	0.33 (±0.03)	0.29 (±0.02)	0.31 (±0.03)	0.36 (±0.04) *1.10*	0.30 (±0.02) *1.03*	0.33 (±0.02) *1.07*
	LUE_{NPP}	$kg\ GJ^{-1}$	0.54 (±0.04)	0.58 (±0.02)	0.56 (±0.03)	0.64 (±0.04) *1.18*	0.49 (±0.02) *0.84*	0.56 (±0.03) *0.99*
	LUE_{GPP}	$kg\ GJ^{-1}$	1.12 (±0.06)	0.98 (±0.03)	1.04 (±0.04)	1.31 (±0.08) *1.17*	0.85 (±0.04) *0.87*	1.06 (±0.04) *1.02*
813/6 (tree-wise mixture)	LUE_{VP}	$cm^3\ GJ^{-1}$	787 (±42)	281 (±20)	521 (±30)	768 (±51) *0.98*	450 (±31) *1.60*	600 (±38) *1.15*
	LUE_{LP}	$kg\ GJ^{-1}$	0.27 (±0.01)	0.19 (±0.01)	0.23 (±0.01)	0.35 (±0.02) *1.27*	0.30 (±0.02) *1.60*	0.32 (±0.02) *1.41*
	LUE_{NPP}	$kg\ GJ^{-1}$	0.45 (±0.02)	0.29 (±0.02)	0.37 (±0.02)	0.54 (±0.03) *1.19*	0.47 (±0.03) *1.62*	0.50 (±0.03) *1.37*
	LUE_{GPP}	$kg\ GJ^{-1}$	0.84 (±0.03)	0.48 (±0.03)	0.65 (±0.03)	0.92 (±0.05) *1.10*	0.71 (±0.04) *1.48*	0.81 (±0.04) *1.24*

represented by the plot 813/1. Here, both species increased their NPP in mixture. However, beech profited more than spruce. The species comparison indicated 21.1:17.6 t ha^{-1} year^{-1} for spruce ($me_{sp}^{NPP} = 1.20$) and 18.4:11.4 t ha^{-1} year^{-1} for beech ($me_{be}^{NPP} = 1.62$). In total, the mixed stand exceeded the expected NPP of the neighbouring pure

Fig. 1 Mean periodic (±SE) mixing effects related to VP, WP, NPP and GPP on species and total stand level for plot **a** FRE 813/1 and **b** FRE 813/6. The comparison of beech ($p_{(sp),be}$:p_{be}) is shown by *circles*, spruce ($p_{sp,(be)}$:p_{sp}) by *triangles* and the total stand productivity ($p_{sp,be}$:$\hat{p}_{sp,be}$) by *squares*
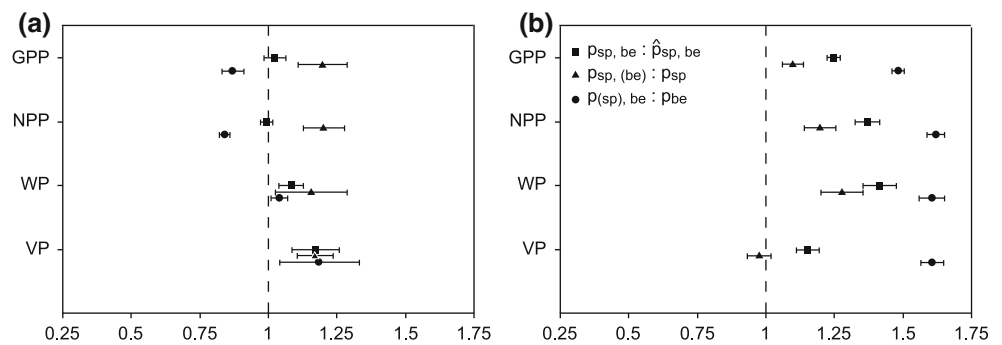
stands by 5.3 t ha^{-1} year^{-1} or 37 % ($me_{sp,be}^{NPP}$ = 1.37). LUE$_{NPP}$ and WUE$_{NPP}$ were also increased in the mixed stands in the case of spruce ($me_{sp}^{LUE_{NPP}}$ = 1.20, $me_{sp}^{WUE_{NPP}}$ = 1.14) and beech ($me_{be}^{LUE_{NPP}}$ = 1.62, $me_{be}^{WUE_{NPP}}$ = 1.74). On a stand level, LUE$_{NPP}$ was 0.50 and 0.37 kg GJ^{-1} and WUE$_{NPP}$ was 6.2 and 4.2 g kg^{-1} in the mixed and the expected pure stand, respectively. Consequently, the mixed stand was more light ($me_{sp,be}^{LUE_{NPP}}$ = 1.35) and water-use efficient ($me_{sp,be}^{WUE_{NPP}}$ = 1.46).

Hence, group-wise mixture seems to be good for spruce, enhancing its superiority over beech, while tree-wise mixture benefits beech more. Similar tendencies were found for VP, WP and GPP (Table 3; Fig. 1), and for LUE and WUE when related to these productivity measures (Tables 4, 5). However, on a stand level, the response variables NPP and GPP indicated a better performance by the tree-wise mixture, while the VP showed superior productivity by the group-wise mixture.

Effects of annual climatic conditions

Figure 2 illustrates the growth (NPP) in the mixed stand, grouped for species, and in the total mixed stand.

Despite the already described different absolute levels, spruce growth over the 9 years followed a similar pattern on the group-wise (FRE 813/1) and the tree-wise mixed plots (FRE 813/6). Of particular interest is the reaction of the trees to the drought in 2003 and the following years. In 2003, the absolute growth reduction of spruce in the group-wise mixture was slightly less pronounced compared with the tree-wise mixture, but the increment losses were extended for another year in the grouped mixture and the recovery took longer. Productivity in the beech stand showed less difference between the group- and tree-wise mixtures in 1999 than in subsequent years. The drought year 2003 caused stronger reductions in the tree-wise mixture, but the recovery was also faster in analogy to the spruce trees. In relative terms, growth dropped about 23 % (spruce) and 21 % (beech) in the group-wise mixture (FRE
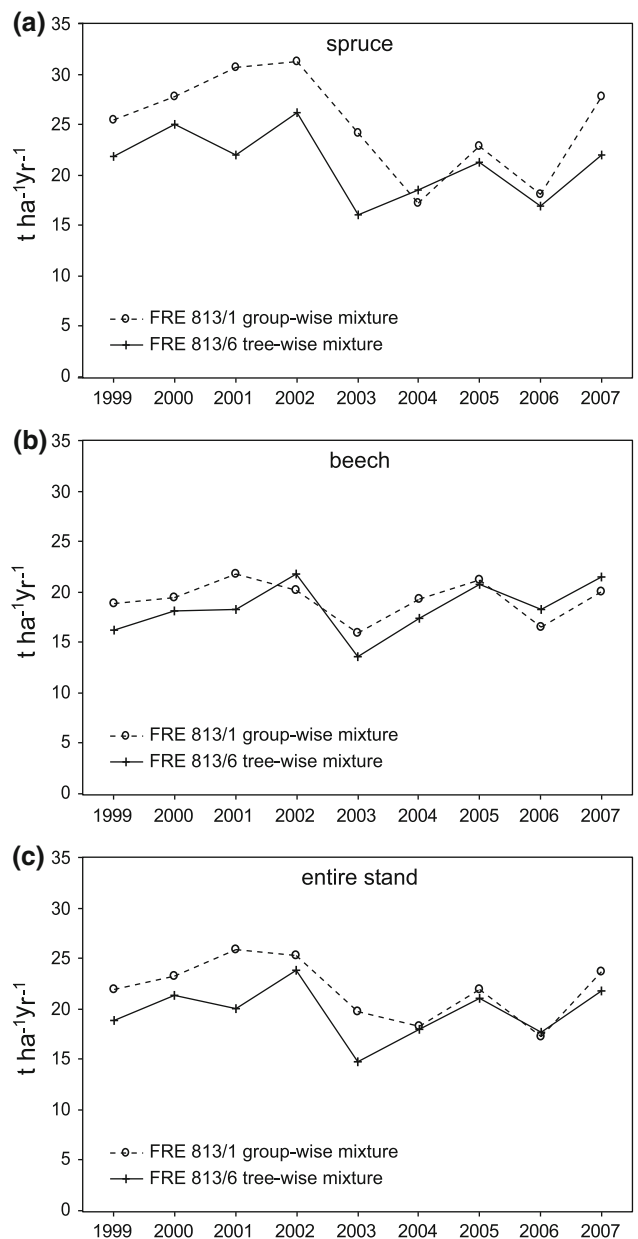

Fig. 2 Annual NPP for the spruce, the beech and the entire stand in group and individual mixture (FRE 813/1, respectively, 813/6)

Table 6 Mean periodic, range and coefficient of variation of NPP and annual NPP–NPP ratios of 2003, 2004 and 2005 to 2002 for FRE 813/1 and 813/6

Plot	Subplot	Mixture type	Productivity		Mean (t ha^{-1})	Range		Var. coeff.	Ratio		
						(min–max)			2003 vs. 2002	2004 vs. 2002	2005 vs. 2002
813/1	Pure		NPP	p_{sp}	21.1	13.7	27.0	0.205	0.51	0.61	0.79
			NPP	p_{be}	22.9	19.8	26.3	0.096	0.86	0.81	1.00
			NPP	$\hat{p}_{sp.be}$	22.1	17.6	25.7	0.140	0.69	0.71	0.90
	Mixed	Group wise	NPP	p_{sp}	25.0	17.2	31.3	0.201	0.77	0.55	0.73
			NPP	p_{be}	19.2	16.0	21.7	0.100	0.79	0.95	1.04
			NPP	$p_{sp.be}$	21.9	17.2	25.8	0.137	0.78	0.72	0.87
813/6	Pure		NPP	p_{sp}	17.6	15.1	21.2	0.102	0.79	0.89	0.99
			NPP	p_{be}	11.4	8.9	13.9	0.150	0.68	0.78	1.06
			NPP	$\hat{p}_{sp.be}$	14.3	11.8	17.2	0.120	0.75	0.85	1.03
	Mixed	Tree wise	NPP	p_{sp}	21.1	16.1	26.1	0.160	0.62	0.71	0.81
			NPP	p_{be}	18.4	13.5	21.7	0.143	0.62	0.80	0.95
			NPP	$p_{sp.be}$	19.6	14.8	23.8	0.137	0.62	0.75	0.88

813/1) compared to the preceding year. The tree-wise mixture (FRE 813/6) lost with 38 % (spruce) and 38 % (beech) about twice as much as the group-wise mixture.

The range of annual growth rates as well as their coefficients of variation (Table 6) indicates that spruce was superior to beech in the peaks; however, over the 9-year period beech grew more consistently and recovered quicker after a drought. The ratios 2003/2002, 2004/2002 and 2005/2002 reflect the growth rate in the extremely dry year (2003) and the two subsequent years in relation to the growth in the rather moist year 2002. In most cases, growth in beech decreased less than in spruce in the dry year and also recovered faster.

A comparison of the ranges and variation between pure and mixed stands showed that mixing lowered the annual growth variation; the coefficient of variation in the mixtures always lay in between the species-specific variation in the neighbouring pure stands (Table 6). This stabilization of the mixed stands mainly originated from beech which decreased less than spruce. Obviously, drought stress and growth reduction in 2003 were at a maximum in the tree-wise mixture (FRE 813/6), while the predicted ratio 2003/2002 for neutral mixing effects is 0.69; as a result of the interaction and mentioned density effect, the tree-wise mixture showed only 62 % of the growth of the previous year. This reduction of 38 % from 2002 to 2003 in the case of the tree-wise mixture applied for spruce, beech and the total stand.

Annual growth reaction patterns of pure and mixed stands

The yearly deviations from the 10-year average of the NPP provide indications of the reaction of spruce, beech and the entire stand with tree-wise and group-wise mixtures in the single years (Fig. 3).

On plot FRE 813/1 with a tree mixture in groups as well as on plot FRE 813/6 with an individual tree-wise mixture, spruce trees produced the highest deviations from the average while beech trees deviated to a lesser degree. Thus, it seems that extreme years modify NPP of spruce stronger than NPP of beech. This was true for years with favourable water supply, as for example for 2001 and 2002, but also for dry years such as 2003 and 2006. Spruce deviated from the mean in NPP more severely in group-wise mixture (2003 was an exception). The reactions of the beech trees were generally smoother. The largest deviations for beech in group-wise mixture were obvious not only in the moist year 2001, but also in the dry years 2003 and 2006. In tree-wise mixture, beech showed the largest positive deviations for the years 2002 and 2007 which both had favourable growing conditions, and the worst negative deviation for the extreme year 2003.

For the entire stand, positive deviations were calculated for the years 2000–2002, all years with high precipitation, >900 mm. In the wet and cold year 2001, the deviation of the group mixture was more than the individual mixture's deviation. In the following 3 years from 2003 to 2006, in which precipitation were below the long-term average, no clear reactions could be detected.

However, if the deviations were related to a drought index as, for example, the climatic water balance (CWB), which is defined as the difference between precipitation and potential evapotranspiration in the summer months June to August, a significant increase in the deviations with increasing CWB became obvious (Fig. 4).

The increase was stronger for the tree-wise mixture (FRE 813/6), meaning that summer drought periods
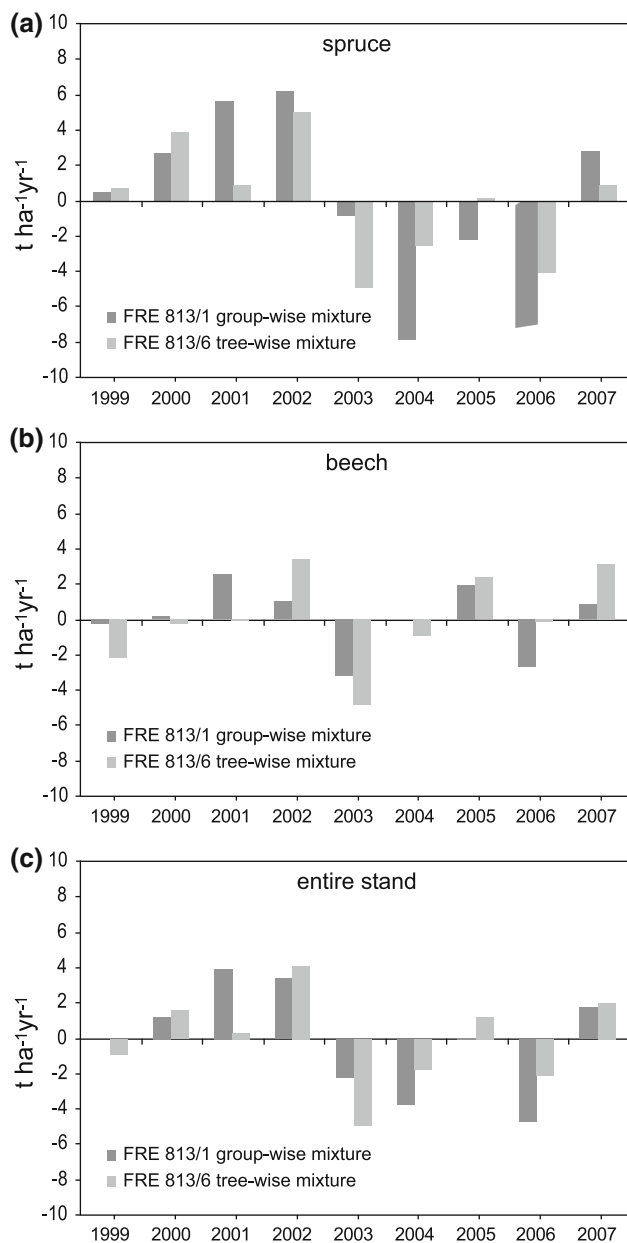
(a)

(b)

(c)

Fig. 3 Annual differences of NPP from the average (1999–2007) for the spruce, the beech and the entire stand in group and individual mixture (FRE 813/1, respectively, 813/6)

influenced NPP of this mixture to a greater extent (2.4 t ha^{-1} per 100 mm increase of CWB, $r^2 = 0.77$). In group-wise mixture (FRE 813/1), on the other hand, the influence of summer droughts was less pronounced (1.5 t ha^{-1} per 100 mm increase of CWB, $r^2 = 0.25$).

In summary, productivity of the stand showed a higher volatility in the individual mixture compared to the group mixture.

The yearly efficiencies WUE and LUE, which are based on water supply and radiation, can assist in finding causal

explanations for the relationships between climatic conditions and productivity (Figs. 5, 6).

On plot FRE 813/1, the yearly efficiencies based on the evapotranspiration of the mixed and the pure stands were similar. The maximum WUEs were calculated for the year 2001, in which the expected WUE based on the pure stand was 7.8 g kg^{-1} while the observed WUE of the mixed stand was 8.5 g kg^{-1}, which implies an efficiency increase of 9 %. For the dry and hot year 2003, the respective efficiencies with 5.0 g kg^{-1} for the pure stand and 5.4 g kg^{-1} for the mixed stand were the lowest values for the given period, the resulting WUE increase was again 9 %.

On plot 813/6 with tree-wise mixture, the lowest WUE was computed for the year 2003 at 3.3 and 4.2 g kg^{-1}. Considerable differences can be noted between the annual values of the expected WUE based on the pure stand and the measured WUE of the mixed stand. Based on the tree species proportions (m) the mixed stand was more efficient than the corresponding pure stand for up to 69 %. The lowest WUE increase was found in 2003 with 27 %.

The LUE showed the same pattern as the WUE (Fig. 6). On plot FRE 813/1 with group-wise mixture, the annual expected LUE based on the pure stand and the measured LUE of the mixed stand were almost identical. On plot FRE 813/6, on the other hand, huge differences were obvious in the annual values. The lowest LUE for both stands at both plots were calculated for the dry year 2003. High LUE values can be found in years with favourable growing conditions such as 2002 or 2007.

The mixing effect showed the biggest increases in NPP, WUE and LUE 2003 with its unfavourable growing conditions. Under favourable growing conditions (e.g. 2002), no differences between mixed and pure stands were detected. The advantage of the tree-wise mixture with respect to the corresponding pure stand was high in years with favourable growing conditions (e.g. 2002) and low in years with unfavourable growing conditions (e.g. in 2003). This was true for both the productivity and the efficiencies.

Discussion

Basic species interactions between Norway spruce and European beech

A mixture of spruce with beech usually has negative as well as positive effects on the growth of spruce (compared with spruce growth in a pure spruce stand). A well-documented negative competition effect of beech on spruce trees are the shading effect of beech, which can slow down the development of spruces in mixed compared with pure
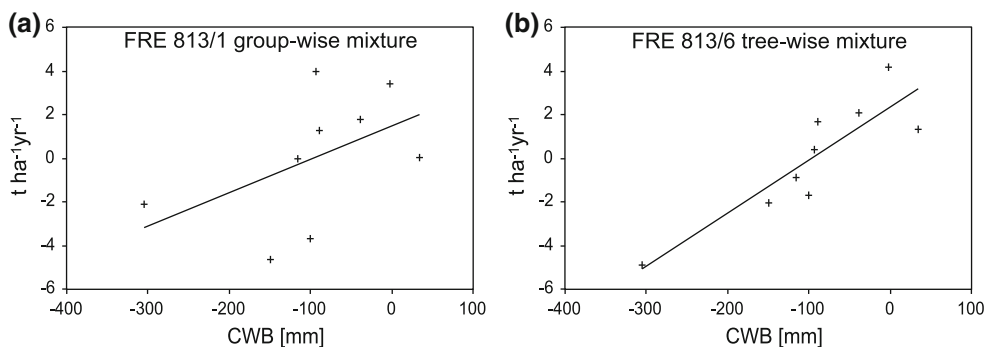
Fig. 4 Climatic water balance (CWB) of the summer months June to August and annual deviations of the NPP from the average for the group (FRE 813/1, *left*) and the individual mixture (FRE 813/6, *right*). The results of the regression analysis were $\Delta NPP = 0.015*CWB + 1.46$ ($r^2 = 0.25$) for group-wise mixture and $\Delta NPP = 0.024*CWB + 2.32$ ($r^2 = 0.77$) for tree-wise mixture
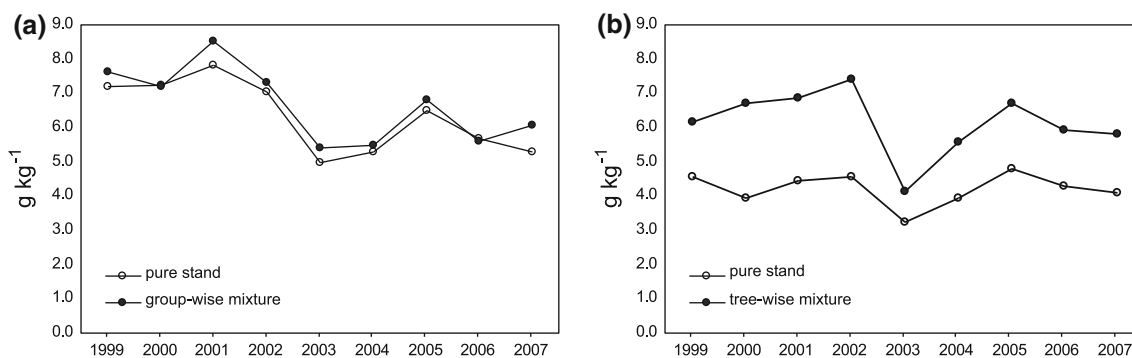

Fig. 5 Annual water-use efficiencies (WUE$_{NPP}$) for pure and mixed stands on plot **a** FRE 813/1 and **b** FRE 813/6
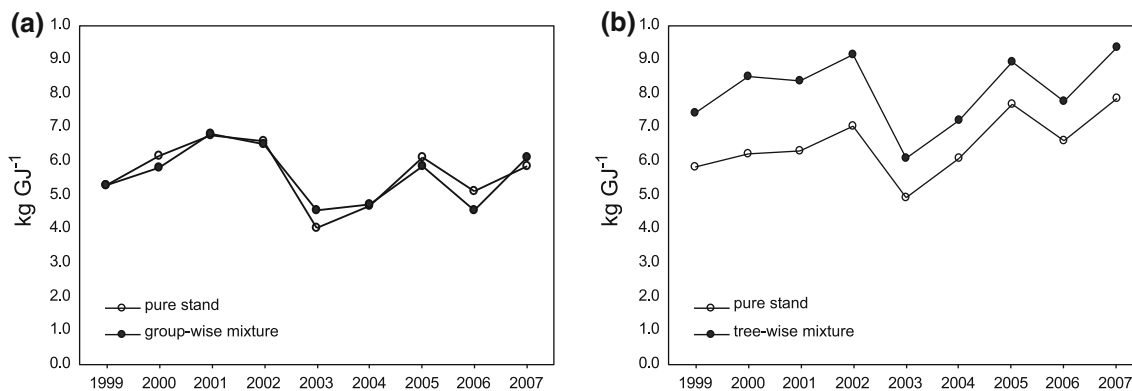

Fig. 6 Annual light-use efficiencies (LUE$_{NPP}$) for pure and mixed stands on plot **a** FRE 813/1 and **b** FRE 813/6

stands (Kennel 1965). Competition can also be induced by the deep rooting system of beech which can restrict the rooting space of spruce and its access to water and mineral nutrient supply (Rothe 1997, pp. 35–38).

Mixture can have positive and negative effects on beech as well: competition and growth reduction in beech could be the result of the superior height growth of spruce trees, which increases shading (Pretzsch and Schütze 2005, 2009). However, significant support of beech in the mixture can be induced by competitive reduction (Kelty 1992).

More current results obtained with a set of different admixed species suggest that the admixture of other species to a pure beech stand means competitive reduction, and thus positive growth reaction compared with pure beech stands. A likely reason is the high intra-specific competition in pure beech stands and the low self-tolerance of beech compared with other central European species (Pretzsch and Biber 2005; Zeide 1985). While in a pure beech stand a mono-layered structure dominates because of the low self-tolerance, any admixture opens and changes

the canopy space towards a multi-layered structure with light gaps where understory trees can grow (Otto 1994, p 210–216).

Despite mounting evidence of competition and facilitation effects, analyses of mixtures of Norway spruce and European beech up to now barely yielded a general understanding of the mixing effect on productivity and resource consumption. The main reasons for this are: (1) the results of the scattered studies could hardly be compared, since they reported different indicators of productivity; (2) the mixing structure of the experiments was seldom taken into consideration; and (3) in most studies only the mixing effect on productivity in total was reported rather than the species-specific contributions to and reasons for it.

The production ecology equation as a starting point

Our results showed marked differences in the productivity of pure and mixed stands indicating that species mixing affects at least one of the three factors in the production ecology equation

GPP = resource supply
$\times$ proportion of resource captured
$\times$ efficiency of resource use

(Monteith 1977).

Richards et al. (2010) provided nine main hypothesis of changes productivity based on an extensive review of published results with a focus on effects correlated with nutrient supply. Using Monteith's production ecology equation as a framework, they identified nine major hypothesis, how a change in productivity could be explained. In a meta-analysis, the main findings of Richards et al. (2010) were changes in resource-use efficiency, which were found in 65 % of the studies. They outlined the need for further research in order to assign the improved resource-use efficiencies to canopy photosynthetic capacities, changes in carbon allocation or changes in nutrient residence times. They also stressed the necessity of experiments spanning site gradients.

The approach in this study is complementary. While it focused on one site only, it was based on longitudinal data over 9 years to detect possible influences of the water availability on productivity and resource-use efficiency. The novel contribution of this study is the explicit description of the influence of the spatial mixing structure of trees within the stand and its influence on productivity and efficiency indicators. According to the current literature, the majority of changes in the resource availability would usually be connected with nutrient availability, which was not tested in our study (see "Basic species interactions between Norway spruce and European beech"). Our investigation also did not allow for addressing the proportion of nutrients captured. However, spruce should be facilitated in its resource capturing mixed with deciduous beech stands, because it can photosynthesize in warm spring and autumn periods when beech trees have no leaves. Extensive analyses of light intensity and spectra have shown the phenological effects on these variables and their temporal change (Leuchner et al. 2011). These effects should be reflected to a higher degree in the growth of the individual mixture compared to growth in the group mixture. However, we were not able to detect significant differences here. Moreover, we cannot disregard that effect since the advantage could be balanced out by a higher competitive pressure by beech on spruce in the individual mixture.

Mass productivity indicates evidence of mixing effects, but volume productivity the relevance

Analyses of productivity in mixed stands certainly should be based on aboveground or total tree and stand biomass instead of stem volume or tree volume. Even the small number of dominating tree species in Central Europe differs considerably in the ratio between aboveground volume and stem volume and in their specific wood gravity. The expansion factor (ratio between aboveground volume and stem volume), e.g. for trees at age 100 ranges from 1.36 for Scots pine, 1.37 for Sessile oak, 1.38 for European beech and 1.45 for Norway spruce (Burschel et al. 1993, pp. 10–11). Recent allometric studies stress an even wider intra- and interspecific crown plasticity and variation in branch and stem wood depending on tree size, and lateral and vertical crown restriction by neighbours (Pretzsch and Dieler 2012). The specific gravity is on average 390 kg m^{-3} for Norway spruce and 560 kg m^{-3} for European beech. Behind a given growth of tree volume there can be significantly different amounts of biomass, depending on the species-specific crown morphology and wood density. The latter is known to vary between species, and is intra-specific between sites and trees and within trees. Reliable information of tree species mixing on basic density is sadly lacking, what justifies the application of an average value in this study. As the over- or under-yielding of mixed versus pure stands in terms of biomass growth ranges frequently within ±10 %, the above-mentioned considerable differences in expansion factors and wood density can easily disguise real benefits or losses in mixed stands when evaluations are based on volume units. As in the past forest practice was mainly interested in wood volume, and biomass functions or wood density for trees in mixed stands were missing, most information on mixing effects is thus based on volume productivity. With just a few exceptions (Forrester et al. 2006, 2010; Kennel 1965; Pretzsch et al.

2010) most available studies mentioned the shortcoming of using volume units but are nevertheless based on volume productivity (Assmann 1961; Petri 1966; Spellmann 1996; Wiedemann 1942). Our study addresses this shortcoming of previous studies and reports both volume and biomass productivity, and by doing so reveals how the results differ depending on the applied scaling method.

Methodological strengths and weaknesses of this study

We were able to make a contribution to the body of knowledge concerning mixed stands with a comparison of different productivity and efficiency measures and of different spatial mixing patterns. In comparison, all tested response variables (GPP, NPP and WP) yielded similar results, except for the merchantable stem volume VP. However, the deviation in the reaction pattern if VP was used as a response variable is a crucial factor since the majority of previous work on productivity in mixed forest stands was and still is usually based on volume. Knowledge pertaining to mixing effects on merchantable volume productivity is highly relevant for discussion of pros or cons in mixed stands for timber production. The mixing effects on GPP, NPP and WP, in contrast, rather contribute to understanding and modelling mixed species stands.

Analyses based on VP omit stem compartments under 7 cm diameter, and therefore lacks substantial proportions of the production in the juvenile phase of the tree. For this reason, specific effects were observed when VP was applied for analysis. If the growth was faster in a mixed stand, the application of VP overrates the differences between pure and mixed stands, because in the slower growing pure stand a substantial number of trees <7 cm remained unconsidered, while more trees are taken into account in the faster growing mixed stand. If the pure stand has the superior growth, the reverse applies.

GPP, NPP and WP were applied in order to provide baseline information on different productivity indicators, and to evaluate compare the influence of the choice of the indicator on the mixing effects. Some of these indicators were modelled based on measured variables according to the state of the art. A minor bias in the increment calculations with regards to merchantable wood volume, biomass, NPP and GPP could have resulted from the fact that volume and biomass functions were applied, which were not explicitly developed to cover stem form differences and shifts in biomass proportions in mixed and pure stands. Since such functions were not available at the time, these assumptions had to be made. The same applies for changed wood density since only a fixed average value was used in the calculations.

For the reasons of data availability, our study was limited to radiation and water to characterize resource-use efficiency. However, over-yielding in mixed stands is known to be also influenced by improved nutrient availability, nutrient uptake and nutrient-use efficiencies (Rothe and Binkley 2001; Richards et al. 2010). This is obvious when nutrient fixing tree species are admixed (Forrester et al. 2006, 2007), which is not the case in our stands. However, there is evidence of several further nutrient-related effects. Conifers have higher surface areas than broadleaved trees and are thus more efficient at filtering for atmospheric depositions (Augusto et al. 2002). This leads inter alia to higher N-deposition rates in spruce-dominated forests compared to beech-dominated forests (Rothe et al. 2002a, b; Berger et al. 2008). Particularly, the intercept of atmospheric NO_3^- and NH_4^+ seems to lead to an increased nitrogen input if spruce is mixed with beech, compared to a pure beech forest (Berger et al. 2009).

There might also be positive mixing effects resulting from specific constellations of the radiation budget in spruce–beech forests, which were not considered in our study. New results obtained by Leuchner et al. (2012) or Rötzer et al. (2012) provide evidence of the complex spatio-temporal changes of radiation during the year and its interaction with biomass in mixed spruce–beech stands.

Our investigation was limited to six plots, with only two mixed plots where the spatial mixing pattern was varied. For this reason, this study is rather a first approach for causal analysis of mixing effects and not generalizable in its results. Further empirical and scenario-based investigations have to follow.

Modification of the mixing reactions by the spatial mixing pattern

The mixture of spruce and beech yielded 37 % more to 1 % less NPP compared to the pure stand. Part of the variation can be explained by the spatial pattern of the mixture: a group-wise mixture increased production and resource-use efficiencies to a lesser degree than an individual tree-wise mixture. The tight interlocking crowns of spruce and beech in the tree-wise mixture resulted in a higher resource capture of light and a substantial plus in growth, which was not achieved in the group-wise mixture. The reason is that there are less overlap zones in the crown of both species. In the tree-wise mixture, it seems that the beech is the benefitting tree species because of a competitive reduction. The inter-specific competition of beech with spruce seems less than the intra-specific competition in the pure beech stand. The fact that the beech in mixed stands outperformed beech in pure stands, regardless of the mixture type, allows the conclusion that there is an interaction with spruce on the nutrient level which is positive for beech. While for better LUEs a strong interlocking is mandatory, nutrient effects can also be realized in less intense mixtures.
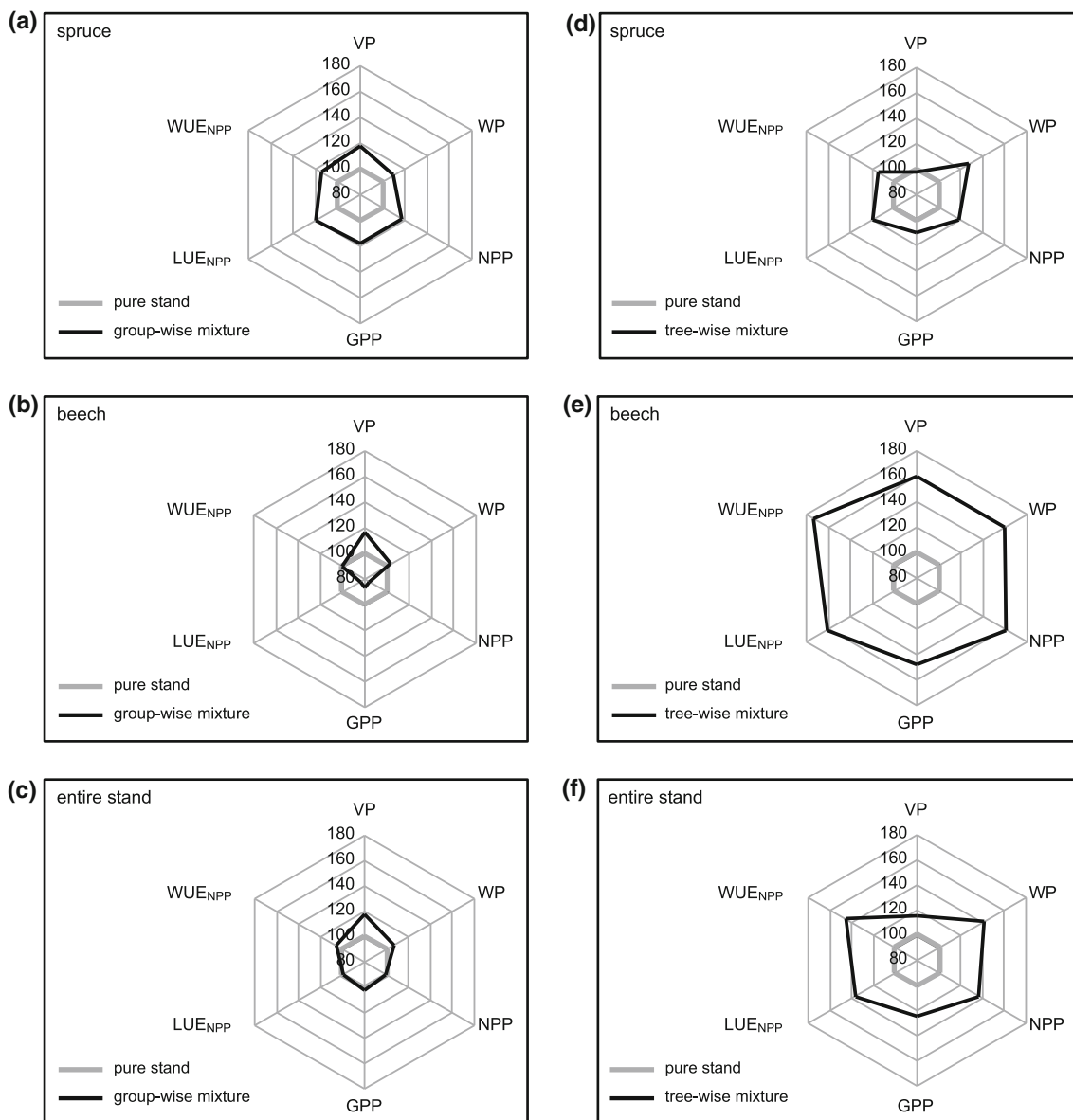
Fig. 7 Average productivity and efficiency changes (1999–2007) of the mixed stands compared to the pure stands, the spruce stands (**a**, **d**), the beech stands (**b**, **e**) and for the entire stands (**c**, **f**) in group-wise mixture FRE 813/1 (*left*) and tree-wise mixture FRE 813/6 (*right*)

Effect of temporal climatic conditions on the mixing reactions

Based on our results, it can be stated that the two species under investigation have an increased production in mixed stands because of improved LUEs and WUEs (Fig. 7).

Higher LUE and WUE in the tree-wise mixture were particularly apparent. The higher volatility in productivity, exhibited by the tree-wise mixture in years with very favourable and with rather unfavourable growing conditions is evidence that the facilitation processes between the species were sensitive to water availability and that in particular the beech trees profited from the tree-wise

mixture. This observation might be related to the different strategies used to cope with extremes. Nikolova et al. (2009a) demonstrated in the case of fine root growth in the drought year 2003 on stand FRE 813/1 that Norway spruce fine root respiration and growth were substantially reduced as opposed to the growth and respiration of roots of European beech. The more pronounced effects in tree-wise mixed plots observed in this study may also have their origins in the different species-specific morphological strategies for water storage and conductance as described by Nikolova et al. (2009b). In a comparison of small roots of Norway spruce and European beech Nikolova et al. (2009b) found clear differences in the potentially

conductive cross-sectional area and in the specific conductivity of the sapwood. While beech showed sapwood on the full cross section, spruce roots had already developed a significant amount of inactive heartwood, which limited the conductance substantially. The water containing cross section of beech may not be fully conductive but may serve as an intermediate water buffer.

Also temporal aspects have to be considered. It seems evident that analyses conducted in comparably unfavourable years would yield different results than in good growth years. In our case, beech showed only a superior growth in mixed stands in good years. In unfavourable years, growth in mixed stands dropped to the level or below the level of pure stands reference. This fact points out once more the necessity of long-term experiments, which cover time periods with a good balance of favourable and unfavourable years.

The analysis of annual productivity values and resource efficiencies substantiates the perception that improved light capture is the reason for the increased growth in years with favourable growing conditions. In such years, the tree-wise mixture is particularly better than the pure stand reference. The group-wise mixture is better as well, but to a smaller extent. In contrast, drought years lead to a reduced advantage of the tightly interlocked individual mixture. Then particularly spruce trees seem to suffer from water competition with beech trees. An inverse pattern was observed in group-wise mixed stands. Here, the drought years resulted in an over proportional advantage of growth of mixed compared to pure stands. Apparently, the benefits of better resource availability can be utilized without negative effects caused by the inter-specific competition. However, it is important to mention that while the group mixture had the lower amplitude of under-yielding and over-yielding, the individual tree-wise mixture had a higher average over-yielding in the long term.

Interactive effect of the spatial pattern and climatic conditions on mixed stand growth

The results of this study suggest that the intensive interlocking of spruce and beech not only increased LUE, which could reasonably have been expected, but also improved WUE compared to group-wise mixed stands, particularly in years with favourable water supply. This indicates a close spatial interaction, which should be investigated in future studies.

The observed higher resource-use efficiencies, however, cannot be generalized and applied to other species combinations. Even though higher WUE in mixtures has also been reported previously by Forrester et al. (2010). It is likely that in cases where LUE is the dominant factor in over-yielding, the spatial vertical and horizontal structure of the forest is decisive. This is mainly a consequence of the directional character of light. If we look at other possible reasons for over-yielding, as for example nitrogen fixation, improved humus mineralization, etc. the spatial structure might be less relevant. There is mounting evidence that the competition for edaphic resources such as nutrients or water leads to size-symmetric growth, while competition for light favours the bigger trees (Schwinning and Weiner 1998; Pretzsch and Biber 2010; Pretzsch and Dieler 2011). Therefore, depending on the limiting resource, there might be different effects of mixing to be expected.

Our investigation made the step from pure diagnosis of under-yielding or over-yielding of mixed stands to a causal analysis employing the concept of Binkley et al. (2004). Their approach characterized the mixing effects based on the generic production balance of ecosystems. Our study combined existing concepts of competition and facilitation (Vandermeer 1989) with causal explanations and a solid quantification of data obtained from two research plots. In this context, it is important to state that equal productivity at stand level does not necessarily indicate neutral behaviour of the mixed plants, since mixing reactions at species, individual or organ level can counteract and cancel each other with respect to stand level productivity.

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