Nova Acta Leopoldina NF *114*, Nr. 391, 159–174 (2013)

Facilitation and Competition in Mixed-Species Forests Analyzed along an Ecological Gradient

Hans Pretzsch (München)

With 8 Figures

Abstract

Long-term experiments, with many of them under survey since the 1880's, are applied for analyzing the extent of over- and underyielding of mixed *versus* pure stands. Firstly, a method for quantification of over- and underyielding and for indication of effects of facilitation and competitive reduction in mixed stands is introduced. Secondly, the extent of over- and underyielding in terms of productivity and the relevance of positive and negative interactions is presented for the mixtures of Norway spruce (*Picea abies* (L.) H. Karst.) with European beech (*Fagus sylvatica* L.) as well as for beech with oak (*Quercus petraea* (Mattuschka) Liebl. and *Quercus robur* L.). Thirdly, the mixing reactions are analyzed in dependence on site conditions. The discussion is focused on the relevance of the revealed effects for forest practice and ecological theory.

Zusammenfassung

Versuchsflächen, von denen viele seit den 1880er Jahren unter Beobachtung stehen, werden für die Analyse von Mehr- bzw. Minderzuwächsen von Mischbeständen gegenüber Reinbeständen verwendet. Zunächst werden Methoden für die Quantifizierung von Mehr- und Minderzuwächsen und Indikation von Facilitation und Konkurrenz eingeführt. Anschließend wird das Ausmaß der Mehr- und Minderproduktion quantifiziert und die Relevanz von Interaktionen zwischen den Mischbaumarten Fichte (*Picea abies* (L.) H. Karst.) und Buche (*Fagus sylvatica* L.) bzw. Buche und Eiche (*Quercus petraea* (Mattuschka) Liebl. und *Quercus robur* L.) aufgedeckt. Schließlich werden Mischungseffekte in Abhängigkeit von den Standortbedingungen untersucht. Die Diskussion konzentriert sich auf die Relevanz der aufgedeckten Mischungseffekte für die Praxis und die ökologische Theoriebildung.

1. Introduction

The strong influence of agronomy on forest practice resulted in extended forest monocultures in the past, however, mixed-species stands are receiving more attention at present (Scherer-Lorenzen et al. 2005). The reason for this increasing interest is that close-to-nature mixed species stands are widely held to supply ecological, economical and socio-cultural forests goods and services in a way similar to or even better than far-from-nature monocultures (Hector and Bagchi 2007, Hooper et al. 2005). A crucial question regarding the progressive currency of mixed stands is about how the productivity of poly-cultures compares with that of monocultures. Knowledge on the advantages or disadvantages of mixed *versus* pure stands with respect to productivity decisively influences the forest owner's decision in favor or against tree species poly-culture (Olsthoorn et al. 1999).

However, sound knowledge about mixing effects even for the most common tree species combinations is rather rare and scattered. Just in the last few years, after failure of lots of monocultures and rethinking on risk distribution (Knoke et al. 2005), resource efficiency (Richards et al. 2010), functional significance of species diversity (Scherer-Lorenzen et al. 2005) and mixed stand dynamics returned into the focus of forest science (see e. g., Forrester et al. 2006, Pretzsch et al. 2010, 2013). Most available works on mixed stand's growth and yield were searching for overyielding of mixed *versus* pure stands. In Norway spruce-European beech (*Picea abies* (L.) H. Karst. respectively *Fagus sylvatica* L.) mixtures in northern Germany Wiedemann (1942, 1943, 1951) found approximately the same dry biomass as in corresponding pure stands on sites of mediocre quality. However, on poorer sites with moderate growth of European beech the mixed stand biomass production is about 19 % less than in pure stands on neighboring sites. Kennel (1965) studied mixtures of Norway spruce and European beech in the Bavarian alpine foothills, the Bavarian Forest and the Harz in Lower Saxony as Burger (1941) did in Switzerland. Their results range from slight overyielding to underyielding of mixed *versus* pure stands. Zöhrer (1969) provides evidence that the biomass production of European larch-Norway spruce mixtures in the Salzburger Land is superior to that of neighboring pure stands of both tree species. The European larch-Norway spruce mixture therefore surpasses the pure Norway spruce stand by 22 to 28 % and the pure European larch stand by 2 to 13 %. In mixed stands of Sessile oak and European beech, Scots pine and Norway spruce and Scots pine European beech Bonnemann (1939) and Wiedemann (1943, 1951) found similar beneficial effects from species interactions after 50 years of observation. In the case of long-term Scots pine and European beech experimental areas in the Dübener Heide, Dittmar et al. (1986) note beneficial interaction effects compared with the pure stands of 7 to 25 % depending on the age and structure of the mixture. Burger (1941) and Wimmenauer (1941) note similar superiority in European larch-European beech mixtures.

Only a very few works deal with the dependency of mixing effects on site conditions: The study by Jensen (1983) along a West-East-transect through Jutland/Denmark gives a model example of site condition effects on the growth relationship between Norway spruce and silver fir. In the coastal dune belt silver fir is superior to Norway spruce, the adjacent Riss-glacial landscape leads to equivalent growth in silver fir and Norway spruce, whereas on the old inland moraines of the Würm-glacial period silver fir is inferior to Norway spruce in dry biomass production. The probable factor for the inland superiority of Norway spruce is its adaptability to low water supplies on acidic sites. By contrast, silver fir profits from better water availability and the more favorable nutrient supply in the coastal region. Frivold and Kolström (1999) studied silver birch (*Betula pendula*), Scots pine and Norway spruce growth in Finland, Sweden and Norway. Like Jensen (1983) they emphasize that the over- or underyielding of mixed *versus* pure stands is related to site conditions. In Southern and Central Finland Scots pine-silver birch mixtures surpass pure Scots pine and pure silver birch stands by 10 % and 14 %, respectively (Mielikäinen 1980). For Norway spruce-silver birch mixtures a 10 to 15 % increase in production compared to corresponding pure stands of these species may occur depending on the site (Mielikäinen 1985). In the oceanic regions of Norway and Sweden silver birch loses some of its increment capacity compared with coniferous species. There, Scots pine-silver birch mixtures do not achieve greater yield than pure stands whereas Norway spruce-silver birch mixtures show a beneficial effect only during early stand development (Frivold and Frank 2002).

The objective of this paper is to analyze the effect of species mixing on forest productivity at the stand level, exemplifying the two very common species mixtures of European beech (*Fagus sylvatica* L.) with Norway spruce (*Picea abies* (L.) H. Karst.) and of European beech with oak (*Quercus petraea* (Mattuschka) Liebl. and *Quercus robur* L.). To this end, first a method for quantifying over- and underyielding is introduced. Second, long-term mixing experiments are analyzed for indicating the extent of over- or underyielding of mixed versus pure stands. Third, mixing experiments located along an ecological gradient through Europe reveal how mixing effects are modified by site quality.

2. Methodological Considerations

The results in this paper base on long-term experimental plots in forest stands. From repeated measurements by 5 to 10-year intervals, the mean annual increment in stem volume and biomass growth (as "m^3 ha^{-1} yr^{-1}" and "t ha^{-1} yr^{-1}", respectively) can be derived for pure stands and neighboring mixed stands. The presentation encompasses analysis of two-species mixture where the results are based on triplets of plots (species 1 in monoculture, species 2 in monoculture, species 1 and 2 in mixed culture) and three-species mixtures based on quadruples (species 1, 2, and 3 in pure stand and species 1–3 in mixture). The comparison of the growth in mixed *versus* pure stands provides information of whether the mixed stand's productivity is higher, equal or lower relative to that of respective pure stands. Such a comparison for a great number of stands enables statements on the extent of over- or underyielding of mixed *versus* pure stands. Comparison for stands along an ecological gradient from rich to pure sites indicates the way by which mixing effects are modified through site conditions.

In the following, I will focus on such variables, algorithms and graphs which are essential for understanding the analyses of the triplets and quadruples of the included plots with respect to mixing effects. For a more detailed introduction into the nomenclature and the quantification of over- and underyielding in mixed *versus* pure stands, see Pretzsch (2003, 2009) and Pretzsch et al. (2010).

2.1 Quantification of Over- and Underyielding

First, the relative productivity $RP_{1,2}$ for a mixed stand as a whole will be considered as a ratio of observed productivity of the mixed stand $p_{1,2}$ divided by the productivity expected for the mixed stand $\widehat{p}_{1,2}$ in the absence of net mixing reactions $RP_{1,2} = p_{1,2} / \widehat{p}_{1,2}$. The expected productivity $\widehat{p}_{1,2}$ is derived from the productivity of both species in the neighboring pure stands, p_1 and p_2, and their mixing portions m_1 and m_2 ($\widehat{p}_{1,2} = m_1 \times p_1 + m_2 \times p_2$). The mixing portions m_1 and m_2 are calculated on the basis of the species' share of the stock of dry mass ($m_1 = W_1 / (W_1 + W_2)$, $m_2 = W_2 / (W_1 + W_2)$).

Second, the relative productivity *RP* of species 1 and 2 in mixed *versus* pure stands is of interest. For species 1, the relative productivity in mixed *versus* pure stand is $RP_{1,(2)} = pp_{1,(2)} / m_1 / p_1$, 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. Regarding species 2, $RP_{(1),2} = pp_{(1),2} / m_2 / p_2$ applies accordingly. Notice, that $pp_{1,(2)}$ and $pp_{(1),2}$ are the parts of the productivity of species 1 and 2 in the mixed stand which add up to $p_{1,2}$ ($p_{1,2} = pp_{1,(2)} + pp_{(1),2}$). By contrast $p_{1,(2)}$ and $p_{(1),2}$

are the parts 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 $p_{(1),2} = pp_{(1),2} / m_2$).

Third, the relationships $RPP_{1,(2)} = pp_{1,(2)} / p_1$ and $RPP_{(1),2} = pp_{(1),2} / p_2$ are of interest. The relative productivity on the basis of the portions (RPP) result from division of the parts of the productivity of species 1 and 2, $pp_{1,(2)}$ and $pp_{(1),2}$, respectively, by the productivity of the same species in the pure stand. Note that $RP_{1,2} = RPP_{1,(2)} + RPP_{(1),2}$.

2.2 Graphical Representation of Growth Reactions in Mixed Stands

For visualization of the mixing reactions, cross-diagrams according to Harper (1977, pp. 776–778) and Kelty (1992) are indicative. In such diagrams (Fig. 1) the productivity of species 1 in the pure stand is plotted on the left-hand ordinate, while that of species 2 is plotted on the right-hand ordinate. The broken straight lines represent the expected productivity of the mixed stand in total (horizontal 1.0-line) as well as the share of species 1 and 2 in the stand productivity (descending line connecting (0|1) with (1|0), and accordingly, rising line connecting (0|0) with (1|1)) in dependence on the mixing portion (scaled on the abscissa). The observed productivity is represented by the following three drawn functions: The observed productivity at the total stand level by the upper curve, the share 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. As Figure 1 shows cross-diagrams for the relative productivity, in analogy, cross-diagrams are common also for comparing absolute productivity (see Fig. 2*B*).

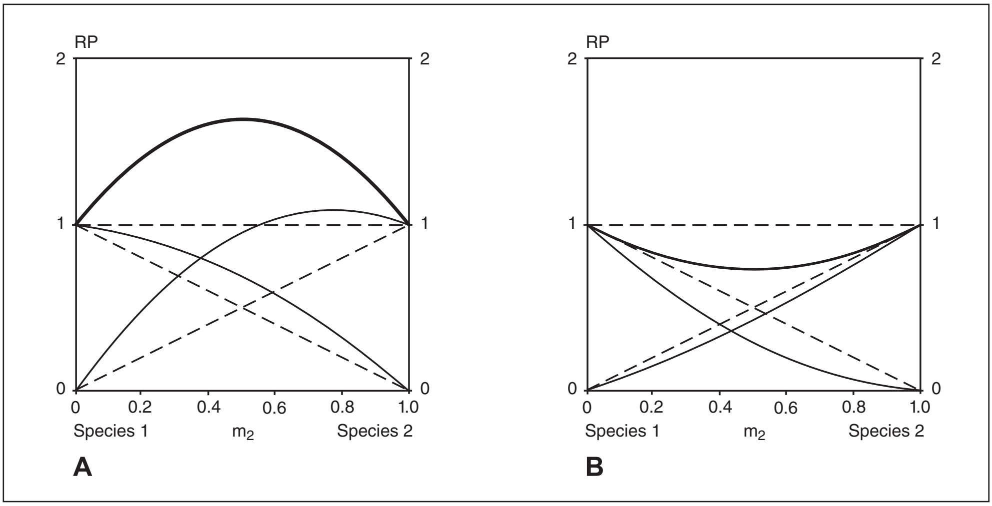

Fig. 1 Cross diagrams for display of mixing effects on productivity in two-species mixtures with overyielding (*A*) and underyielding (*B*). The left respectively right ordinates represent the relative productivity of the species in the pure stand. The range in between represents the relative productivity in the mixture depending on the mixing portion. Broken lines represent the productivity expected for neutral mixing effects on stand level (horizontal 1.0-line) and species level (decreasing resp. increasing lines). The solid lines show the observed productivity on stand level (upper bold curve) and species level (lower thin curves).

With growth-neutral mixture effects, the production of the mixed plot will lie on the straight horizontal lines connecting the two pure stands (Fig. 1). Positive or negative deviations from the reference lines reveal whether the mixed stand gains or losses in productivity. The concave (seen from below) upper lines in Figure 1*A* indicate positive mixing effects at the stand level, i.e. overyielding. In Figure 1*A* the species-specific functions are concave as well and indicate that both species contribute positively to the overall positive mixing effect. Hence, both species have a mutual benefit from the mixture: Species 1 in mixture lies above the species specific reference line, and species 2 in mixture even exceeds the productivity of the pure stand of species 2. In contrast, Figure 1*B* indicates antagonism. The convex functions (seen from below) at the stand as well as at the species level indicate mutual inhibition of growth in mixture. Species 1 suffers more in mixture than species 2 do. While the profit in relation to the pure stand in terms of productivity amounts to 60–70 % in the case depicted in Figure 1*A*, the mixture shown in Figure 1*B* reduces productivity by 20–30 %. The individual species lines (forming a cross) indicate whether a species gains or losses in productivity by mixing. Again concavity indicates benefit, and convexity loss due to the mixing. When the stand productivity of species 1 in a mixed stand comprising species 1 and 2 exceeds the productivity of species 1 in the adjacent pure stand, such a phenomenon is then interpreted as facilitation of species 1 by species 2. When the performance of a species in the mixed stand is lower than expected on the basis of productivity in the neighboring pure stand, this indicates that inter-specific competition exceeds intra-specific competition. Hence, the stand productivity of mixed *versus* pure stands is used as an indication for facilitation or competition at the stand level and separately for species 1 and 2.

Analyses of mixing effects based on the above shown algorithms and cross-diagrams are widely available for tree species mixtures were one species can fix atmospheric nitrogen (e.g. Forrester et al. 2006) and make mixing effects on productivity evident. For example, Figure 2 shows overyielding in mixed *versus* pure stands of *Eucalyptus globulus* Labill and *Acacia mearnsii* De Wild., the N-fixing species, stressing the difference between the *relative* productivity of a species in mixture (Fig. 2*A*) *versus* its performance in a pure stand (and the *absolute* gain or loss of productivity of a species or stand under conditions of mixed culture *versus* such of neighboring monoculture; Fig. 2*B*).

Forest science is primarily interested in species productivity in mixture *relative* to the pure stand productivity and to which extent two or more species benefit or lose under mixture. Conversely, forest practice is mainly interested in the amount of biomass (t ha^{-1} yr^{-1}) or volume (m^3 ha^{-1} yr^{-1}) by which mixed stands exceed pure stands. While the absolute outcome determines management decisions (production economy), the relative outcome contributes to the understanding of species-specific competitiveness and fitness at a given site (production ecology). As in central-European forests, combinations with atmospheric nitrogen-fixing species are still rare, it will be examined in the following as to whether stimulation of similar extent may be found in mixed stands of beech, oak and spruce which occur across large areas and are of considerable ecological and economical importance.

3. Extent and Relevance of Mixing Effects in Central-European Forest Stands

The prevailing reductionism in science continuously advances towards detailedness and tends to overwhelm us with amazing and often breathtaking mosaic pieces of facts on species mixing at the organ, tree and stand level (e. g., Richards et al. 2010, Rothe and Binkley 2001).

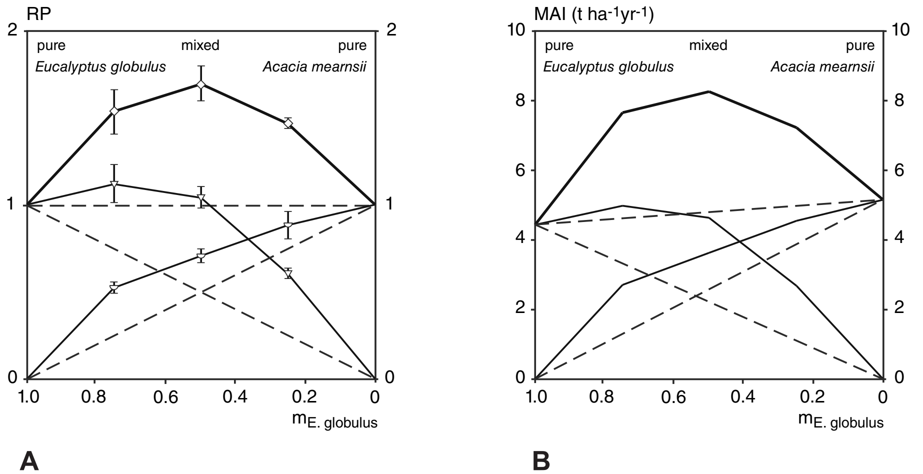

Fig. 2 Overyielding in mixed *versus* pure stands of *Eucalyptus globulus* Labill and *Acacia mearnsii* De Wild in terms of (*A*) the *relative* productivity of a species in mixture *versus* its performance in a pure stand and (*B*) the *absolute* gain or loss of productivity of a species or the stand as a whole in mixed compared with a neighbouring pure stand (courtesy of David Ian Forrester, see also Forrester et al. 2006)

However, the relevance of the observed high resolution in mixing effects in terms of the productivity of stands is hardly being addressed. In the following, the extent will be demonstrated to which mixing effects, which are evidenced by reductionistic research, are relevant for stand productivity.

3.1 Extent of Mixing Effects on Productivity

In order to unify the somewhat scattered sources of information about mixing effects, Pretzsch et al. (2010) compiled and analyzed existing growth and yield plots of pure and mixed stands of Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.). The database contains information from 23 long-term plots, covering an ecological gradient from nutrient-poor and dry to nutrient-rich and moist sites throughout Central Europe. Depending on site condition, dry mass growth in mixed stands can range from –46 % to +138 % of the growth yielded by neighboring pure stands. Figure 3 shows the observed relative volume productivity of mixed *versus* pure stands. On average the relative productivity of the mixed stand amounts to 120 % of the productivity expected on the basis of the neighboring pure stand (Fig. 3*A*). The gain of productivity in terms of absolute biomass productivity amounts to 1.5 t ha^{-1} yr^{-1}. The analysis at the species level (Fig. 3*B* and *C*) shows, that Norway spruce can profit but also suffer from mixture and comes off neutral on average (Fig. 3*B*). European beech also shows broad variation in performance, however, on average the outcome is positive. The latter result is indicated in Figure 3*C* by the transgression of the concave solid model line above the level of the increasing broken straight reference line. The functions representing the mean observed relative productivity in dependence of the mixing share result from model fitting by nonlinear regression analysis.

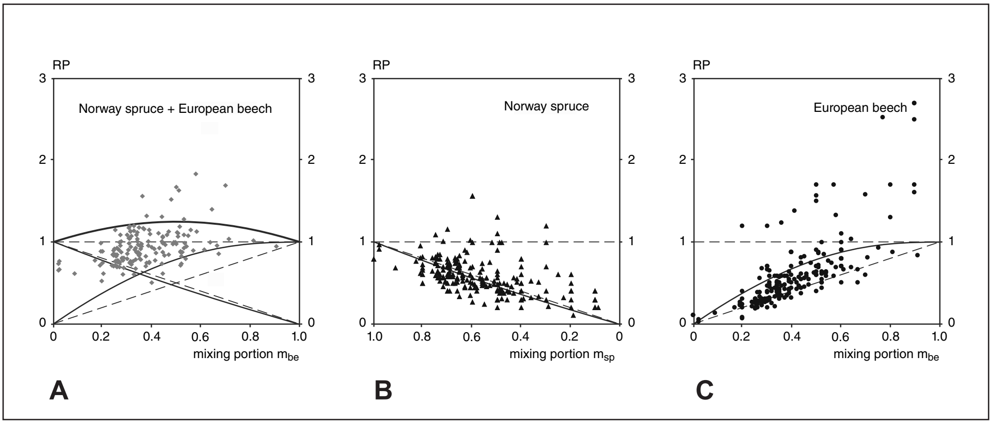

Fig. 3 Relative productivity of volume growth of (*A*) the mixed stand in total, (*B*) spruce and (*C*) beech in relation to the neighboring pure stands. The points represent the observed relative volume productivity of mixed *versus* pure stands. The curves represent the average mixing reactions of spruce, beech and total stand according to Pretzsch et al. (2010).

The species combination of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and beech (*Fagus sylvatica* L.) is of considerable importance at present, but will become even more relevant in forests under climate change. Data from 37 long-term mixing experimental plots in Poland, Germany and Switzerland were pooled for analysis of mixing effects on stand productivity, as depending on mixing share and site conditions. On average mixed stands of oak and beech produce 30 % or 1.7 t ha^{-1} yr^{-1} more than the respective pure stands, as both species profit from the mixture (Pretzsch et al. 2013).

Based on 15 long-term experiments in mixed stands of Norway spruce (*Picea abies* (L.) H. Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.) in the mountainous areas of the Bavarian Forest and the Bavarian Alps comprising a total of 46 plots, mixing effects of combinations of three species can be evaluated. The mean relative productivity amounts to 124 % of the neighboring pure stands while the absolute gain in productivity on average amounts to 1.60 t ha^{-1} yr^{-1}. Figure 4 shows a considerable variation around the mean mixing effect. A similar evaluation for 2 experiments with 6 plots and 3-species mixtures of Sessile oak (*Quercus petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus silvestris* L.) in the hill country of Steigerwald and Spessart yielded, on average, a productivity in relation to the pure stands of 143 % and an absolute gain of productivity of 1.89 t ha^{-1} yr^{-1}. Although based on a rather small database, these results are indicative, given the scarce information to date on the effect of 3-species mixtures. The extent of mixing reactions (on average 124 to 143 % in relation to the neighboring pure stands) stresses, that in three-species mixtures the absolute gain as well as the variation is even higher than in 2-species mixtures. Hence, such outcome is attractive to forest science as well as to sustainable forest ecosystem management.

3.2 Dependency on Site Conditions

The above mentioned 37 long-term mixing experimental plots of oak (*Quercus petraea* (Matt.) Liebl and *Quercus robur* L.) and beech (*Fagus sylvatica* L.) in Poland, Germany

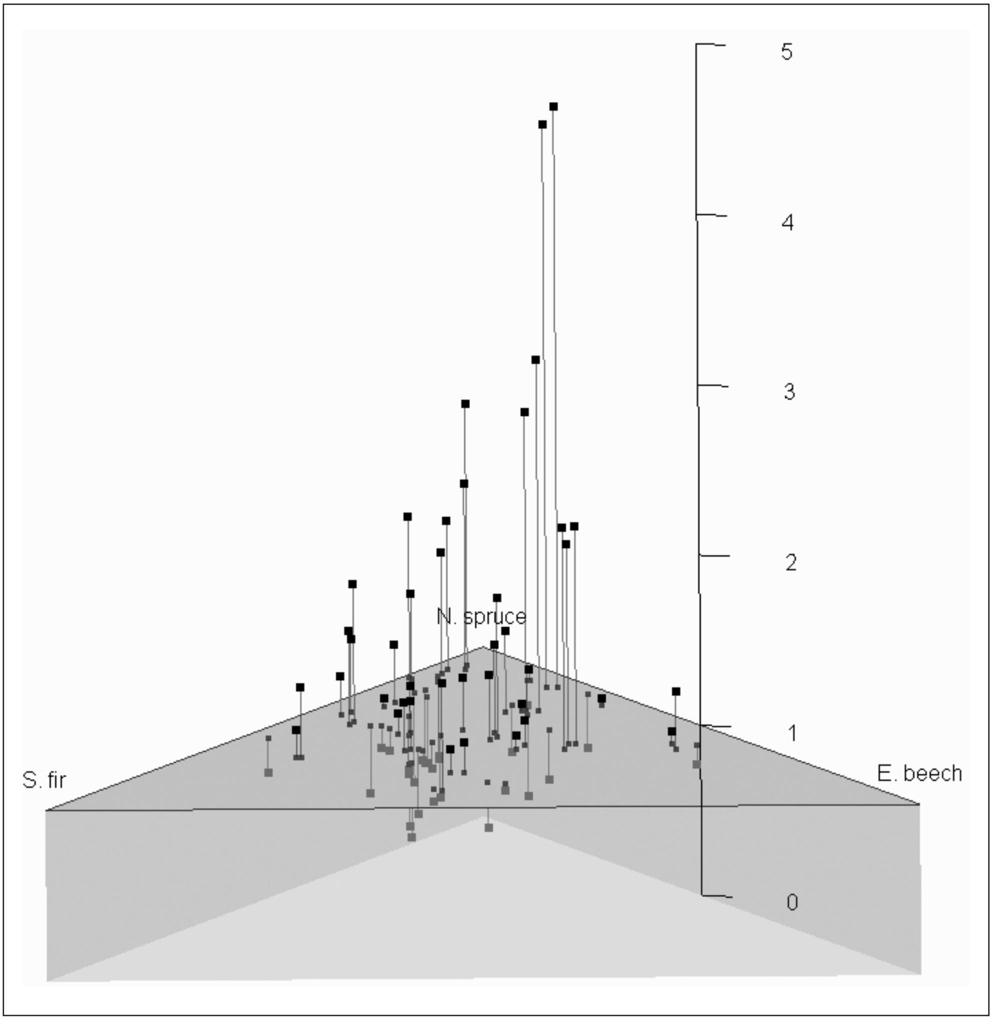

Fig. 4 Productivity of mixed stands with Norway spruce (*Picea abies* (L.) H. Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.) *versus* pure stands. The horizontal lines framing the upper surface of the grey box represent the expected productivity in the pure stands (1.0-line). Each vertical bar in the center indicates the relative productivity of one mixed stand in relation to the pure stands. Overyielding is indicated by bars which reach out the 1.0-plane, while underyielding is evident when the bars remain under the plane. The relative productivity of the mixed stand as a whole amounts to 1.24 (+24 %) and the absolute gain of productivity amounts to 1.60 t ha^{-1} yr^{-1}.

and Switzerland cover a broad range of site conditions. For analyzing any dependencies of mixing effect on site quality, the quadratic mean height of oak and beech was used at an age of 100 years, being the so-called site indices hq_{oak} and hq_{be}, respectively (see Pretzsch 2009, pp. 200–203, for the definition and calculation of h_q) and surrogates for site quality. As most of the survey series included species up to the age of 100 years, observed hq_{oak} and hq_{be} were available from the pure-stand plots. Height of oak at age 100 ranges from 20 to 35 m, in the case of beech the range is between 20 and 45 m and even beyond. Based on the relative productivities (i.e. mixed *versus* pure stands), the mixing portion and the site index PRETZSCH et al. (2013) fitted the model shown in Figure 5. Volume growth in mixed stands is revealed as changing from gains of 50 % to losses of 10 % in dependence on site condition and mixing share. In both species an increase in site index has a significantly negative effect on the relative productivity. Figure 5 shows the model functions against the scattergrams for oak and beech (Fig. 5*A* and *B*) in mixture. In order to demonstrate the site effect we inserted height values of 10 to 40 m into the model. On sites of low quality (hq < 25 m) both species profit considerably from the mixture. Their relative productivity even exceeds the 1.0-lines and indicates a facilitation effect. On mediocre sites (hq = 25 m – 30 m) the species still show a positive mixing effect, but do not exceed the level of the neighboring pure stands. On fertile sites (hq > 35 m) mixing causes a loss of productivity in relation to neighboring pure stands, reflecting exacerbating inter-specific competition.

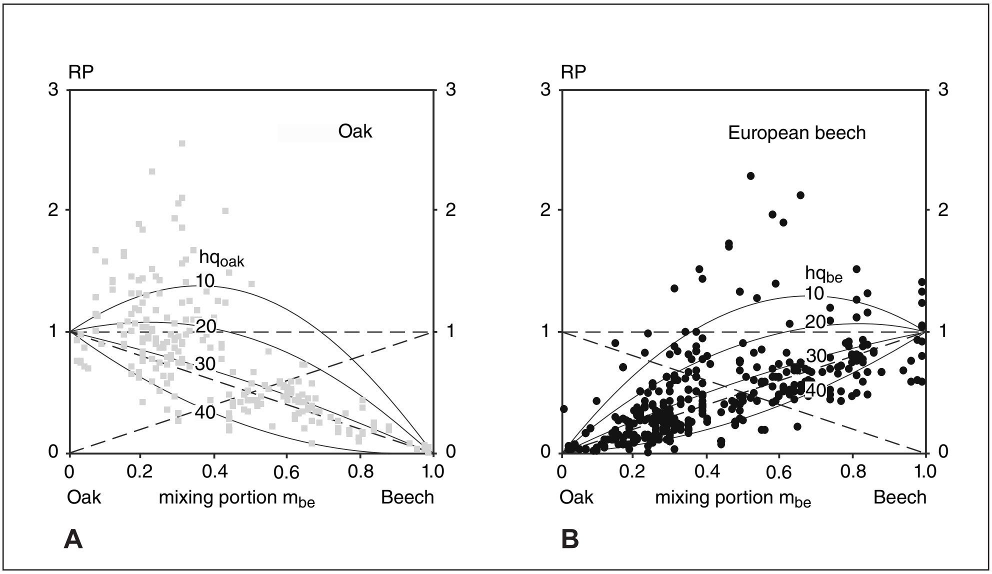

Fig. 5 Species-specific relative productivity in mixed *versus* pure stands of (*A*) oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and (*B*) European beech (*Fagus sylvatica* L.) depending on mixing portion, m, and quadratic mean height at age 100, hq, as indicator for site fertility. (*A*) Observed relative productivity for oak plotted over mixing portion of beech, m_{be}, (filled rectangles) and model prediction in dependence on admixture of beech and site fertility (curves with h_q= 10 … 40 m). (*B*) Observed relative productivity for beech plotted over mixing portion of beech, m_{be}, (filled circles) and model prediction in dependence on admixture of oak and site fertility (curves with h_q= 10 … 40 m).

Figure 6 makes the relationship between site quality and mixing reactions of oak and beech (Fig. 6*A*) and the mixed-stand performance (Fig. 6*B*) even more apparent. The dependency of the relative productivity (mixed *versus* pure stand) is displayed on the quadratic mean height at age 100 of oak hq_{oak} and beech hq_{be} as fitted by a simple linear equation. In the case of oak as well as of beech, the relative periodic annual volume increment decreases significantly with increasing site quality, indicated by significantly negative slopes. Insertion of hq = 20 m in the linear model yields $RP_{oak,be}$ = 1.49 and $RP_{(oak),be}$ = 1.38, being equivalent to a surplus of productivity by mixing of 49 % in relation to the pure stand in the case of oak and 38 % in the case of beech. Mediocre site conditions (indicated by hq = 30 m) yields + 11 % and 15 % in the productivity of oak and beech in mixture *versus* that under pure-stand conditions. On nutrient-rich site (hq = 40 m) the model predicts a loss of 27 % for oak and 8 % for beech. At the stand level the gains and losses in total for hq_{oak} of 20, 30, 40 m result in + 32 %, +7 % and –18 %, respectively. The mostly positive total stand reaction shown in Figure 6*B* can be interpreted as a mutualistic mixing reaction between oak and beech on poor sites, a neutral reaction on mediocre sites and an antagonistic reaction along with a reduction in productivity on fertile sites.

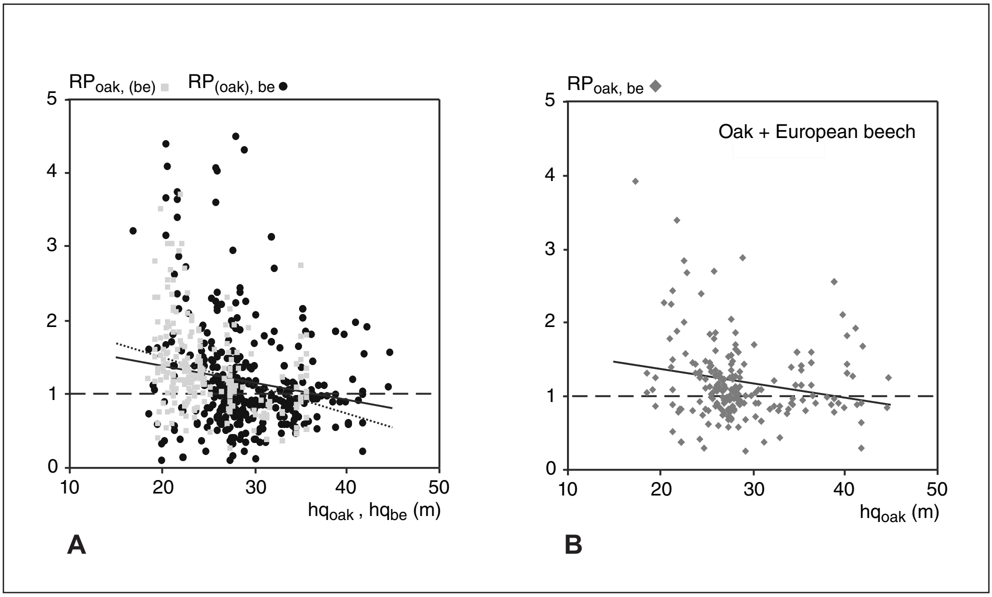

Fig. 6 Relationship between (*A*) species-specific relative productivity and (*B*) whole stand relative productivity of mixed *versus* pure stands of oak and beech (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. respectively *Fagus sylvatica* L.) in dependence on site fertility, indicated by quadratic mean height at age 100, hq. The graph shows the relative productivity expected for neutral mixing reactions (broken 1.0-line), the observed relative productivity of oak (rectangles), beech (circles) and the stand as a whole (rhombi), and the regressions lines for oak (Fig. 7*A*: broken line), beech (Fig. 7*A*: solid line) and total stand (Fig. 7*B*: solid line).

4. Discussion

Systematic overyielding up to 50 % reported by Caspersen and Pacala (2001), Hector et al. (1999), Loreau et al. (2001) and Pfisterer and Schmid (2002) for grasslands can hardly be found in managed forests in Central Europe. Presumably, in temperate forests of Central Europe niche differentiation is comparatively low due to species reduction in the course of the ice ages and due to the much slower evolutionary and co-evolutionary processes of long-lived trees. This may be a reason why the surplus of productivity of mixed stands compared with pure stands is much lower in long-lived forests than in short-lived herbaceous stands. Many of the European forest stands are "artefacts" designed with very productive species such as Norway spruce and Douglas fir cultivated outside their natural habitats. Often, genetic variation in these species no longer reflects natural selection but is a consequence of commercial selection criteria. Managed forests are therefore not designed for optimum niche utilization by the species in mixture. Compared with overyielding found in the subtropics and tropics (DeBell et al. 1989, Forrester 2006, 2007, Kelty 1992) the reported mixture effects of about ± 30 % for commercial tree species in temperate and boreal zones appear to be rather moderate. However, beyond the potential of direct increase or decrease of productivity, species mixing may indirectly change productivity by risk distribution and enhanced stand resilience in view of a broad set of forest functions and services (Hector and Bagchi 2007, Pretzsch 2005, Scherer-Lorenzen et al. 2005).

4.1 Site Conditions as Modifier of Mixing Reactions

As shown for the mixture of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and beech (*Fagus sylvatica* L.), scattered and seemingly contradictory findings on mixing reactions may fit into an ecological continuum from poor sites with mainly positive interaction (overyielding) to rich sites with neutral or even negative mixing reactions (underyielding). In order to stress the site-specificity of relative mixing effects, cross-diagrams were introduced as demonstrated in Figure 1. Use of statistical relationships between mixing effects and site conditions allow to predict interaction between oak and beech on a poor site (represented by quadratic mean height at age 100 of hq_{oak}= 21 m, hq_{be}= 25 m), on a mediocre site (hq_{oak}= 26 m, hq_{be} = 29) and on a rich site (hq_{oak} = 33 m, hq_{be} = 36; Fig. 7). The reaction at the stand level (bold curve in the upper part of the cross-diagrams) results from the sum of the species-specific functions. Depending on site conditions, mixing can trigger a strong mutual facilitation with a relative productivity on stand level of about 1.66 (+ 66 %) on poor sites, a moderate mixing effect of 1.35 (+ 35 %) on mediocre sites, or a negative effect indicated by a relative productivity of 0.88 (–12 %) on fertile sites (Fig. 7*A*, *B* and *C*, respectively). While on the poor and mediocre site both species contribute to the productivity gain, on the rich site both react slightly negative and contribute to the overall loss. Accordingly, parts of the variation of the mixing effects observed to date can be explained by the site conditions of the analyzed stands.

4.2 Correspondence with the Stress-gradient Hypothesis

The observed mixing reactions correspond with the stress-gradient hypothesis (Callaway and Walker 1997) which predicts, that facilitation dominates on poor rather than rich sites whereas it is the latter sites where competition might prevail (Fig. 8*A*). In mixture both oak (*Quercus petraea* (Matt.) Liebl and *Quercus robur* L.) and beech (*Fagus sylvatica* L.) are more productive than in neighboring pure stands on poor sites and less productive on fertile sites. Only on mediocre sites mixed and pure stands are similar in productivity. Facilitation and competition between neighboring trees may occur simultaneously (Vandermeer 1989), however, the net effect is indicated by productivity gains or losses at the tree and stand level. The analysis of the productivity relationships suggest that on poor sites facilitation prevails, even mutual facilitation. The observations represented by data above the broken 1.0-line in Figure 5*A* and *B* indicate mutual facilitation. Such data reflect that the productivity of a fully stocked, closed oak stand can be increased in the presence of beech, and *vice versa* with oak

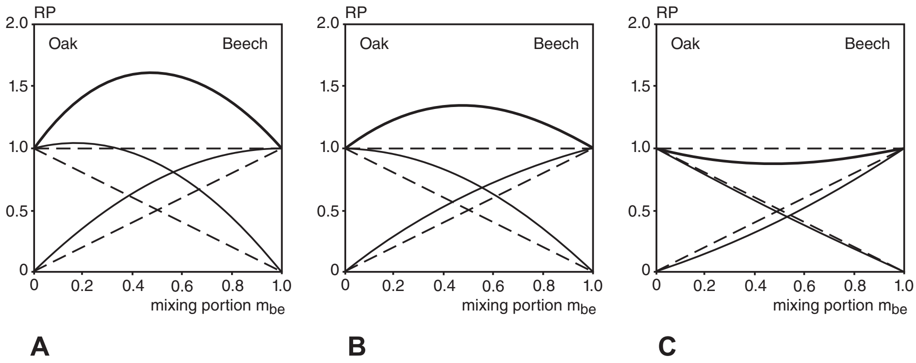

Fig. 7 Essential mixing reaction patterns of oak and beech observed along a gradient from poor to fertile sites. The site indices of oak resp. beech (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. respectively *Fagus sylvatica* L.) are 25 m and 21 m (*A*), 29 m and 26 m (*B*), and 36 m and 33 m (*C*). The cross-diagrams reflect that the relative productivity is modified by site conditions.

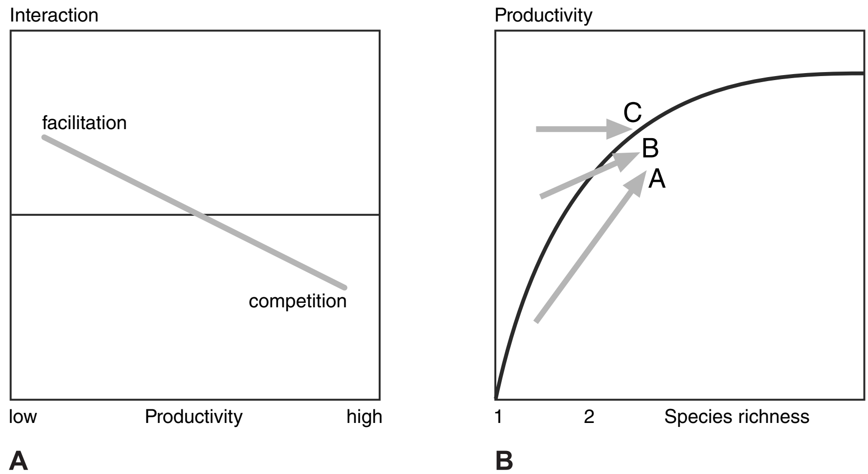

Fig. 8 Essential results of this study in schematic representation. (*A*) Change from facilitation dominated interactions to competition along the gradient from low to high productivity sites. (*B*) Site dependent relationships between productivity and species richness observed for oak and beech (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. respectively *Fagus sylvatica* L.) in this study (broken lines A, B, C for poor, mediocre and rich sites) and expected relationship (solid saturation curve) according to Körner (2002).

in beech stands. In other words, the competition effect by adding the other species is overcompensated by a supportive effect, yielding facilitation at the tree and stand level.

Other tree species mixtures behave differently, e.g. in mixed stands of Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) the former conforms with the stress-gradient hypothesis, with beech profiting most from mixture on fertile sites (Pretzsch et al. 2010). The response behavior probably depends on covariates such as species traits, kind of limiting resources, and environmental factors. Scrutiny in testing the stress-gradient hypothesis for forest stands requires integrative analyses of species mixture, covering different functional groups of tree species, environmental conditions and resource availability (Callaway and Walker 1997, Holmgren et al. 1997).

4.3 Contribution to the Relationship between Species Richness and Productivity

It is an ongoing debate as to whether the relationship between productivity and species richness is represented by an increasing straight line, a saturation curve, an optimum curve or even a stepped, non-continuous trajectory (Körner 2002, p. 985). Figure 8*B* shows the saturation curve assumed according to Hector et al. (1999). In addition the graph reflects the relationships between mixing and productivity observed on our oak-beech long-term experimental plots on poor, mediocre and rich sites. The transition from pure to two-species stands results 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 experiments striving for relationships between productivity and species richness 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. The phenomenon that the more fertile the initial site conditions the shallower the slope of the observed trajectories (A > B > C) reflects the predominantly positive but attenuating feed-back between stand and local environment: The mixture improves the site conditions, so that the additional benefit gradually becomes smaller. This kind of attenuating feed-back effect supports the hypothesis that the species richness-productivity curve follows a saturation curve.

4.4 Perspectives

Growth rates change with plant size. Pretzsch and Schütze (2005, 2009) show species mixing to alter tree size and as a consequence the expected growth rates of mixed *versus* pure stands. The analysis of this study is restricted to stand-level data, aims at providing a first overview on the extent of over- and underyielding, but neglects the above said effect of tree size on growth rate. Although descriptive, the outcome summarizes the existing knowledge on effects of tree species mixing at the stand level. The data of the long-term experimental plots used here has the potential for advanced analyses of mixing effects on productivity: Ontogenetic size effects on growth are to be separated from complex mixing effects. Furthermore, mixing effects will have to be decomposed into stand density and growth rate components of trees. Such components will be traceable to the individual tree level, using respective data on tree growth, crown size and competition. Although neither resource supply, nor resource uptake, nor resource use efficiency were measured directly on the long-term plots further detailed analysis of, e.g., density, growth rate, crown allometry and leaf area will functionally clarify the mixing reactions.

Compared to effects of thinning, tending, or fertilization the shown productivity increase by mixing is easy to achieve. Just knowledge is required about which species on which sites may pay off in terms of mixing. This article underlined the relevance of tree species mixing in forestry and the potential of further clarifying underlying mechanisms.

Acknowledgement

Thanks are due to Kamil BIELAK, Joachim BLOCK, Arkadiusz BRUCHWALD, Hans-Peter EHRHART, Ulrich KOHNLE, Jürgen NAGEL, Hermann SPELLMANN, Michał ZASADA, and Andreas ZINGG for providing data from long-term experimental plots in Switzerland, Poland and Germany for this study. Thanks are also due to Ulrich KERN for the graphical artwork and Jochen DIELER for thoroughly reviewing the manuscript. I 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".

References

BINKLEY, D., STAPE, J. L., and RYAN, M. G.: Thinking about efficiency of resource use in forests. Forest Ecol. Managem. *193*, 5–16 (2004)

BONNEMANN, A.: Der gleichaltrige Mischbestand von Kiefer und Buche. Mitt. Forstwirtsch. Forstwiss. *10*/4, 1–45 (1939)

BURGER, H.: Beitrag zur Frage der reinen oder gemischten Bestände. Mitt. d. Schweiz. Anst. f. d. Forstl. Versuchsw. *XXII*, 164–203 (1941)

CALLAWAY, R. M., and WALKER, L. R.: Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology *78*/7, 1958–1965 (1997)

CASPERSEN, J. P., and PACALA, S. W.: Successional diversity and forest ecosystem function. Ecol. Res. *16*, 895–903 (2001)

DEBELL, D. S., and WHITESELL, C. D., and SCHUBERT, T. H.: Using N_2-fixing *Albizia* to increase growth of *Eucalyptus* plantations in Hawai. Forest Sci. *35*, 64–75 (1989)

DITTMAR, O., KNAPP, E., und ZEHLER, H.: Die langfristige Versuchsfläche Tornau im StFB Dübener Heide, ein Beispiel für den Weg vom Kiefernreinbestand zum Buchennaturverjüngungsbetrieb. Soz. Forstw. *36*, 344–348 (1986)

FORRESTER, D. I., BAUHUS, J., COWIE, A. L., MITCHELL, P. A., and BROCKWELL, J.: Productivity of three young mixed-species plantations containing N_2-fixing *Acacia* and non-N_2-fixing *Eucalyptus* and *Pinus* trees in South-eastern Australia. Forest Sci. *53*/3, 426–434 (2007)

FORRESTER, D. I., BAUHUS, J., COWIE, A. L., and VANCLAY, J. K.: Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: A review. Forest Ecol. Managem. *233*, 211–230 (2006)

FRIVOLD, L. H., and FRANK, J.: Growth of mixed birch-coniferous stands in relation to pure coniferous stands at similar sites in South-eastern Norway. Scan. J. Forest Res. *17*, 139–149 (2002)

FRIVOLD, L. H., and KOLSTRÖM, T.: Yield and treatment of mixed stands of boreal tree species in Fennoscandia 37–45. In: OLSTHOORN, A. F. M., BARTELINK, H. H., GARDINER, J. J., PRETZSCH, H., HEKHUIS, H. J., and FRANC, A. (Eds.): Management of Mixed-Species Forest: Silviculture and Economics. IBN Scientific Contributions *15* (1999)

HARPER, J. L.: Population Biology of Plants. London, New York: Academic Press 1977

HECTOR, A., and BAGCHI, R.: Biodiversity and ecosystem multifunctionality. Nature *448*, 188–190 (2007)

HECTOR, A., SCHMID, B., BEIERKUHNLEIN, C., CALDEIRA, C. M., DIEMER, M., DIMITRAKOPOULOS, P. G., FINN, J. A., FREITAS, H., GILLER, P. S., GOOD, J., HARRIS, R., HÖGBERG, P., HUSS-DANELL, K., JOSHI, J., JUMPPONEN, A., KÖRNER, C., LEADLY, P. W., LOREAU, M., MINNS, A., MULDER, C. P., O'DONOVAN, G., OTWAY, S. J., PEREIRA, J. S., PRINZ, A., READ, D. J., SCHERER-LORENZEN, M., SCHULZE, E. D., SIAMANTZIOURAS, A. S. D., SPEHN, E. M., TERRY, A. C., TROUMBIS, A. Y., WOODWARD, F. I., YACHI, S., and LAWTON, J. H.: Plant diversity and productivity experiments in European grasslands. Science *286*/5442, 1123–1127 (1999)

HOLMGREN, M., SCHEFFER, M., and HUSTON, M. A.: The interplay of facilitation and competition in plant communities. Ecology *78*/7, 1966–1975 (1997)

HOOPER, D. U., CHAPIN, F. S., EWEL, J. J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J. H., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A. J., VANDERMEER, J., and WARDLE, D. A.: Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. *75*/1, 3–35 (2005)

Jensen, A. M.: Growth of silver fir (*Abies alba* Mill.) compared with the growth of Norway spruce (*Picea abies* (L) Karst.) in pure and mixed stands on sandy soils in the Western parts of Denmark. Reports from Department of Forestry, Royal Veterinary and Agricultural University *14*, 1–498 (1983)

Kelty, M. J.: Comparative productivity of monocultures and mixed stands. In: Kelty, M. J., Larson, B. C., and Oliver, C. D. (Eds.): The Ecology and Silviculture of Mixed-Species Forests; pp. 125–141. Dordrecht: Kluwer Academic Publishers 1992

Kennel, R.: Untersuchungen über die Leistung von Fichte und Buche im Rein- und Mischbestand. AFJZ *136*, 149–161, 173–189 (1965)

Körner, C.: Ökologie. In: Sitte, P., Weiler, E. W., Kadereit, J. W., Bresinsky, A., und Körner, C. (Eds.): Strasburger Lehrbuch für Botanik. 35. Ausgabe. S. 886–1043. Heidelberg, Berlin: Spektrum Akademischer Verlag 2002

Knoke, T., Stimm, B., Ammer, C., and Moog, M.: Mixed forests reconsidered: A forest economics contribution on an ecological concept. Forest Ecol. Managem. *213*, 102–116 (2005)

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grimr, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A.: Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science *294*, 804–808 (2001)

Mielikäinen, K.: Mänty-koivusekametsiköiden rakenne ja kehitys. Summary: Structure and development of mixed pine and birch stands. Commun. Inst. Forest Fenn. *99*, 1–82 (1980)

Mielikäinen, K.: Koivusekoituksen Vaikutus Kuusikon Rakenteeseeen ja kehitykseen, Effect of an admixture of birch on the structure and development of Norway Spruce Stands. Commun Inst. Forest Fenn. *133*, 1–79 (1985)

Olsthoorn, A. F. M., Bartelink, H. H., Gardiner, J. J., Pretzsch, H., Hekhuis, H. J., and Franc, A. (Eds.): Management of Mixed-Species Forest: Silviculture and Economics. IBN Scientific Contributions *15*, 389 pp. (1999)

Pfisterer, A. B., and Schmid, B.: Diversity-dependent production can decrease the stability of ecosystem functioning. Nature *416*, 84–86 (2002)

Pretzsch, H.: Diversity and productivity in forests. In: Scherer-Lorenzen, M., Körner, C., and Schulze, E.-D. (Eds.): Forest Diversity and Function. Ecol. Studies Vol. *176*; pp. 41–64. Berlin, Heidelberg: Springer 2005

Pretzsch, H.: Forest Dynamics, Growth and Yield. From Measurement to Model. Berlin, Heidelberg: Springer 2009

Pretzsch, H.: Diversität und Produktivität von Wäldern. AFJZ *174*, 88–98 (2003)

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., and Zingg, A.: 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. Eur. J. Forest Res. DOI 10.1007/s10342-012-0673-y (2013)

Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J., Spellmann, H., and Zingg, A.: Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. Forest Sci. *67*, DOI:10.1051/forest/2010037 (2010)

Pretzsch, H., and Schütze, G.: Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. Plant Biol. *7*, 628–639 (2005)

Pretzsch, H., and Schütze, G.: Trangressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: Evidence on stand level and explanation on individual tree level. Eur. J. Forest Res. *128*, 183–204 (2009)

Richards, A. E., Forrester, D. I., Bauhus, J., and Scherer-Lorenzen, M.: The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol. Tree Physiol. *30*/9, 1192–1208 (2010)

Rothe, A., and Binkley, D.: Nutritional interactions in mixed species forests: a synthesis. Can. J. Forest Res. *31*, 1855–1870 (2001)

Scherer-Lorenzen, M., Körner, C., and Schulze, E.-D.: Forest Diversity and Function. Ecol. Studies Vol. *176*, Berlin, Heidelberg: Springer 2005

Vandermeer, J.: The Ecology of Intercropping. Cambridge: Cambridge University Press 1989

Wiedemann, E.: Der gleichaltrige Fichten-Buchen-Mischbestand. Mitt. Forstwirtsch. Forstwissensch. *13*, 1–88 (1942)

Wiedemann, E.: Der Vergleich der Massenleistung des Mischbestandes mit dem Reinbestand. AFJZ *119*, 123–132 (1943)

Wiedemann, E.: Ertragskundliche und waldbauliche Grundlagen der Forstwirtschaft. Frankfurt (Main): J. D. Sauerländer's Verlag 1951
Wimmenauer, K.: Zur Frage der Mischbestände. AFJZ *90*, 90–93 (1941)
Zöhrer, F.: Bestandeszuwachs und Leistungsvergleich montan, subalpiner Lärchen-Fichten-Mischbestände. Forstw. Cent.bl. *88*, 1–64 (1969)

Prof. Dr. Dr. h. c. Hans Pretzsch
Lehrstuhl für Waldwachstumskunde
Wissenschaftszentrum Weihenstephan
Technische Universität München
Hans-Carl-von-Carlowitz-Platz 2
85354 Freising
Germany
Phone: +49 8161 714710
Fax: +49 8161 714721
E-Mail: H.Pretzsch@lrz.tum.de, http://www.wwk.forst.tu-muenchen.de