

# Productivity of mixed versus pure stands of oak (*Quercus petraea* (MATT.) LIEBL. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient

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Received: 8 August 2012 / Revised: 4 December 2012 / Accepted: 4 December 2012  
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**Abstract** The mixture of beech (*Fagus sylvatica* L.) and oak (sessile oak, *Quercus petraea* (MATT.) LIEBL., and pedunculate oak, *Q. robur* L.) is of considerable importance in Europe and will probably become even more important under climate change. Therefore, the performance of oak and beech in mixture was compared with the species'

growth in pure stands. Data from 37 long-term mixing experiments in Poland, Germany and Switzerland were pooled for analysis of mixing effects on stand productivity and possible interrelationships with mixing portions or site conditions. We found that on average, mixed stands of oak and beech exceeded biomass productivity in pure stands by 30 % or  $1.7 \text{ t ha}^{-1} \text{ year}^{-1}$ , as the growth of both species was benefitted by the mixture. However, that the interaction actually ranged from facilitation and overyielding on poor sites to underyielding on fertile sites triggered by competition. An empirically derived interaction model showed volume and dry mass growth changing in mixed stands from gains of 50 % to losses of 10 % depending on site conditions. It is concluded that the analysed mixture grows in accordance with the stress-gradient hypothesis and that our results suggest a site-specific relationship between species mixture and biomass productivity. As a consequence, an adequate species mix should result in increased productivity under steady state as well as climate change.

Communicated by R. Matyssek.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10342-012-0673-y) contains supplementary material, which is available to authorized users.

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**Keywords** Facilitation · Competitive reduction ·  
Competition · Stress-gradient · Overyielding ·  
Mixing effect · Long-term mixing experiments ·  
Climate change

## Introduction

In the past, the mixture of beech and oak has been highly relevant for Central European forestry and its importance will most probably increase under climate change. Despite this importance, growth and productivity of oak–beech mixtures have only rarely been subject to analyses. This paper examines productivity of mixed stands of European beech (*Fagus sylvatica* L.; termed “beech” in the following)

and oak (*Quercus* sp.) consisting of two major representatives in Central Europe: pedunculate and sessile oak, respectively. The taxonomic status of these two members of the oak group has since long been subjected to ongoing discussions and repeated reassessment. Pedunculate and sessile oak have either been described as two distinct species, *Q. robur* L. and *Q. petraea* (MATT.) LIEBL., respectively, or are currently placed within the species *Q. robur* L. as two subspecies *Q.r. robur* and *Q. r. petraea* (Roloff and Bärtels 2008, pp. 506–507). To avoid possible taxonomic pitfalls, we either use in the following “oak” as a generic term summarizing both members or their colloquial names to distinguish species/subspecies with “pedunculate oak” referring to the *robur* type and “sessile oak” to the *petraea* type, respectively.

Oaks started to spread across Europe immediately after the end of the last glaciation and were the dominating forest species around 5,000 BC (Atlantikum/Subboreal). At that time, beech occupied not more than approximately 50 % of the area potentially occupied today. The species colonized the remainder of today’s native range during the following millennia (Huntley 1988; Lang 1994). Since human influence on European forests, oak as well as beech has been severely decimated by clearings for agricultural land or, during the last centuries, by replacing them in the forest by faster and straighter growing conifers such as spruce, fir or pine species (Mantel 1961). Without human interference, beech would currently most probably cover more than 2/3 of the Central European forest area (Bohn et al. 2003). Their current share in the forested lands has been reduced to less than 1/5 by human interference (Fischer and Fischer 2012).

Most probably, ongoing climate change will again reinforce the relevance of beech and oak mixtures in Central European forestry in the nearer future. The predicted changes towards increasingly drier and warmer climate conditions are generally expected to reduce vigour and resilience of less-adapted species like spruce and pine (Pretzsch 1999; Pretzsch and Ďurský 2002; Spellmann et al. 2011). Lately, regimes adhering to the general principles of close-to-nature silviculture (Leibundgut 1987) have been introduced in practical forestry on a broad basis (e.g. Schütz 1999; Kenk and Guehne 2001). These principles enhance—among others—the importance of the tree species dominant in the potential natural forest cover, that is, mainly beech in Central Europe. Forest science as well as forest practice scrutinizes currently whether stands of beech and other species of the natural vegetation are better adapted to prevalent climatic trends and events than stands dominated by artificially promoted spruce or pine. Although close-to-nature mixed stands of beech and oak may be inferior in growth in the short term, their performance might prove superior over the long term due to potentially higher stress tolerance, stability and resilience (Kölling and Zimmermann 2007; Manthey et al. 2007; Pretzsch et al. 2012).

Natural mixtures of oak and beech occur within the Central European beech region under certain site conditions (Mayer 1984). The physiological optima regarding productivity of oak and beech are rather similar on fertile soils which are well supplied with water under mild climatic conditions. However, the ecological optima differ considerably and their ecological niches appear almost complementary. In most parts of the European beech region, beech displays superior competitive vigour enabling the species to outcompete oak and to dominate forests across a considerable gradient of ecological site characteristics ranging from dry sites and very moist sites to sites with extremely low temperatures in winter and or late frost in spring (Leuschner 1998). As a consequence, pedunculate oak is restrained by beech competition mostly to very wet and heavy alluvial soils in river lowlands rich in nutrients but short in macropores, while the ecological optimum of sessile oak is restricted to dry and acidic sites of more hilly country (Ellenberg and Leuschner 2009; Körner 2002).

Mixed stands of oak and beech occur naturally on sites where combinations of either drought and warmth or moistness and low temperatures restrict the competitive potential of beech to such an extent that oak can compete successfully. The competitive balance between oak and beech can be expected to respond to climate change and may be favourable for oak if temperatures rise or precipitation is reduced during the vegetation period resulting in a tendency of increasing water-stress levels.

Considering the high relevance of beech and oak as potential forest vegetation at present and considering their expected increasing role under climate change scenarios, detailed knowledge on the species’ performance and performance-modifying site conditions is important. However, such information is rather scant. Notwithstanding, this statement is the fact that a variety of above-ground (André et al. 2008; Valladares et al. 2002) as well as below-ground mechanisms (Aranda et al. 1996; Jonard et al. 2008; Hein and Dhôte 2006) in mixed stands of oak and beech have been analysed on tree or stand level. Studies by Jensen (1983) and Pretzsch et al. (2010) demonstrate that mixing effects can hardly be understood without consideration of site conditions. Callaway and Walker (1997) and Holmgren et al. (1997) actually assume that underlying inter-species interactions such as facilitation, reduction of competition or competition may only emerge if the prevailing site conditions are adequately considered.

As the aim of our study was to contribute to the understanding of inter-species interactions in mixed oak–beech stands, we attempted to cover a wide range of site conditions by pooling data from oak and beech long-term experiments in the German state of Bavaria, with similar data sets from long-term experiments maintained by other German forest research stations in the states of Lower

Saxony, Rhineland-Palatinate, Baden-Württemberg, as well as from Switzerland and Poland for this study. This provides a unique database. Although several of the included experiments have been under survey since the late nineteenth century, their data have not been combined so far, and some have never been published.

In the study presented here, we use the data set to (1) investigate the productivity of mixed stands in comparison with adjacent pure stands, (2) analyse how site conditions may modify mixing effects and (3) develop a basic model which describes how site conditions and mixing portions modify mixing effect in terms of relative and absolute productivity changes compared with adjacent pure stands. We then discuss results in relation to facilitation and competition in mixed versus pure stands in view of the stress-gradient hypothesis, present some causal interpretations practical for silvicultural implications of the revealed over- and underyielding effects and finally use the species-specific behaviour along the ecological gradient to hypothesize on the dynamics of oak–beech forests under climate change.

## Materials and methods

### Study area and experimental plots

Data were pooled from 37 experimental plots with mixed stand of oak and beech. The geographical distribution of the experiments ranges from 54° N in the diluvial north of Germany to 46° N in the Jurassic centre of Switzerland (Fig. 1). The westernmost experiments are located at 6° W in the devonian mountains close to the German–French border and the easternmost locations at 14° W in the quaternary north of Poland. All experiments are located in the Central European oak–beech forest region which reaches from Poland, Bohemia and Moravia in the east to Münsterland, Hunsrück, French Vosges and Swiss Jura Mountains in the west and extends from southern Sweden and Norway in the north to Lake Geneva in the south (Mayer 1984, pp. 14–18 and 124–132). The experiment locations range in elevation from 30 to 585 m a. s. l., the mean annual temperature from 6.0 to 9.3 °C and the annual precipitation from 550 to 1,120 mm year<sup>-1</sup> (Online Resource 1).

A broad variety of geology and soils characterizes this region: rich diluvial soils in the Polish and Baltic north, acidic soils on quartzite in the west along the German–French border, alkaline limestone-derived soils in the Jurassic mountains of Swiss Jura, Swabian and Bavarian Alb in the south-west and south, and rather poor soils in the sandstone and Keuper highlands of Spessart and Steigerwald.

Precipitation increases gradually from north to south, and continental climates (deep winter frost, large amplitude of temperature and concentration of precipitation on the summer

months) gain importance going from west to east. At low elevations in the planar and colline climate zones, oak is sufficiently competitive to either form pure stands or grow in mixture with beech. At higher elevations (submountainous and mountainous climate zones), beech generally outcompetes oak, and oak may only be maintained in beech stands through repeated human interference (e.g. tending and thinning).

Due to the differences in geological material at the different locations, the experiments represent growth dynamics developing on very nutrient poor and dry diluvial loamy sands as well as on quite fertile and moist calciferous loess loams (Online Resource 1).

The 37 experiments listed in Online Resource 1 represent the locations with mixed species plots near Barlohe, Trittau, Gryfino, Chojna, Ankum, Hochstift, Herborn, Schlüchtern, Lahnstein, Jossgrund, Schweinfurt, Lohr, Trier, Rothenbuch, Soonwald, Rohrbrunn, Ebrach, Waldbrunn, Bad Mergentheim, Schöntal, Fischbach, Kelheim, Winterthur, Winznau, Gunzgen, Neuendorf, Boudry, Galmiz, Greng and Concise (see Fig. 1). The plot size varied between 0.25 and 1.0 hectare. In one case, the experiment comprises seven mixed plots within a distance of 1–2 km from a specific location (Zwiesel 111). For the mixed stand plots, we chose pure stands of oak or beech as reference plots (for reasons of brevity not listed in Online Resource 1) growing at the same location. In most cases, these reference plots were a part of the experimental set-up including the mixed plots. In other cases, pure stand plots from experiments in the immediate neighbourhood served as reference, and in a few cases, we used successive surveys from inventory plots conducted in suitable neighbouring pure stands of oak or beech. The analysis is based on fully stocked pure and mixed stands which were continuously lightly or moderately thinned from below or above according to Verein Deutscher Forstlicher Versuchsanstalten (1902). That ensures a standardized treatment on all included plots and a stocking density close to the optimal stand density and maximum growth (Assmann 1961).

Since the foundation of the “Verein Deutscher Forstlicher Versuchsanstalten” (Association of German Forest Research Stations) in 1872 and its international successor organization “International Union of Forest Research Organizations” (IUFRO) in 1892, Central European forest research institutions have been cooperating based on standardized research plans. The associated institutions early took into consideration that the effect of silvicultural treatment (e.g. spacing, thinning, species mixing) on stand growth and yield can be significantly modified by site conditions and that reliable results and generalizations can only be achieved when experiments cover a broad range of site conditions. Consequently, questions regarding the relationship between species mixing and productivity have been investigated by establishing disjunct experiments

**Fig. 1** Location of the 37 long-term mixed stand observation plots of pure oak (sessile oak and pedunculate oak), pure beech, and mixtures of oak and beech included in this study (see Online Resource 1 for further information)



since the very beginning of experimental forestry (Jensen 1983; Kennel 1965; Wiedemann 1951). Such disjunct experiments replicate the treatment variants to be tested (species combination, mixing proportion, thinning) on experimental plots on different sites in different growth regions. Common research plans standardized the establishment (e.g. Ganghofer von 1881; Hausrath 1927), the silvicultural treatment (Verein Deutscher Forstlicher Versuchsanstalten 1902) and even the data evaluation (Johann 1993) allowing for the compilation of trans-institutional experiment series.

Our paper draws decisively on the result of this long-standing process of observation techniques harmonized among cooperating institutions. The crucial value of this cooperation is the provision of a unique database of long-term observations along wide geographical or ecological gradients, which could only be achieved by pooling data sets of several research organizations. The majority of the experiments included in this study had been established between 1900 and 1950 and was kept under survey to date.

This means that our results apply for the growing conditions within the twentieth and the beginning of the twenty-first century. It needs to be recognized that this database became only feasible by gathering information from research plots, which had been established, treated, measured and documented by previous generations of forest researchers to whom we are deeply grateful.

#### Overview on stand characteristics and data preparation

Two-thirds of the plots with oak comprise of sessile oak, the remainder of pedunculate oak or a mixture of both (Online Resource 2). For the comparison with beech growth, we pooled the data from both oaks. This appears appropriate as both are taxonomically closely related, often mixed within the same stand, tend to cross-breed rather often and even appear to display genetic introgression (Kremer et al. 2002). In addition, they are similarly inferior as competitors compared to beech on the whole range of sites covered by our database. Only when beech competition suffers by drought,

coldness or lack of oxygen in the soil, oaks increase in relative competition vigour finally gaining superiority over beech (Aas 2000, 2002; Levy et al. 1992; Epron and Dreyer 1993). However, sites with clear oak superiority were not included in our database. The following differences in the oaks' ecology should also be kept in mind: sessile oak in tendency appears to avoid compact soils and is rather shade tolerant. Winter frosts are tolerated less by sessile oak compared with pedunculate oak. In contrast, pedunculate oak is more tolerant with respect to waterlogging, scarcity of soil oxygen and compact soils.

The comparison of attributes of mixed versus pure stands requires different approaches for mean values like quadratic mean diameter,  $d_q$ , quadratic mean height,  $h_q$  and sum values like standing volume or periodic annual volume increment, PAIV (PAIV = average annual increment within a given period). For both types of stands, we use the same notation. For example, if we wanted to investigate attribute  $x$  in mixed or pure stands, then  $x_{\text{oak}}$  and  $x_{\text{be}}$  address this attribute in the pure oak stand, respectively, the pure beech stand; in the mixed beech–oak stand, the attribute is denoted  $x_{\text{oak,(be)}}$  when oak is addressed in the mixture, or  $x_{\text{(oak),be}}$  when beech is addressed in the mixture.

For analysing dependencies between mixing effect and site index, we use the quadratic mean height of oak and beech at an age of 100 years,  $hq_{100 \text{ oak}}$  and  $hq_{100 \text{ be}}$ , as a surrogate for site quality. As most of the experiment series included stands of ages up to 100 years,  $hq_{100 \text{ oak}}$  and  $hq_{100 \text{ be}}$  were directly available as observed values from the pure stand plots. For plots younger than 100 years, site index was referenced or extrapolated from yield tables by Jüttner (1955) and Schober (1967) for oak and beech, respectively.

The analysis of mixing effects was based on triplet experimental set-ups: one plot represented pure oak, one plot pure beech and the third plot containing both species in mixture. Stand productivity was analysed on the basis of the periodic annual increment of stem volume, PAIV, in  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  (merchantable stem volume  $\geq 7$  cm over bark).

On the one hand, comparison of species with respect to growth and quantification of mixing effects remains somewhat fragmentary when based solely on stem volume as this assessment does not account for species-specific differences, for example, in wood density or branch-wood portion (Kennel 1965). On the other hand, any approach trying to upscale stem volume to stem or total tree biomass necessarily needs assumptions in addition to technically sound original measurements and will thus inevitably result in increased levels of inaccuracy. Fortunately, beech and oak are quite similar with respect to volume densities (Knigge and Schulz 1966, p. 135) with beech characterized by a volume density (=wood dry mass per volume of fully swelled wood) of 0.554 and oak 0.561  $\text{g cm}^{-3}$ . Furthermore, according to Burschel et al. (1993, p. 10), both species display almost equal

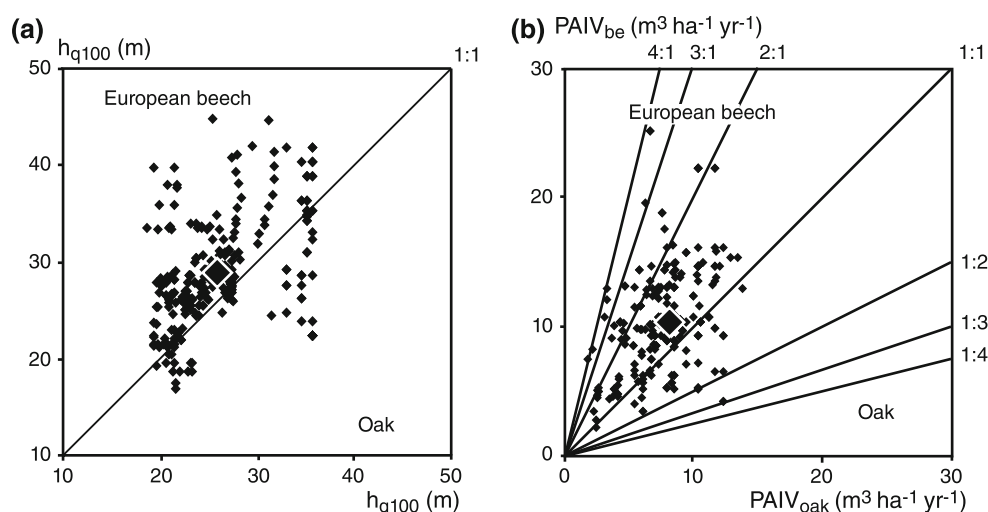
expansion factors for converting stem to total biomass (beech: 4.00–1.39 and oak: 4.00–1.34; factors are listed from young to mature stands). As we wanted to base our analyses with the least possible conversion of the original measurement data, we carried out the analysis on the basis of merchantable wood volume ( $>7$  cm in diameter at the smaller end). Overyielding as well as underyielding by mixing is therefore reported for the periodic annual growth of stem volume ( $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ). However, whereas volume is the more relevant parameter for applied forest management, investigations on ecological growth aspects are usually benefitted by using information on dry mass production. For purposes of discussion, we therefore attempted to scale up from stem volume to biomass production ( $\text{t ha}^{-1} \text{year}^{-1}$ ) based on general assumptions concerning volume density and branch-wood portions (see Pretzsch and Dieler 2012).

In order to sketch the relative performance of oak and beech, we plotted mean height at age 100 of the pure beech stand against the pure oak stand of the same triplet (Fig. 2a). Height at age 100 years ranged in oak stands from 20 to 35 m; the range of beech was approximately 20–45 m. The scattering pattern around the bisectoral line indicated that in most cases of the triplets, beech exceeded oak by far with respect to height. Only in about 10 % of the triplets, height of beech at age 100 years is 5–10 m lower than oak (indicated by the points below the bisectoral line). An analogous plot of the stem volume productivity of pure beech versus pure oak (Fig. 2b) confirmed that the data set really covered a considerable range of site conditions and stand development phases: PAIV ranged from 1 to 15  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  in oak and from 1 to 25  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  in beech. On average, PAIV amounted to 7.81 (standard error:  $\pm 0.16$ )  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  in the pure oak stands and to 10.42 ( $\pm 0.26$ )  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  in the pure beech stands. This means that in pure stands, which served as the reference for the analysis of mixing effects, beech outgrew oak in most cases with respect to height and PAIV. However, due to the wide range of site and stand constellations covered by the experiments, the database also covers situations where this relation was reversed in favour of oak (for further stand-level information, see Online Resource 2).

As the included stands and surveys cover an age span from about 30 to 370 years with a concentration between 50 and 150 years (see Online Resources 1 and 2), our results with respect to mixing reactions apply to middle-aged and mature stands and may be different in young stands.

### Quantification of mixing effects

We restrict the following specifications of variables and calculation to those which are deemed indispensable for understanding the concept and results of the mixing analysis. For a more detailed introduction into nomenclature



**Fig. 2** Characteristics of the pure stands of oak and beech. These stands serve as reference for the investigation of mixing effects in the neighbouring mixed stands. Shown are **a** mean height at age 100 years of oak and beech,  $hq_{100}$ , and **b** periodic mean annual

volume increment of oak,  $PAIV_{oak}$ , and beech,  $PAIV_{be}$ . The large rhombi indicate species-specific mean values ( $\pm$ standard errors) of  $hq_{100}$  (oak  $24.05 \pm 0.29$  m; beech:  $28.16 \pm 0.40$  m) and  $PAIV$  (oak  $7.81 \pm 0.16$   $m^3$   $ha^{-1}$   $year^{-1}$ ; beech  $10.42 \pm 0.26$   $m^3$   $ha^{-1}$   $year^{-1}$ )

and quantification approaches for over- and underyielding in mixed versus pure stands, see Pretzsch (2003) and Pretzsch et al. (2010). In order to be able to read the cross diagrams and to understand the models (Eqs. 5–9) presented in this paper, there are only three different relative productivity measures needed:

Firstly, we considered the relative productivity  $RP_{1,2}$  for the stand as a whole. It resulted from the observed productivity of the mixed stand  $p_{1,2}$  divided by the productivity expected for the mixed stand  $\hat{p}_{1,2}$

$$RP_{1,2} = p_{1,2} / \hat{p}_{1,2} \tag{1}$$

The expected productivity  $\hat{p}_{1,2}$  was derived from the productivity of both species in the neighbouring pure stands,  $p_1$  and  $p_2$ , and their mixing portions  $m_1$  and  $m_2$  ( $\hat{p}_{1,2} = m_1 \times p_1 + m_2 \times p_2$ ). The mixing portions  $m_1$  and  $m_2$  were calculated on the basis of the species' share of the stocking dry mass  $W$  ( $m_1 = W_1 / (W_1 + W_2)$ ,  $m_2 = W_2 / (W_1 + W_2)$ )

Secondly, the relative productivity  $RP$  of species 1 and 2 in mixed versus pure stands was of interest. For species 1, the relative productivity in mixed versus pure stand was

$$RP_{1,(2)} = pp_{1,(2)} / m_1 / p_1, \tag{2}$$

with the share of productivity of species 1 in the mixed stand,  $pp_{1,(2)}$ , mixing portion,  $m_1$ , and productivity of the pure stand,  $p_1$ . For species 2, the following formula applied:  $RP_{(1),2} = pp_{(1),2} / m_2 / p_2$ . Notice that  $pp_{1,(2)}$  and  $pp_{(1),2}$  were the contribution of species 1 and 2 in the mixed stand to the total productivity which added up to  $p_{1,2}$  ( $p_{1,2} = pp_{1,(2)} + pp_{(1),2}$ ). In contrast,  $p_{1,(2)}$  and  $p_{(1),2}$  were the contributions of both

species in the mixed stand scaled up to 1 ha using their mixing portion ( $p_{1,(2)} = pp_{1,(2)} / m_1$  and  $p_{(1),2} = pp_{(1),2} / m_2$ ).

Thirdly, for completion of the cross diagrams for species 1 and 2, we needed the relationships

$$RPP_{1,(2)} = pp_{1,(2)} / p_1 \text{ and } RPP_{(1),2} = pp_{(1),2} / p_2. \tag{3}$$

The relative productivity on the basis of the portions,  $RPP$ , resulted from division of the contribution of the productivity of species 1,  $pp_{1,(2)}$ , respectively, species 2,  $pp_{(1),2}$ , by the productivity of the same species in the pure stand. Notice that  $RPP_{1,2} = RPP_{1,(2)} + RPP_{(1),2}$ .

The following equations showed how the species-specific relative mixing reactions  $RP_{1,(2)}$  and  $RP_{(1),2}$  had to be weighted by the species-specific productivity and mixing proportions in order to calculate the stand-level response  $RP_{1,2}$ .

$$RP_{1,2} = RPP_{1,(2)} \times [p_1 / (p_1 \times m_1 + p_2 \times m_2)] + RPP_{(1),2} \times [p_2 / (p_1 \times m_1 + p_2 \times m_2)] = [pp_{1,(2)} + pp_{(1),2}] / [p_1 \times m_1 + p_2 \times m_2]. \tag{4}$$

In order to illustrate the mixing reactions in terms of relative and absolute productivity of mixed versus pure stands in section “Causal explanation of the mixing effects” and “Implication for ecological theory,” we derived auxiliary relationships which reflected  $PAIV$  of pure stands depending on age,  $a$ , and site index,  $hq_{100}$ , for oak

$$PAIV_{oak} = 2.232 + 0.229 \times hq_{100_{oak}} - 0.008 \times a_{oak}, \tag{5}$$

and for beech

$$PAIV_{be} = 2.682 + 0.243 \times hq100_{be} + 0.005 \times a_{be}. \quad (6)$$

Cross diagrams for analysing the mixing effect

We use cross diagrams according to Harper (1977, pp. 776–778) and Kelty (1992) to disclose possible mixing effects on productivity in mixed stands composed of two different species. In such diagrams (Fig. 3), the relative productivity of species 1 in the pure stand is plotted on the left-hand ordinate, and for species 2 on the right-hand ordinate. The broken straight lines represent the expected productivity of the mixed stand in total (horizontal line 1.0-line) as well as the share of the species 1 and 2 in the stands' productivity [descending line connecting (0|1) with (1|0), respectively, and rising line connecting (0|0) with (1|1)] depending on the mixing portion, which is scaled on the abscissa. The observed productivity is represented by the following three continuous curves: the observed productivity on total stand level by the upper curve, the contribution of species 1 by the lower curve descending from left to right and the share of species 2 by the lower curve rising from left to right.

If varying portions of the species in mixture do not impact on the species' respective growth potential (growth neutral), the production of the mixed plots should more or less follow the straight lines connecting the two pure stands. In contrast, systematic positive or negative deviations of observed growth values from the straight reference lines would indicate whether overall stand production gains or loses in the mixture. In such diagrams, the individual species lines of

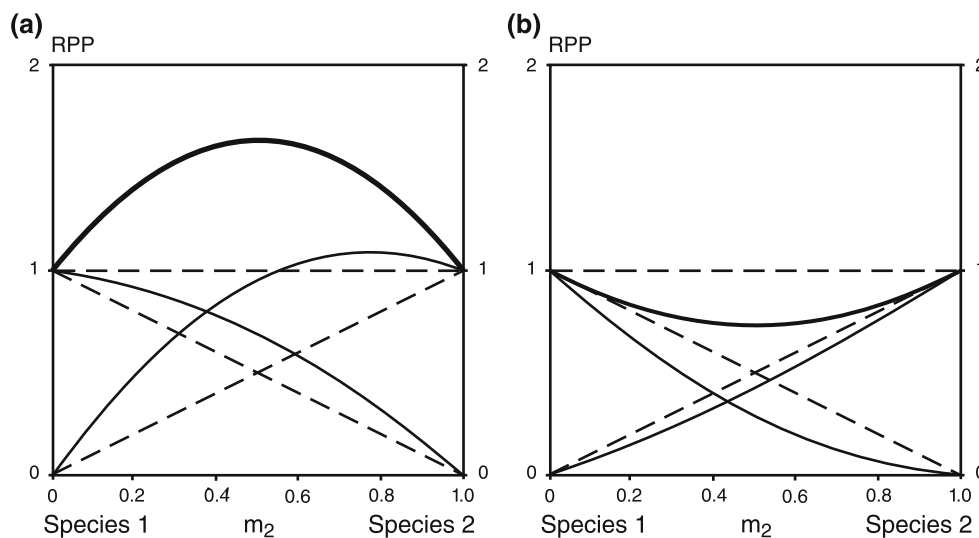
$RPP_{1,(2)}$  and  $RPP_{(1),2}$  form a cross (hence the name “cross diagram”) and indicate whether a species gains or loses by mixing. Concavity indicates benefits, and convexity losses due to the mixing of the two species in one stand.

The curves shown for the upper lines in Fig. 3a indicate positive mixing effects on the stand level. Overall productivity of the mixed stand exceeding the reference line expected based on productivity in the pure stands and indicates overyielding. Similarly, the species-specific curves are also concave and exceed the species-specific reference lines indicating that both species contribute positively to the overall positive mixing effect. In this case, both species mutually benefit from the mixture. Such mutual facilitation is generally called mutualism.

In contrast, Fig. 3b indicates an example of antagonism. The convex curves (seen from below) on stand as well as on species level indicate mutual inhibition of growth in mixture. Species 1 suffers more in mixture than species 2. While the benefit in terms of productivity amounts to 60–70 % in the stand depicted in Fig. 3a, the mixture shown exemplarily in Fig. 3b corresponds to a reduction in productivity by 20–30 %.

Statistical analysis and models

The first of the three models focused on the prediction of the relative productivity of the species' portion in the mixed stands  $RPP_{oak,(be)}$  and  $RPP_{(oak),be}$  depending on the mixing portions  $m_{oak}$  and  $m_{be}$ , respectively



**Fig. 3** Cross diagrams according to Harper (1977) and Kelty (1992) for display of mixing effects on productivity in two-species mixtures with overyielding due to mutual facilitation (a) and underyielding due to antagonistic interactions between the two species (b). The left and right ordinates, respectively, represent the relative productivity of species 1 and 2 ( $RPP_1$  and  $RPP_2$ ) and the abscissa the mixing portion

of species 2 ( $m_2$ ). Broken lines represent the productivity expected for neutral mixing effects on the level of the stand as a whole (horizontal 1.0-line) and on the level of the two contributing species (decreasing with respect to increasing lines). The solid lines show the observed productivity on stand level (upper bold curve) and species level (lower thin curves), respectively

$$\text{RPP}_{\text{oak,(be)}} = m_{\text{oak}} \times (1 + a_1 \times m_{\text{be}})$$

and

$$\text{RPP}_{(\text{oak}),\text{be}} = m_{\text{be}} \times (1 + a_1 \times m_{\text{oak}}), \text{ respectively.} \quad (7)$$

Equation 1 was chosen as it represents the simplest connection between the boundary points (011) and (110) of the cross diagram (Fig. 3) and can become concave ( $a_1 > 0$ ), convex ( $a_1 < 0$ ) or just straight ( $a_1 = 0$ ). The first factor in this equation ( $m_{\text{oak}}$  and  $m_{\text{be}}$ , respectively) describes the expected proportional decrease of the productivity of the respective species, when its share is reduced and simultaneously substituted by another species. The second factor,  $(1 + a_1 \times m_{\text{be}})$  and  $(1 + a_1 \times m_{\text{oak}})$ , respectively, describes whether and how the addition of the second species actually impacts on the growth of the initial species.

The second model is similar to the first, but extended by the covariate height at age 100 years ( $h_q$ ),

$$\begin{aligned} \text{RPP}_{\text{oak,(be)}} &= m_{\text{oak}} \times (1 + b_1 \times m_{\text{be}} + b_2 \times m_{\text{be}} \times \text{hq}100_{\text{oak}}) \\ \text{RPP}_{(\text{oak}),\text{be}} &= m_{\text{be}} \times (1 + b_1 \times m_{\text{oak}} + b_2 \times m_{\text{oak}} \times \text{hq}100_{\text{be}}) \end{aligned} \quad (8)$$

Equation 2 also connects the boundary points (011) and (110) of the cross diagram (Fig. 3). However, in this case, the deviation from a straight line ( $b_1$  and  $b_2 = 0$ ) is determined by mixing portion and site quality.

The third model approach is a simple linear model estimating the species-specific relative productivity of oak and beech,  $\text{RP}_{\text{oak,(be)}}$  and  $\text{RP}_{(\text{oak}),\text{be}}$ , and the relative productivity of the mixed stand as a whole,  $\text{RP}_{\text{oak,be}}$ , in dependence on the mean height,  $h_q$ .

$$\begin{aligned} \text{RP}_{\text{oak,(be)}} &= c_1 + c_2 \times \text{hq}_{\text{oak}}, \\ \text{RP}_{(\text{oak}),\text{be}} &= c_1 + c_2 \times \text{hq}_{\text{be}}, \\ \text{RP}_{\text{oak,be}} &= c_1 + c_2 \times \text{hq}_{\text{oak}} \end{aligned} \quad (9)$$

To fit the models (Eqs. 10–13), we applied the non-linear regression procedure based on the Levenberg–Marquardt algorithm, and for the models (Eqs. 14–16), we used the OLS-linear regression algorithm. In this way, we kept the model simple. The application of mixed models appeared to be unnecessary and too sophisticated in our case as a nesting of plots within locations was rare. Out of the repeated measurements on the plots, we sampled those with period length  $>5$  years and which did not follow each other in order to get sound means of the periodic annual increment and avoid intercorrelation between successive periods. By using the periodic-specific stand characteristics (e.g., stand age, site index, stand density, mixing proportion at the beginning of each period) as covariates in the model for predicting the mixing effects we took into account any inter-correlation between successive survey periods. However, this approach enables an exhaustive exploitation of the given data set with

respect to interactions between periodic-specific stand characteristics and mixing effects. All calculations were carried out using the software package PASW Statistics (Version 18.0).

## Results

### Stand and mean tree characteristics of mixed versus pure stands

Figure 4a shows the observed  $\text{PAIV}_{\text{oak,be}}$  ( $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) values of the mixed stands plotted against the expected values  $\hat{\text{PAIV}}_{\text{oak,be}}$  derived from the respective pure oak and beech stands. The mixed stands produced on average  $9.31$  (standard error:  $\pm 0.22$ )  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  thus exceeding the productivity expected from the pure stands ( $8.99 \pm 0.17 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) on average by  $0.32 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  (+4 %). The maximum overyielding observed for mixed stands was  $13.46 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  and maximum underyielding was  $9.94 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ .

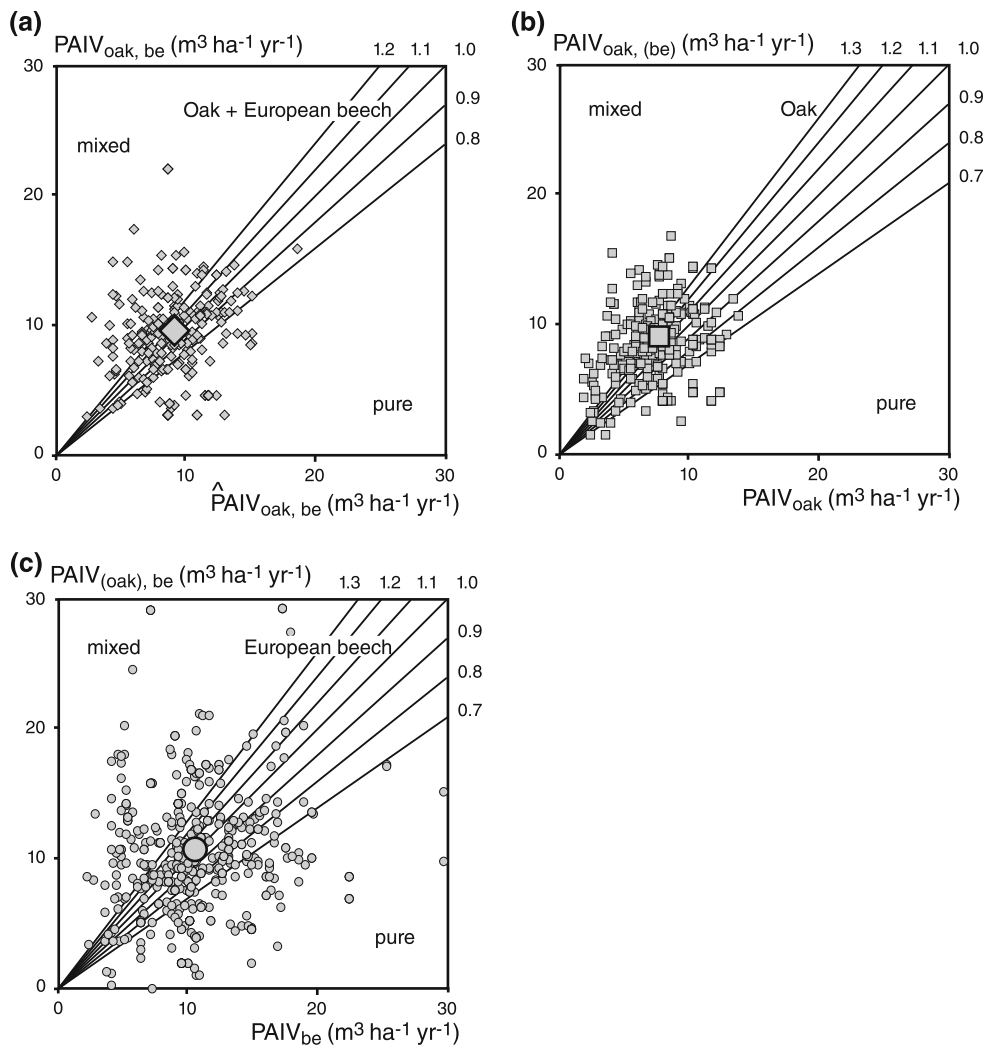
The species-specific analysis (Fig. 4b, c) showed that oak produced on average 11 % ( $0.83 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) more in mixed stands ( $8.39 \pm 0.17 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) as compared to pure stands ( $7.56 \pm 0.15 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ). For beech, overyielding in mixed stands amounted on average to  $0.10 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  which was similar to oak. However, due to the higher growth level of beech, this represented merely an increase of 0.1 % from pure beech ( $10.65 \pm 0.20 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) to mixed stands ( $10.75 \pm 0.25 \text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ).

On average, total standing volume of oak per hectare was higher in the mixed stands ( $316 \pm 9.43 \text{m}^3 \text{ha}^{-1}$ ) compared to the pure stands ( $255 \pm 6.70 \text{m}^3 \text{ha}^{-1}$ ), while the opposite was true for beech ( $264 \pm 6.70 \text{m}^3 \text{ha}^{-1}$  in mixture versus  $393 \pm 8.60 \text{m}^3 \text{ha}^{-1}$  in pure stand; see Online Resource 3). Total standing volume amounts to  $295 \pm 9.95 \text{m}^3 \text{ha}^{-1}$  in the mixed stands, and  $309 \pm 9.50 \text{m}^3 \text{ha}^{-1}$  in the pure stands. So, the increased volume of growing stock of 24 % at the stand level was compensated by a reduction of 23 % of growing stock volume in beech. Overall, the mixed stands within the triplets exhibited growing stock volumes as expected from the adjacent pure stands. Furthermore, there were no statistically significant differences with respect to above-ground dry biomass of the total stand (oak + beech), with values of  $248 \pm 8.31 \text{t ha}^{-1}$  in mixed stands and  $260 \pm 7.99 \text{t ha}^{-1}$  in the pure stands (see Online Resource 4).

For further interpretations of possible mixing effects, species-specific mean diameters achieved in mixed versus pure stands may be of interest (see Online Resource 5): mean diameter of oak was 2 % higher in the mixed stand



**Fig. 4** Comparison of periodic mean annual increment (PAIV) of the mixed stands with neighbouring pure stands. Depicted is **a** the observed  $PAIV_{oak,be}$  over the expected  $\hat{PAIV}_{oak,be}$  for stem volume at the level of the stand as a whole, **b** the analogue relationship  $PAIV_{oak,(be)}$  versus  $PAIV_{oak}$  for oak and **c** for  $PAIV_{(oak),be}$  versus  $PAIV_{be}$  for beech



(33.20 ± 0.81 cm) compared with the pure stand (32.59 ± 0.72 cm). Most probably caused by silvicultural treatment in favour of oak, the mean diameter of beech was 39 % lower in the mixed stand (19.88 ± 0.57 cm) than in the pure beech stand (32.41 ± 0.67 cm). In particular on the fertile sites where beech tended to outgrow oak with respect to height and diameter, stand dominating beech which impede growth of oak had been quite often removed to release oak from adverse competition. As a result of such interventions, mean diameter of the remaining stand decreases.

Productivity of mixed stands compared to adjacent pure stands

For closer analysis of mixing effects and their dependency on species, mixing portion or site conditions, the relative mixing responses at the level of the individual stand are useful parameters for being displayed in cross diagrams (Fig. 5). The scatter plots separated for oak and beech (Fig. 5a, b) as well as for the stand in total (Fig. 5c) display

a high amount of variation among the RPP values with positive as well as negative deviation from the neutral reference line (broken line).

In order to analyse the potential effect of the mixing portion on the relative volume growth of oak and beech in the mixed stands as well as to depict the mean mixing effect, we used the following functions (standard error of the parameters in brackets):

$$RPP_{oak,(be)} = m_{oak} \times (1 + 0.827(\pm 0.124) \times m_{be}) \quad (10)$$

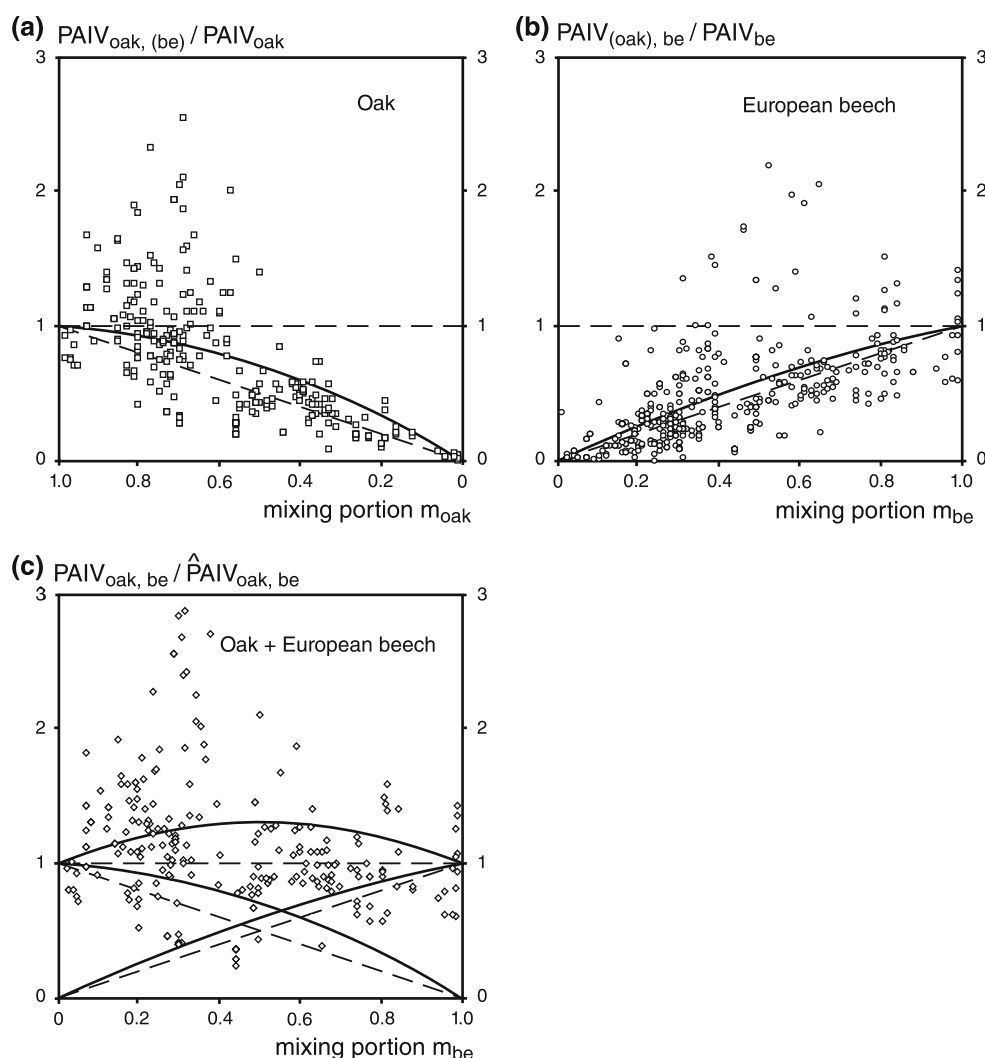
$n = 297, R^2 = 0.38, p < 0.001$

$$RPP_{(oak),be} = m_{be} \times (1 + 0.363(\pm 0.077) \times m_{oak}) \quad (11)$$

$n = 464, R^2 = 0.33, p < 0.001$

The cross diagram shows the species-specific response patterns (Fig. 5a, b) to mixing as well as the sum  $RPP_{oak,be} = RPP_{oak,(be)} + RPP_{(oak),be}$  (Fig. 5c). The latter represents the relative overall productivity of the mixed stand as a whole in relation to the adjacent pure stands.

**Fig. 5** Relative productivity on the basis of the portions of volume growth of **a** oak, **b** beech and **c** the mixed stand in total in relation to the productivity of the neighbouring pure stands. The *points* represent the observed relative volume productivity of mixed versus pure stands. The *curves* represent the average mixing reactions of oak, beech and total stand according to model Eqs. 10 and 11. For explanation of the included reference lines (*broken*), see Fig. 2 and text



Both models (Eqs. 10, 11) were significant at level  $p < 0.001$ . The first factor in the two equations ( $m_{oak}$  and  $m_{be}$ , respectively) describes the decrease in productivity of the respective species, which can be expected when reducing a species' share in the mixture. The second factor is displayed in the two equations in brackets and addresses whether and how the added species impacts on the growth of the initial species in addition to simply proportion-based effects. If the estimated slope for factor two is zero, then an admixture would have no additional effect on a stands' productivity, whereas positive values of the slope parameter (as  $+0.827$  and  $+0.363$  in Eqs. 10, 11) would indicate an additional positive mixing effect besides the proportion-based impacts. In contrast, negative slope values can be interpreted as deteriorative effects of the admixture on the growth of the initial species.

The concave curves (seen from below) in Fig. 5a–c indicate that productivity of oak and beech in the mixed stand and therefore the mixed stand as a whole benefitted from the mixture with respect to productivity. Species-specific as well as stand-specific RPP curves deviated

positively from the productivity predicted for neutral mixing response to varying species proportions in the mixture (broken lines). Assuming a mixing portion of 0.5, the models yielded values of  $RPP_{oak,(be)} = 0.7067$  (oak in mixed stand; Eq. 10) and  $RPP_{(oak),be} = 0.590$  (beech in mixed stand; Eq. 11), which resulted in an overall  $RPP_{oak,be} = 1.296$  on the level of the total mixed stand. This means that at species level, oak achieved in the mixed stand 141 % ( $=0.7067/0.50 \times 100$ ) and beech 118 % ( $=0.590/0.50 \times 100$ ) of the respective species' pure stands. That means that the mixed stands as a whole exceeded total productivity as expected from pure stands according to  $\hat{p}_{1,2} = m_1 \times p_1 + m_2 \times p_2$  (see section "Quantification of mixing effects") by 29.6 % ( $=1.296/1.00 \times 100$ ).

#### Effect of site conditions on the mixing effect

For analysis of possible site-related effects on mixing response, we extended the models (Eqs. 12, 13) by an

interaction effect between mixing proportion and site index as follows:

$$\begin{aligned} \text{RPP}_{\text{oak,(be)}} &= m_{\text{oak}} \times (1 + 4.685(\pm 0.583) \times m_{\text{be}}) \\ &\quad - (0.145(\pm 0.021) \times m_{\text{be}} \times \text{hq}100_{\text{oak}}) \quad (12) \\ n &= 296, R^2 = 0.46, p < 0.001 \end{aligned}$$

$$\begin{aligned} \text{RPP}_{(\text{oak),be}} &= m_{\text{be}} \times (1 + 4.033(\pm 0.468) \times m_{\text{oak}}) \\ &\quad - (0.122(\pm 0.016) \times m_{\text{oak}} \times \text{hq}100_{\text{be}}) \quad (13) \\ &= 428, R^2 = 0.37, p < 0.001 \end{aligned}$$

For both species, site index had a significant negative effect ( $p < 0.001$ ) on relative productivity, RPP. Figure 6 shows the model curves against the scatter plots for oak and beech (Fig. 6a, b) in mixture. In order to evaluate the magnitude of the site effect, we inserted height values from 10 to 40 m into the model Eqs. 12 and 13. The results indicate that on sites with low productivity levels ( $\text{hq} < 25$  m at age 100 years), both species profit considerably from the mixture. Under these conditions, the RPP curves even exceed the 1.0-lines and indicate a significant facilitation effect. On sites with medium productivity levels ( $\text{hq} = 25\text{--}30$  m), a positive mixing effect was still visible in both species, but did not exceed the level of the neighbouring pure stands. For sites with high growth potential ( $\text{hq} > 35$  m) Fig. 6 shows a negative mixing effect; productivity in mixtures was reduced in comparison with the productivity in neighbouring pure stands.

In this context, we point out that statistical analysis of the growth rates clearly showed age- and site index-specific effects on RPP of both species. However, the mixing effect itself between oak and beech changed significantly only with site index, but not with stand age.

By using the quadratic mean height at age 100 years of oak ( $\text{hq}100_{\text{oak}}$ ) and beech ( $\text{hq}100_{\text{be}}$ ) as site index we were able to test the modifying impact of site productivity on mixing response with respect to the actual stand-level productivity either for each species separately or the stand as a whole. For oak as well as for beech, RP values decreased significantly ( $p < 0.001$ ) with increasing site quality, as indicated by the significantly negative slope values in Eqs. 14 and 15 (Fig. 7a):

$$\begin{aligned} \text{RP}_{\text{oak,(be)}} &= 2.250(\pm 0.155) - 0.038(\pm 0.006) \times \text{hq}100_{\text{oak}} \\ n &= 289, R^2 = 0.14, p < 0.001^{***} \quad (14) \end{aligned}$$

$$\begin{aligned} \text{RP}_{(\text{oak),be}} &= 1.841(\pm 0.207) - 0.023(\pm 0.007) \times \text{hq}100_{\text{be}} \\ n &= 420, R^2 = 0.05, p < 0.001^{***} \quad (15) \end{aligned}$$

For the total stand, the result was

$$\begin{aligned} \text{RP}_{\text{be,oak}} &= 1.816(\pm 0.165) - 0.025(\pm 0.006) \times \text{hq}100_{\text{oak}} \\ n &= 242, R^2 = 0.07, p < 0.001^{***} \quad (16) \end{aligned}$$

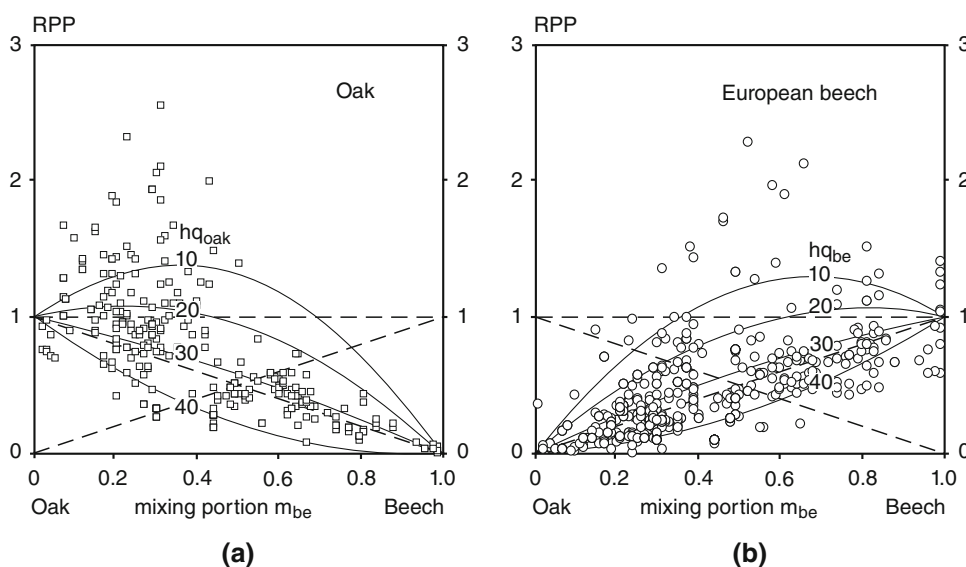
In the latter model (Eq. 16), we used  $\text{hq}100_{\text{oak}}$  as an indicator for the site fertility of the stand in total. Analysis of the relationship between  $\text{hq}100_{\text{oak}}$  and  $\text{hq}100_{\text{be}}$  showed a correlation of  $r_{\text{Pearson}} = +0.48$  ( $p < 0.01$ ,  $n = 282$ ). With respect to height growth, both species obviously displayed similar qualitative responses along the examined ecological gradient. As a consequence, site indices expressed through height development corresponded closely between oak and beech and might even be mutually substituted (see Fig. 2a).

A quadratic mean height of 20 m at a stand age of 100 years represents poor site conditions. Insertion of  $\text{hq}100 = 20$  m in Eq. 14 (oak) results in  $\text{RP}_{\text{oak,(be)}} = 1.49$ ; insertion of  $\text{hq}100 = 20$  m in Eq. 15 (beech) yields  $\text{RP}_{(\text{oak),be}} = 1.38$ . This is the equivalent of a gain in productivity brought along by mixing effects in the magnitude of 49 % (oak) or 38 % (beech). Medium site conditions ( $\text{hq}100 = 30$  m) yielded +11 and 15 % for the productivity of oak and beech in mixture versus pure stands. In contrast, for highly productive sites ( $\text{hq}100 = 40$  m), Eqs. 14 and 15 predicted a loss of 27 % for oak and 8 % for beech.

On the stand level, the gains and losses at the different levels of site-specific productivity (present values of site indices  $\text{hq}100_{\text{oak}} = 20, 30$  and 40 m) ranged from gains of +32 % ( $\text{hq}100_{\text{oak}} = 20$  m), or +7 % ( $\text{hq}100_{\text{oak}} = 30$  m), to a loss of -18 % ( $\text{hq}100_{\text{oak}} = 40$  m) according to Eq. 16. The responses of total production at the stand level displayed in Fig. 7b may be interpreted as a mutually beneficial mixing interaction between oak and beech on poor sites, a neutral response on medium sites and a partially antagonistic effect resulting in reduced productivity reduction on prime sites.

## Discussion and conclusions

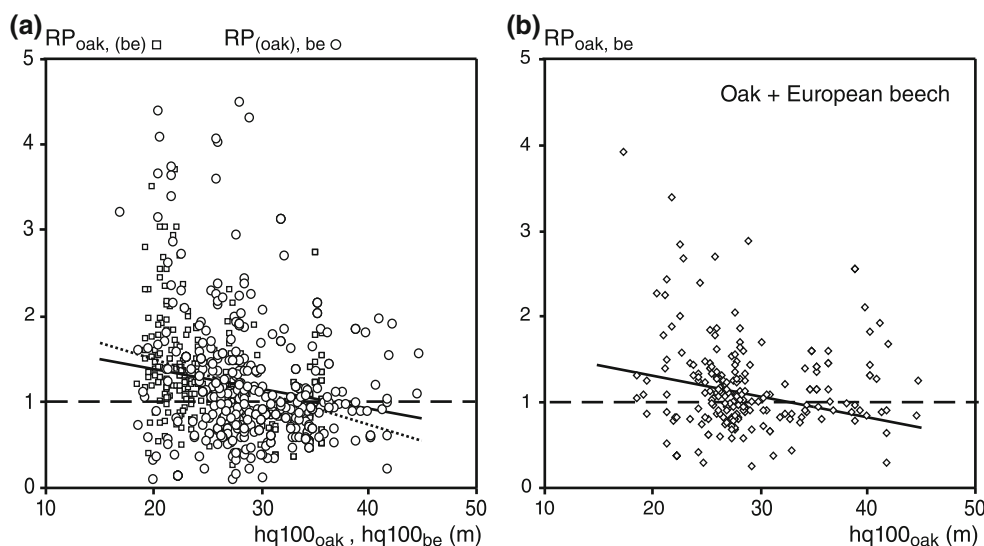
The strong influence of agronomy on forest practice has resulted in widespread establishment of forest monocultures. At present, after failure of lots of monocultures and rethinking on risk distribution (Griess and Knoke 2011), resource efficiency (Richards et al. 2010) and the functional significance of species diversity (Scherer-Lorenzen et al. 2005), mixed stand dynamics has returned into the focus of forest science (see e.g. Forrester et al. 2006, 2007; Pretzsch et al. 2010; Schütz 1999) after a long break since the 1940–1960s (Kennel 1965; Wiedemann 1942). However, overarching studies along ecological gradients which deliver sound information based on pooled data sets have not been available until recently. Comprehensive knowledge about



**Fig. 6** Species-specific relative productivity in mixed versus pure stand of **a** oak and **b** European beech depending on mixing portion,  $m$ , and quadratic mean height at age 100,  $hq_{100}$ , as indicator for site fertility. **a** Observed relative productivity ( $RPP = PPAIV_{oak,(be)}/PAIV_{oak}$ ) for oak plotted over mixing portion of beech,  $m_{be}$ , (rectangles) and model prediction (see Eq. 12) in dependence on

admixture of beech and site fertility (curves with  $h_{q100} = 10$  to 40 m). **b** Observed relative productivity ( $RPP = PPAIV_{(oak),be}/PAIV_{be}$ ) for beech plotted over mixing portion of oak,  $m_{oak}$ , (circles) and model prediction (see Eq. 13) in dependence on admixture of oak and site fertility (curves with  $h_{q100} = 10$  to 40 m)

**Fig. 7** Relationship between **a** species-specific relative productivity of annual volume increment of oak and beech and **b** total relative productivity of annual volume increment of mixed versus pure stands in dependence on site fertility, indicated by quadratic mean height at age 100,  $hq_{100}$ . Shown is the relative growth expected for neutral mixing reactions (broken 1.0-line), observed relative productivity of oak (rectangles), beech (circles) and the stand as a whole (rhombi), and regressions lines for oak (a broken line), beech (a solid line) and total stand (b solid line)



mixing effects between oak and beech is not yet available in scientific literature and therefore not integrated in guidelines for forest management and silvicultural treatment. The results of our study remain rather descriptive but summarize what we can learn from long-term experimental plots about the performance of this species mixture in Central Europe. The finding that the mixed stands of oak and beech produce on average 30 % more than neighbouring pure stands, that both species benefit from the mixture and that the benefit is the highest on poor sites and decreases with site quality tempts causal explanation, suggests silvicultural conclusions and promotes ecological theory.

The analysis is based on fully stocked pure and mixed stands which were continuously lightly or moderately thinned from below or above according to Verein Deutscher Forstlicher Versuchsanstalten (1902). In course of the stand development and silvicultural treatment, the mixing proportions and the site index changed on most of the plots. We distinguished between silvicultural treatment effects and mixing effects as follows. To all periodic annual increments which were used in the analysis, we assigned the mixing proportion at the beginning of the respective survey period, and the mixing effect for each survey period was evaluated based on the periodic-specific mixing

proportion. Suppose the mixing proportion of a species is reduced by thinning at the beginning of a period that is coupled with a reduction of the share of the pure stand which is used as reference. In this way, treatment effects were eliminated and confusion between species mixing effects and silvicultural treatment can be avoided.

#### Causal explanation of the mixing effects

Differences in the productivity between mixed and pure stands in terms of biomass growth indicate that species mixing affects at least one of the factors in the production ecology equation  $GPP = \text{resource supply} \times \text{proportion of resource captured} \times \text{efficiency of resource use}$  (Binkley et al. 2004; Matyssek et al. 2010; Richards et al. 2010).

In relation to comparable pure stands of the same area, mixing of oak and beech might increase the resource supply due to a higher atmospheric deposition (e.g.  $\text{NO}_x$ ,  $\text{NH}_3$ ,  $\text{SO}_x$ , Ca, K, Mg) (André et al. 2008), a higher nutrient content and decomposition in the leaf litter (Jonard et al. 2008), or a higher mineralization due to changed root depths, mycorrhiza and soil chemistry. The resource capture might be higher as a result of an improved temporal and spatial presence of the two species: from spring to autumn and from the canopy to the root space. Finally, the resource-use efficiency might be increased due to a higher nutrient content in leaves of mixed versus pure stands (Richards et al. 2010).

In the following discussion, we consider the three factors in the production ecology equation as possible causes for mixing reactions. As measurements of resource supply, resource uptake, and resource use efficiency were not conducted on the included experimental plots, all following considerations about the causes for mixing effects remain speculative.

That in the majority of the experiments both species are more productive in mixture compared with their performance in pure stands suggests a site-overarching complementarity between their ecological niches (Morin et al. 2011). Most obvious is their different light ecology; while oak is rather light demanding, beech is much more shade tolerant (Assmann 1961). According to Lyr et al. (1967), the ranking of European species regarding their light compensation point is European beech < Norway spruce < Sessile oak < Scots pine. We speculate that oak's light use is highest efficient in the upper canopy layer and decreases distinctly from top to bottom. In case of beech, the decrease is less distinct; it can be rather beneficial for European beech to forage for light within or even under an oak crown. Due to this complementarity, the proportion of light captured may be higher in mixed versus pure stands. Over the long term in the lower canopy, the more light-efficient beech may out-compete and replace the less light-efficient oak. In addition, this replacement may increase the efficiency of light and space use in mixed compared with pure stands (Kelty 1992).

That both species profit from each other, most of all on sites with low nutrient supply, supports the hypothesis that increased productivity is related to improved availability to and access to below-ground resources (nutrients and water).

The input of nutrients via atmospheric deposition depends particularly on the interception capacity of the stands. Important factors for nutrient interception are leaf area index, vertical structure and for broad-leaved stands also leaf life time span. André et al. (2008) investigated the effects of canopy characteristics on throughfall chemistry in an oak–beech stand. They found higher deposition rates under mixed canopies compared with pure canopies. Breda (2003) reported that LAI in mixed oak–beech stands was higher than in pure oak stands and similar to the LAI in pure beech stands. The interception capacity in multilayered canopies, often establishing in mixed oak–beech forests, should be larger than in single-layered pure stands. Deposition measurements in the Rhineland-Palatinate forest monitoring programme have shown higher throughfall and bulk deposition ratios for nutrients in an oak stand mixed with beech and ash than in pure beech stands and an oak stand with beech only in the understorey (FAWF 2011a). In most years, beech sprouted several days or weeks earlier than oak. In autumn, leaf fall of oak began and ended much later than leaf fall of beech. Therefore, in mixed stands, the time span with interception capacity may be elongated, presumably resulting in higher nutrient input in mixed compared with pure stands.

Nutrient cycling and availability to trees may be accelerated in mixed versus pure stands via higher rates of litter production or decomposition. Litterfall measurements in the Rhineland-Palatinate forest monitoring programme showed higher yearly leaf fall rates in an oak stand with admixed beech and ash than in pure beech stands and an oak stand with beech only in the understorey (FAWF 2011b). Jonard et al. (2008) found that decomposition of oak litter and turnover was much faster than that of beech litter. However, beech contained more P and K. Otherwise, Augusto et al. (2002) described in a review article that no clear evidence can be found for differences in C/N ratio of litter on the forest floor in beech compared with oak stands. Also, the litterfall amount seemed to be similar between beech and oak provided that the stands are kept at the same stand density. But in most research plots, the litter weight on the forest floor under beech was higher than under oak, showing a higher decomposition rate of oak litter (Augusto et al. 2002). In mixed oak–beech stands, a higher variability of microhabitats, decomposer organism and a longer-lasting period of litterfall can be assumed than in a one species stand resulting in an accelerated nutrient turnover. Talkner et al. (2009) studied the soil phosphorus status and turnover in Central European beech forest ecosystems with differing tree species diversity. The turnover

rate of litter was much shorter in mixed stands than in pure beech stands.

The ability of trees to utilize nutrients depends largely on soil exploration. Leuschner et al. (2001) investigated root competition between beech and oak in a mature Central European beech–oak forest. They found that beech outnumbers oak three to five times in fine-root biomass and root tip and ectomycorrhiza numbers, in areas where stem density and leaf area of the two species were similar. They concluded that there exists an asymmetric inter-specific root competition in favour of beech. However, Meinen et al. (2009) have not found below-ground overyielding in terms of higher fine-root biomass up to 40 cm soil depth in species-rich temperate broad-leaved forests as compared to pure beech forests. Fölster et al. (1991) investigated the root distribution in a mixed beech–oak–spruce stand on a site with stagnant water in the subsoil. They found a much deeper rooting for oak than for beech or spruce, but fine-root density in the topsoil was lower for oak than for the other species. Taking into account the deeper rooting of oak and the denser surficial rooting of beech, a mixing of both species should enhance soil exploration. A presumably deeper rooting zone in mixed stands might substantially improve the availability of nutrients via mineral weathering. Tyler (1992) found that many ectomycorrhizal macrofungi grow solely in oak or in beech stands. Thus, mixing of both tree species may increase mycorrhiza diversity resulting in an improved acquisition of soil nutrient stocks. All these findings support the assumption that mixing of oak and beech, especially in poor soils, can improve soil exploration and exploitation of soil nutrient in comparison with pure stands.

The finding that the species' benefit of mixing was higher on poor than on rich sites is in line with recent findings by Pretzsch et al. (2012) who showed that the benefit of mixing is also higher in years with drought than in years with normal growing conditions. A common explanation of this remarkable spatial and temporal variation of mixing effects might be the phenomenon of hydraulic lift which has a much higher marginal benefit on poor and dry sites, respectively, in dry years compared with rich sites or years with ample supply of water and nutrient.

Caldwell et al. (1998) listed *Quercus* among other genera which exhibit hydraulic lift in the field, and they stressed that all deep-rooting plants with low resistance to water loss from roots might provide this facilitative feature. According to Dawson (1993), hydraulic lift is the passive movement of water from deep, moist soil layers through the root system upwards. Under extremely dry conditions, the water potential in upper soil layers is lower than in the root system and the roots lose water to the soil. Shallower rooting species like beech or spruce can benefit from this increase of soil moisture both directly as their water supply

increases and indirectly as the nutrient availability increases with soil moisture. Körner (2002) stressed that the indirect effect of water surplus via nutrient availability on plant growth may be much more relevant as the direct effect.

#### Practical relevance of mixing effects

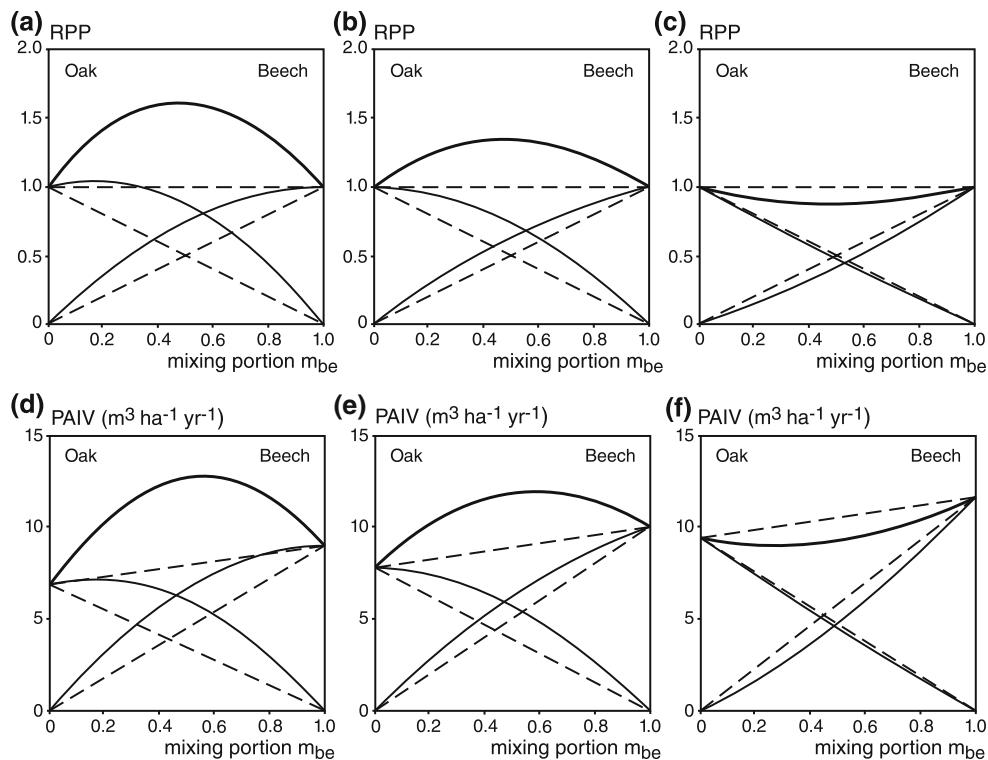
At first glance, the scattered case studies published on mixing effects between oak and beech so far (Hein and Dhôte 2006; Wiedemann 1942, 1951) seemingly provided contradictory findings. Actually, they would fit into a concept of mixing effects shifting from facilitation to inhibition along an ecological gradient from poor to prime growing sites indicated by our investigations.

In order to stress and discuss the site-specific relative mixing effects, we used cross diagram introduced in section “Cross diagrams for analysing the mixing effect” (see Fig. 3). Using Eqs. 12 and 13, we predicted the expected mixing reaction on a poor site (represented by  $hq100_{oak} = 21$  m,  $hq100_{be} = 25$  m), mediocre site ( $hq100_{oak} = 26$  m,  $hq100_{be} = 29$ ) and a rich site ( $hq100_{oak} = 33$  m,  $hq100_{be} = 36$ ). The results are shown on Fig. 8a–c above. The reaction on stand level (bold curve in the upper part of the cross diagrams) results from the sum of the species-specific curves. Depending on site conditions, mixing yielded a mutual facilitation (mutualism) with a relative productivity on stand level of about 1.66 (+66 %). Oak contributed 0.41 and beech 0.25 (Fig. 8a). In a moderate mixing effect, which occurs on mediocre site conditions amounted to 1.35 (+35 %), oak contributed 0.23 and beech 0.12 (Fig. 8b), and 0.88 (–12 %) on fertile sites with both a negative contribution of oak (–0.025) and beech (–0.09) (Fig. 8c). While in the first two cases both species contribute to the productivity gain, in the latter case, both react slightly negatively and contribute to the loss: beech slightly more than oak.

For illustration of the absolute mixing reactions in terms of volume production, PAIV (Fig. 8d–f), we first estimated the productivity of pure oak and pure beech stands on sites with  $hq100_{oak} = 21$  m,  $hq100_{be} = 25$  m,  $hq100_{oak} = 26$  m,  $hq100_{be} = 29$  m,  $hq100_{oak} = 33$  m and  $hq100_{be} = 36$  m at age 100 years by Eqs. 5 and 6. These absolute productivities of the pure stands were the reference values for the respective growth of the pure stands (see values on the left respective right ordinate). To assess the growth in the mixed stands, these benchmark figures were multiplied with the relative mixing reactions (Eqs. 12, 13) in order to quantify the mixing reactions in terms of volume production (Fig. 8d–f).

On the poor site (left:  $hq100_{oak} = 21$  m,  $hq100_{be} = 25$  m) where both species profited from mixing, the cross diagrams indicate mutual facilitation, equivalent to mutualism. The mixing induced transgressive overyielding and more than  $4 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  gain of productivity. On the

**Fig. 8** Essential mixing reaction patterns of oak and beech observed along a gradient from poor to fertile sites. The site indices of oak with respect to beech increase from 25 and 21 m (a, d) to 29 and 26 m (b, e), and 36 and 33 m (c, f). The cross diagrams reflect how the mixing reactions in terms of relative productivity, RPP (top a, b, c), and absolute productivity, PAIV (bottom d, e, f), are modified by site conditions. For interpretation of cross diagrams, see Fig. 3



sites with medium site indices (middle:  $hq100_{oak} = 26$  m,  $hq100_{be} = 29$  m), both species produced more than expected in pure stands, but the positive effect of mixing was less pronounced. On the prime site (right:  $hq100_{oak} = 33$  m,  $hq100_{be} = 36$  m), both species inhibited each other's growth by competition. This caused a loss of  $1\text{--}2\text{ m}^3\text{ ha}^{-1}\text{ year}^{-1}$  in terms of absolute productivity.

The cross diagrams reflect the absolute mixing reactions at the species level (curves in the lower part of the cross diagrams) as well as the reaction at the stand level (bold curve in the upper part of the cross diagrams). These response patterns show that different mixing effects can be expected depending on the site conditions.

For Central Europe, climate change is widely expected to be associated with a trend towards increased stress due to rising summer temperatures and a shift of precipitation to the winter months. Another possible development might be root decline triggered by increasingly stagnant soil water or waterlogging caused by heavy rainfall which might concentrate in autumn and spring (Rennenberg et al. 2004). This change in climate-driven ecological factors probably will be more detrimental for beech than for oak, and the effects will be particularly pronounced on shallow soils and on drier sites at the western and southern periphery of the species' range (Manthey et al. 2007). Assumingly, oaks will suffer less as they are more drought resistant and the depth of their root system is expected to be less impacted by waterlogging than for beech.

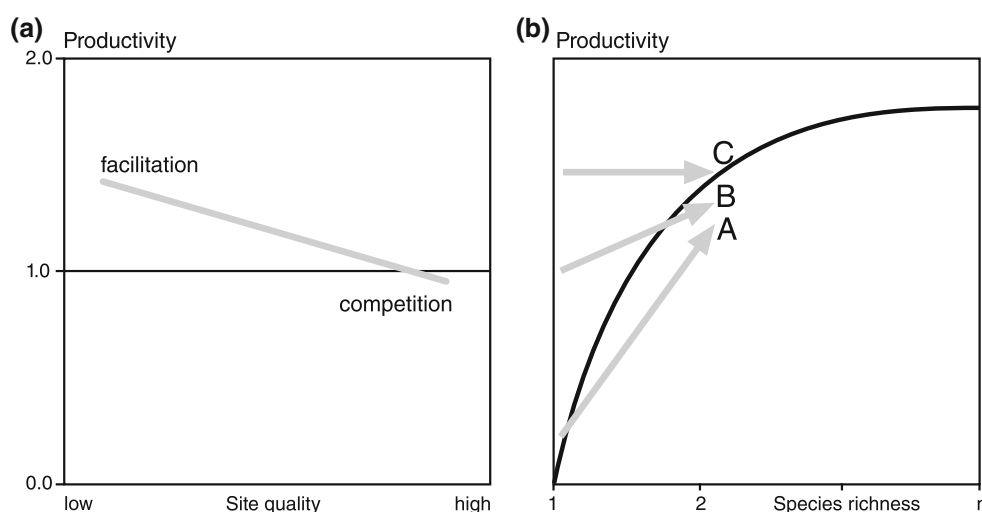
As a consequence, mixing of oak and beech might pay-off if judged from aspects of vulnerability, risk distribution and risk reduction. Furthermore, other effects might be triggered by the mixture of beech and oak and render productivity more stable under stress. Positive interactions (facilitation) between oak and beech will come into play, and a long-term positive feedback between stand and site conditions might improve the humus conditions, water storage and nutrient supply due to an enhanced turnover, resource supply and resource-use efficiency (Binkley et al. 2004; Jonard et al. 2008; Sariyildiz and Anderson 2003).

#### Implication for ecological theory

The observed mixing responses detected in our data set actually correspond to the stress-gradient hypothesis outlined by Callaway and Walker (1997). This hypothesis predicts that facilitation can be expected to occur under poor site conditions, whereas competition is rather more likely to be found on rich sites (Fig. 9a). Our results for mixtures of beech and oak indicate that productivity is clearly enhanced by mixing effects on poor sites (low site index), only little enhanced on medium sites, whereas on prime sites (high site index), mixing effects result in slightly reduced productivity. These observations were similar if productivity responses were either judged on a species basis or on the basis of the stand as a whole.

Facilitation and competition are occurring always simultaneously (Vandermeer 1989); however, the net effect

**Fig. 9** Essential results of this study in schematic representation: **a** change from facilitation dominated interactions to competition along the gradient from low- to high-productivity sites and **b** observed site-dependent relationships between productivity and species richness (*broken lines A, B, C* for poor, mediocre and rich sites) and expected relationship (*solid saturation curve*) according to Körner (2002)



is indicated by productivity gains or losses at stand level. On poor sites, we consider that facilitation, even mutual facilitation synonymous with mutualism, has the upper hand, while competition gets the upper hand on fertile sites. Clearly, more analyses are needed before a general response hypothesis on mixing effects can be developed covering different species groups, environmental conditions and resource supply (Callaway and Walker 1997; Holmgren et al. 1997).

The debate is still open whether the principal relationship between productivity and species richness should best be modelled by a linearly increasing line, a saturation curve, an optimum curve or a non-linear possibly even discontinuous trajectory (Körner 2002, p. 985). For the purposes of our study, we assumed a saturation curve (Fig. 9b) according to Hector et al. (1999) and inserted the trajectories observed on our long-term experimental plots. The transition from pure to two-species stands resulted in strong increase of productivity on poor sites (A), moderate increase on mediocre sites (B) and constant or even slightly decreasing productivity on fertile sites (C). This finding means that productivity-richness experiments may bring different results depending on the initial site conditions and that the apparently contradictory findings might converge when the site conditions are taken into consideration as a modifier and third dimension. On previously poor sites tree species mixing improved the stand productivity and the site conditions the most (A in Fig. 9b). Our study shows that the more favorable the initial site conditions the shallower were the slopes of the observed species richness-productivity trajectories ( $A > B > C$  in Fig. 9b). This suggests that an improvement of the site conditions by mixing may reduce the potential for further positive mixing effects. Such a diminishing feed-back between species mixing and site improvement supports the hypothesis that the relationship between species richness and productivity follows a saturation curve as shown in Fig. 9b (black line).

**Acknowledgments** Thanks to Gregor Aas, Ecological-Botanical Garden, University of Bayreuth, for his advice how to deal with the two different *Quercus* species in this evaluation and to Anton Fischer, Geoecology, Technische Universität München, for revision of the geoecological statements on oak and beech. We further wish to thank the German Science Foundation (Deutsche Forschungsgemeinschaft) for providing the funds for mixed stand research as part of the Collaborative Research Centre 607 (Sonderforschungsbereich SFB 607) “Growth and Parasite Defense” and the Bavarian State Ministry for Nutrition, Agriculture and Forestry for permanent support of the project W 07 “Long-term experimental plots for forest growth and yield research.” The included mixed stand trials belong to the networks of long-term experimental plots in Switzerland, Poland and Germany, and we are deeply grateful to the respective sponsoring forest administrations. Thanks are also due to Ulrich Kern for the graphical artwork.

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