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Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments

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Abstract

Aim of study: The objective of this study was to analyse the effect of species mixing of Scots pine and Norway spruce on the productivity at the stand and species level. We also analysed to what extent the mixing effects is modified by drought stress.

Area of study: The study was conducted in N-E Poland and based on three experiments located in Maskulinskie, Strzałowo and Kwidzyn Forest Districts.

Material and methods: We evaluated long-term mixed-species experiments in Scots pine and Norway spruce which are under continuous survey since more than 100 years. Stand productivity was analysed based on the periodic annual increment and total yield of stem volume. Growth and yield were compared between mixed and neighbouring pure stands. As a substitute for the missing Norway spruce monocultures, we used appropriate yield table data. In order to characterize the effect of water supply on the mixing effects, we correlated the Martonne index of aridity with the ratio of Scots pine growth in mixed versus pure stands.

Main results: We found that the mixed stands exceed the weighted mean of the pure stands' volume productivity on average by 41%. At the species level Scots pine benefits from the mixture by 34% and Norway spruce by 83%. Growth periods with harsh climate conditions reinforce overyielding, while periods with mild conditions reduce the benefit of mixing. The overyielding of mixed stands, especially when growing under unfavourable conditions, is explained by niche complementarity of both species and discussed in view of the stress-gradient-hypothesis.

Research highlights: The revealed overyielding of mixed compared with neighbouring pure stands, particularly under harsh weather conditions, substantiates the preferences of Scots pine-Norway spruce mixtures regarding climate change.

Key words: drought resilience; mixed stand; pure stand; facilitation; competition; overyielding; underyielding.

Introduction

Many studies underline the importance of species diversity for most forest functions and services (Zhang *et al.*, 2012; Gamfeldt *et al.*, 2013). Close-to-nature mixed species stands are widely held to supply many ecological, economical and social forest goods and services in a similar or even better way than far-from-nature monocultures (Hector & Bagchi, 2007; Piotto, 2008; Forrester, 2014). A crucial question for the pro-

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Abbreviations: PAIV (periodic annual increment of stem volume, in $m^3\ ha^{-1}\ yr^{-1}$); RPAIV (relationship between PAIV of a species in pure versus mixed stands); TY (total yield of merchantable stem volume ≥ 7 cm over bark, in $m^3\ ha^{-1}$); RTY (ratio between TY of a species in pure versus mixed stands); Ma (Martonne index of aridity).

gress of the mixed stand currency is how the productivity of polycultures comes off compared with monocultures. Recent studies in temperate and boreal forests frequently found overyielding of mixed *versus* pure stands of 20-30% in terms of stand volume productivity, due to the niche complementary of associated species (Morin *et al.*, 2011; Pretzsch *et al.*, 2010, 2013a). The reviews by Piotto (2008) and Zhang *et al.* (2012) summarize that mixtures are often much more productive than monocultures. Such reported findings of advantages of mixed *versus* pure stands with respect to productivity, decisively influence the forest owners decision in favour of mixed species stands (Olsthoorn *et al.*, 1999). The knowledge about mixtures frequently cultivated in Europe, such as Norway spruce and European beech, sessile/pedunculate oak and European beech (Pretzsch *et al.*, 2010, 2013a), and European beech and Scots pine (Condés *et al.*, 2013) is gradually improving. In contrast, information on species combination like Scots pine and Norway spruce is still very scarce (Lindén & Agestam, 2003; Mason & Connolly, 2014), although this tree species mixture is widely spread in the Central and N-E Europe (Szymanski, 2007). In the continental and boreal climate, this mixture occurs on rather nutrient poor/medium sites where the water supply is still sufficient for Norway spruce to participate, but not enough for its dominance over Scots pine. On poor and medium fertile podsolic sandy soils with precipitation around 600 mm, Norway spruce and Scots pine can grow balanced in association, as none of the species gains dominance over the other (see also Pukkala *et al.,* 1994; Lindén & Agestam, 2003).

In N-E Poland, where our study has been carried out, and Nordic countries like Finland and Sweden, this type of mixture is the most common natural one (Żybura, 1990) and occurs naturally on 13% of the forest area (SILP 2014). However, this mixture has also been artificially established on devastated and extremely poor sites beyond its natural range in Central Germany (Schmidt, 1971; Schmidt-Vogt, 1991), as well as other Central and Western European countries (Spiecker, 2000).

Despite the high relevance of Scots pine-Norway spruce mixed stands in Europe there are only a very few experiments available like the Gisburn Experiment in the United Kingdom (Brown, 1992; Mason & Connolly, 2014) or the network of growth and yield experiments in Germany (Wiedmann, 1943; Pretzsch, 2009). Based on 50 years observation, Wiedemann (1943) found that volume growth in mixtures was higher compared with monocultures of Scots pine, but lower compared with monocultures of Norway spruce. Jonsson (1962) used data from temporary plots in unthinned stands and found that on mesotrophic sites in mixture both species produce more than either Scots pine and Norway spruce alone. Based on data from experiment located in Central Sweden, Jonsson (2001) found that the total volume yield up to stand age of 43 years was higher in mixed stands than the weighted mean yield of the respective monocultures. However, the yield of mixed stands exceeded pure Norway spruce, but not pure Scots pine stands, which indicates an overyielding but not "transgressive overyielding" as defined by Harper (1977, p: 268) and Pretzsch (2009, p: 349). Individual-tree growth model presented by Pukkala *et al.* (1994), fitted on the basis of data from temporary plots located on medium fertility sites of North Karelia in Finland, suggests that volume productivity may be 10-15% greater in mixed compared to pure Scots pine and Norway spruce stands at the same stand age and basal area. According to Pukkala *et al.* (1994), also total yield will be greater when the proportion of Scots pine is gradually reduced by thinnings compared to the scenario, when the proportions are maintained at a constant level on sites where both tree species are equally productive. Based on data from 20 years observations of a randomized block design experiment in Norway spruce and Scots pine, Lindén & Agestam (2003) found that volume productivity can be higher in mixtures than monocultures. Based on the first rotation of Gisburn trial (northern England) up to age of 26 years, Brown (1992) pointed out 44% greater relative yield total (RYT = 1.44) in mixtures compared with monocultures. After 20 years of the second rotation of the Gisburn experiment Mason & Connolly (2014) still found the same pattern (RYT = 1.42) which points to a strong facilitation effect between both species.

One of the main reasons for the scarce knowledge of mixing effects is the small number of existing experiments including pure and mixed species stands with equal stand age, site conditions, and silvicultural treatment (Lindén and Agestam, 2003; Condés *et al.*, 2013). The above studies meet this requirement, however, they reflect the mixing effects on productivity just in a rather short period and hardly cover a whole rotation period of about 100 years. In contrast, this study is based on long-term mixing experiments which were established at the beginning of 20th century in Poland. Most of the analysed plots are under continuous survey since more than 100 years and belong to an essential part of the forest observation network in Central Europe (Dudzinska and Bruchwald, 2008; Pretzsch *et al*., 2013b, 2014). Hence, they enable us to present the evidence of long-term mixing effects of Norway spruce and Scots pine.

The main objective of this paper was to analyse the effect of species mixing of Scots pine and Norway spruce on forest productivity at the stand and species level. Firstly, we quantified the effect of species mixing on growth and yield at the stand and species level. Secondly, we analysed the development of the growth relationships between mixed and pure stands over the stand age. Thirdly, we analysed the effect of temporal growing conditions on the mixing reactions of Scots pine in the respective time periods. The results are discussed regarding their relevance for forest practice in general and mitigation of climate change effects in particular.

Material and methods

Study area

This study is based on three long-term experiments located in Maskulinskie, Strzałowo and Kwidzyn Forest Districts. They have been established in the period of 1911-1932, remeasured 14-16 times since this time, and kept under observation until present (Table 1 and 2). The experiments were initiated by the German growth and yield scientists Adam Schwappach and Eilhard Wiedemann and continued after World War II. by the Polish Forest Research Institute in Warsaw (since 2006 located in Sękocin Stary). The records have been taken mostly in 4-5 years intervals with only one longer break between 1942-1958 caused by World War II. In order not to confuse mixing effects with thinning effects we selected from all available plots only fully stocked ones, *i.e.,* unthinned and A grade plots (see Pretzsch, 2009, p: 171; Pretzsch *et al*., 2013a,b). For each plot we provided a geography-related name, as well as the plot number; *e.g.* "Maskulinskie 1" in Table 1 and 2 means plot number 1 at the location Maskulinskie.

The plots have a square shape and their area vary between 0.25-0.26 ha. Their continuous surveys comprised measurement of all diameters at 1.3 m above ground level (d.b.h.) and tree heights of selected trees. For further information about the history of these so-called Schwappach experiments see Erteld (1958), Trampler (1958), and Dudzinska & Bruchwald (2008). Most of the previous evaluations of these experiments focused on the effect of silvicultural treatments on the species specific growth (Pirogowicz, 1978, 1983; Bruchwald and Zasada, 1995) while mixing effects were hardly considered so far (Pirogowicz, 1990).

All stands are located in N-E Poland in altitudes of 79-151 m a.s.l. and growing on soils of poor-medium fertility. The annual mean temperature lies between 7.1-7.6 °C and the sum of annual precipitation amounts to 593-650 mm yr^{-1}. At the last surveys in 2008 and 2010, respectively, the mean height at age 100 of the stands amounted to 27.3-30.9 m in case of Scots pine and 21.1-25.0 m of Norway spruce; substantiating medium site conditions. The stand density expressed by means of stand density index according to Reineke (1933) ranges between 488-775 tree ha^{-1}. In view of the rather advanced stand age of more than 130 years the current annual volume growth is still rather high

Table 1. Overview of the three mixed pine-spruce long-term experimental trials included in this study. Numbers before slash (/) indicate pure pine plots, while mixed ones are listed after slash. For explanation of eco-regions see Zielony and Kliczkowska (2012)

Experiment: location and plot number	Geographic position		Eco-region	Elevation a.s.l. (m)	Mean annual temp. (°C)	Mean annual precip. (mm yr^{-1})	Substrate
	N-latitude	E-longitude					
Maskulinskie 1, 2, 5, 6/ 7, 9, 12, 13	53° 38'	21° 31'	Great Mazurian Lakes	151	7.1	593	Sand and loamy sand
Strzałowo 23/24	53° 45'	21° 26'	Mazury Forest	148	7.2	594	Weakly loamy sand and fine gravel
Kwidzyn 28/25	53° 50'	18° 58'	Iławskie Lake	79	7.6	650	Sand and sandy loam

Table 2. Growth and yield characteristics related to the last survey for the 12 long-term observational plots in mixed and pure stands of Scots pine and Norway spruce representing three experiments included in this study. The characteristics for pure Norway spruce stands are based on the Polish yield tables (Szymkiewicz, 1966; tables by Schwappach, 1943; site classes III and IV). Site index is calculated on the basis of quadratic mean height at the age of 100 years

Experiment location and plot number	Species	Stand age (year)	First survey (year)	Last survey (year)	Number of surveys	Top height (m)	Site index (m)	Number of trees (ha^{-1})	Mean diameter (cm)	Standing volume (m^3 ha^{-1})	Periodic annual increment (m^3 ha^{-1} y^{-1})	Total yield (m^3 ha^{-1})	SDI
Maskulinskie 1	S. pine	132	1911	2008	16	29.7	27.3	288	39.1	460	3.7	845	590
Maskulinskie 2	S. pine	132	1911	2008	16	30.7	27.7	227	43.2	459	3.8	813	546
Maskulinskie 5	S. pine	132	1911	2008	16	32.7	29.3	177	47.0	451	2.7	786	488
Maskulinskie 6	S. pine	132	1911	2008	16	31.6	28.6	196	44.8	439	2.8	787	500
Strzałowo 23	S. pine	132	1932	2008	14	36.0	30.1	273	40.7	559	4.2	914	597
Kwidzyn 28	S. pine	132	1928	2010	15	35.7	30.7	324	42.4	714	7.0	1,104	756
Maskulinskie 7	S. pine	124	1928	2008	15	33.5	29.7	123	45.3	296	2.6	648	319
	N. spruce	124	1928	2008	15	33.2	23.8	126	36.1	178	4.1	337	227
	Total							249		474	6.7	985	546
Maskulinskie 9	S. pine	124	1928	2008	15	33.1	29.0	158	41.4	311	3.2	637	355
	N. spruce	124	1928	2008	15	31.1	23.6	166	36.0	224	3.6	343	298
	Total							324		535	6.8	980	653
Maskulinskie 12	S. pine	129	1928	2008	15	33.2	27.8	199	38.8	344	2.7	626	403
	N. spruce	129	1928	2008	15	31.8	21.3	260	27.7	210	3.5	320	307
	Total							459		554	6.2	946	710
Maskulinskie 13	S. pine	129	1928	2008	15	35.9	30.2	201	42.8	457	3.7	704	476
	N. spruce	129	1928	2008	15	33.3	21.1	212	28.5	181	3.3	276	262
	Total							413		638	7.0	980	738
Strzałowo 24	S. pine	132	1911	2008	16	36.3	30.9	244	42.2	543	5.4	892	565
	N. spruce	132	1911	2008	16	32.7	25.0	80	36.9	113	2.2	299	149
	Total							324		656	7.6	1,191	714
Kwidzyn 25	S. pine	132	1928	2010	15	34.4	29.3	332	42.1	740	10.9	1,009	766
	N. spruce	122	1928	2010	15	24.6	22.7	8	27.0	5	0.1	38	9
	Total							340		745	11.0	1,047	775
Yield tab. B. III	N. spruce	130	—	—	—	—	25.0	395	33.1	494	5.9	1,039	620
Yield tab. B. IV	N. spruce	130	—	—	—	—	21.0	551	25.8	369	4.6	759	580

SDI: stand density index according to Reineke (1933).

with values up to 11 m^3 ha^{-1} yr^{-1}. According to the last survey the total yield reaches a level up to 1,200 m^3 ha^{-1} (Table 2).

While on each of the three experiments Scots pine is present in pure as well as mixed stands, Norway spruce is available only in mixture. In order to compensate for the missing pure stands we used the growth and yield data from the III and IV site classes of the common yield tables for Norway spruce by Schwappach (1943) as a supplementary reference (see Table 2 and Fig. 1). Latter yield tables are widely used in Poland by forest practice up to this day (Czuraj, 1990). Szymkiewicz (1966) underpinned that they are quite precise under Polish lowlands growing conditions, where our plots are located, but not at all for mountains regions (Bruchwald *et al.,* 1999).

Quantification of mixing effects

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, V,

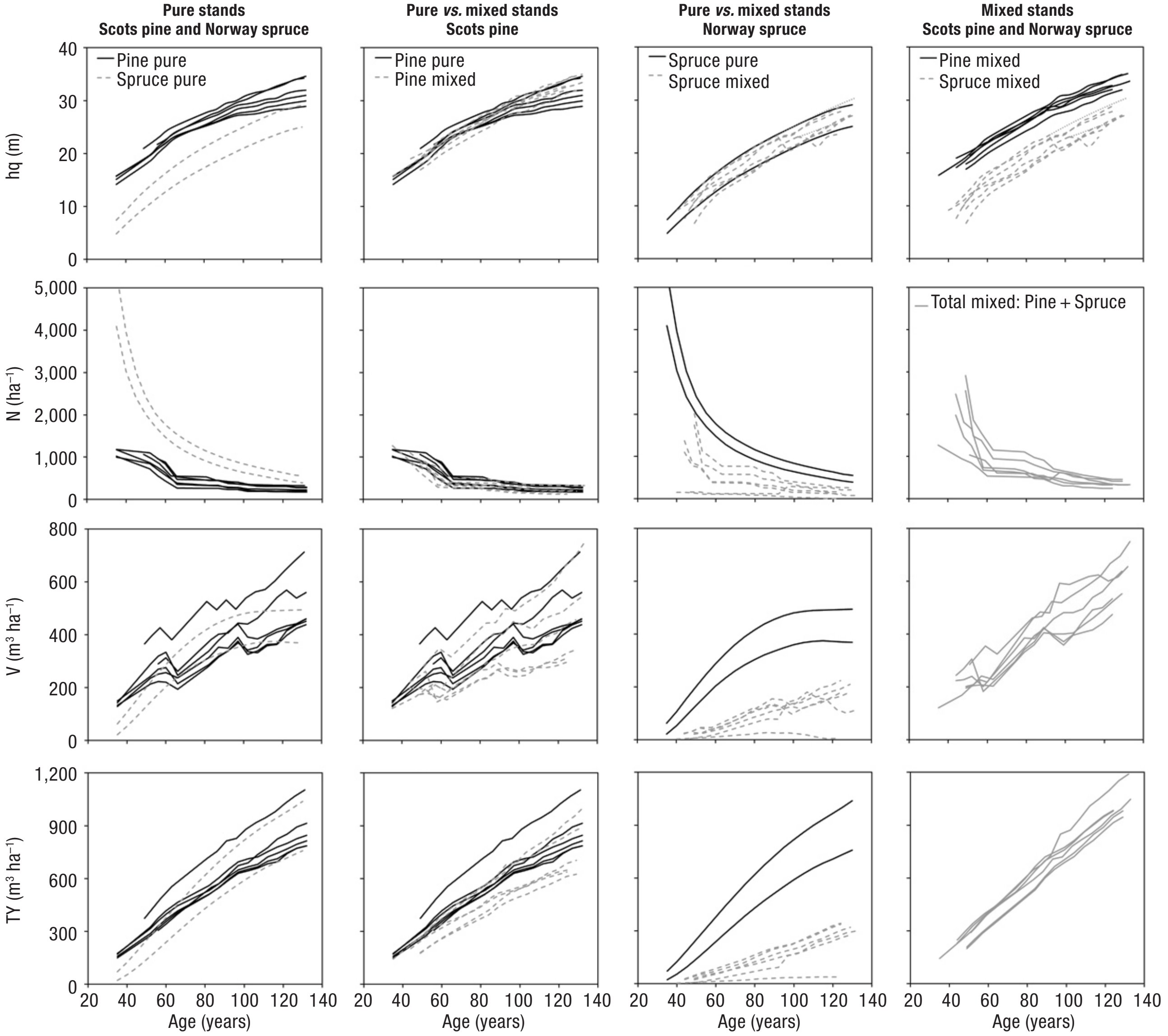

Figure 1. Comparison of growth and yield characteristics over age for the 12 long-term observational plots included in this study. As pure spruce stands were missing we used the Polish yield tables (Szymkiewicz, 1966; tables by Schwappach, 1943; site classes III and IV) as reference. hq: quadratic mean heigh. N: number of trees. V: stand volume. TY: total volume yield. All variables are presented for remaining stand. In two mixed stands for Norway spruce, the extrapolated values hq by means of logarithmic function are presented as well (dotted lines).

total volume yield, TY, or periodic annual volume increment, PAIV (PAIV = average annual increment within a given period). For comparing the growth and yield characteristics of mixed and pure stands we use the following notation. We address for instance the productivity, p, in the pure stands of pine or spruce by p_{pi} and p_{sp}, respectively. In the mixed stand as a whole, the productivity is addressed as $p_{pi,\,sp}$, and this characteristic for pine and spruce in the mixed stand is denoted $p_{pi,(sp)}$ and $p_{(pi),sp}$, respectively.

The analysis of mixing effects was based on triplet experimental setups: one plot represented pure Scots pine, one plot both species in mixture, and for pure Norway spruce we used the yield table values as reference. Stand productivity was analysed on the basis of the periodic annual increment of stem volume, PAIV, in $m^3\ ha^{-1}\ yr^{-1}$ and total yield, TY, in $m^3\ ha^{-1}$. In both cases the analyses relate to merchantable stem volume ≥ 7 cm over bark.

We restrict the following specifications of variables and calculation to those which are indispensable for understanding the concept and results of mixing analysis. For a more detailed introduction into nomenclature and quantification approaches for over- and underyielding in mixed *versus* pure stands see Pretzsch (2009) and Pretzsch *et al*. (2010, 2013a). In order to understand all following figures and cross diagrams mainly three different relative productivity measures are relevant. Firstly, we considered the relative productivity $RP_{pi,sp}$ for the stand as a whole reflected by either PAIV or TY. It resulted from the observed productivity of the mixed stand $p_{pi,sp}$ divided by the productivity expected for the mixed stand $\hat{p}_{pi,sp}$

$$RP_{pi,sp} = p_{pi,sp} / \hat{p}_{pi,sp} \qquad [1]$$

The expected productivity $\hat{p}_{pi,sp}$ was derived from the productivity of both species in the neighbouring pure stands, p_{pi} and p_{sp}, and their mixing portions m_{pi} and m_{sp} ($\hat{p}_{pi,sp} = m_{pi} \times p_{pi} + m_{sp} \times p_{sp}$). The mixing portions m_{pi} and m_{sp} were calculated based on the species' share of the stocking dry mass W [$m_{pi} = W_{pi} / (W_{pi} + W_{sp})$, $m_{sp} = W_{sp} / (W_{pi} + W_{sp})$]. In order to achieve values of W_{pi} and W_{sp}, we converted the standing stem volume, V, of each tree species for a given growth period by its multiplying by the tree species-specific wood density R (R_{pi}=431 kg m^{-3} and R_{sp}=377 kg m^{-3} for Scots pine and Norway spruce, respectively). Thus, $W_{pi} = V_{pi} \times R_{pi}$ and $W_{sp} = V_{sp} \times R_{sp}$ (*cf.* also with Pretzsch, 2009, pp: 66-67 and 354-356).

Furthermore, as in our experimental setup the measured data was only available for Scots pine monoculture and mixture of Scots pine and Norway spruce, we also computed the relative productivity $RP'_{pi,sp}$ referring to the over- or underyielding of the mixed stands compared with only pure Scots pine stands, $RP'_{pi,sp} = p_{pi,sp} / p_{pi}$.

Secondly, the relative productivity RP of both species in mixed *versus* pure stands was of interest. For Scots pine the relative productivity in mixed *versus* pure stand was

$$RP_{pi,(sp)} = pp_{pi,(sp)} / m_{pi} / p_{pi} \qquad [2]$$

with the share of productivity of Scots pine in the mixed stand, $pp_{pi,(sp)}$, mixing portion, m_{pi}, and productivity of the pure stand, p_{pi}. For Norway spruce the following formula applied: $RP_{(pi),sp} = pp_{(pi),sp} / m_{sp} / p_{sp}$. Notice, that $pp_{pi,(sp)}$ and $pp_{(pi),sp}$ were the contributions of the productivity of Scots pine and Norway spruce in the mixed stand which added up to $p_{pi,sp}$ ($p_{pi,sp} = pp_{pi,(sp)} + pp_{(pi),sp}$). In contrast, $p_{pi,(sp)}$ and $p_{(pi),sp}$ were the contributions of both species in the mixed stand scaled up to 1 ha using their mixing portion ($p_{pi,(sp)} = pp_{pi,(sp)} / m_{pi}$ and $p_{(pi),sp} = pp_{(pi),sp} / m_{sp}$).

Values of relative productivity measures at the whole stand or species level above or below 1.0 indicate and quantify the extent of over- or underyielding, respectively.

Thirdly, for completion of the cross diagrams for both species under investigation we applied the relationships

$$RPP_{pi,(sp)} = pp_{pi,(sp)} / p_{pi} \quad \text{and} \quad RPP_{(pi),sp} = pp_{(pi),sp} / m_{sp} \qquad [3]$$

The relative productivity on the basis of the portions, RPP, resulted from division of the contribution of the productivity of Scots pine, $pp_{pi,(sp)}$, respectively Norway spruce, $pp_{(pi),sp}$, by the productivity of the same species in the pure stand. Notice that $RPP_{pi,sp} = RPP_{pi,(sp)} + RPP_{(pi),sp}$ and equals unity, when the neutral effect is observed.

Quantification of drought stress

For characterizing the water supply for each experimental site we calculated the index of Martonne (1926), Ma, in mm °C^{-1}, on the basis of the precipitation (P, in mm) and mean temperature (T, in °C) of the summer months June, July and August

$$Ma = P / (T + 10) \qquad [4]$$

Because of its minimal data requirement, this index has been widely used in modern studies to describe the drought condition or aridity in a given region (Rötzer *et al*., 2012; Pretzsch *et al*., 2013c; Quan *et al*., 2013). The higher the Ma index, the better the water supply for plant growth.

We used the climate datasets from five meteorological stations (Elbląg, Kętrzyn, Mikołajki, Olsztyn and Pisz) that are situated in the vicinity of evaluated experiments and cover two periods: 1932-1944 and 1951-2012. We excluded from our analysis the period between 1945-1950 due to the lack of climate data caused by World War II (see Suppl. Fig. S1). Ma values were interpolated between stations in order to achieve suitable values for each experiment. We used a simple kriging method, where average values were weighted by distance between the location of experiments and surrounding meteorological stations (Matheron, 1963).

Ma values of the sites of the Maskulinkie experiment in the period 1932-2012 (excluding years 1945-

1950) lie in between Ma = 21.7 mm °C^{-1} in 1953 and 48.3 mm °C^{-1} in 1970. The respective values within the growing season amount to Ma = 2.8 mm °C^{-1} in 1992 and 15.7 mm °C^{-1} in 1957. The mean values of Ma amount to 34.6 in the whole year and 8.7 mm °C^{-1} within the growing season. In Strzałowo the mean values of Ma are rather similar to Maskulinkie and add up to 34.7 and 8.6 mm °C^{-1} in the whole year and growing season, respectively. In Kwidzyn the respective values of Ma are slightly higher and amount to 37.2 and 8.9 °C^{-1} .

Regression analyses. Dependency of growth and yield variables on selected stand parameters and drought stress

In order to reveal any mixing effects we analysed the dependency of stand productivity (PAIV) and yield (TY) on stand age (Function 1), Martonne index (Function 2) and set of other stand parameters like mixing portion of Norway spruce, m_{sp}, stand density index, SDI, site index, SI, and mean tree size, $\bar{v}$, as a stand age substitute (Function 3).

$$y = f\,(\text{age}) \qquad \text{Function 1}$$

$$y = f\,(\text{Martonne index}) \qquad \text{Function 2}$$

$$y = f\,(m_{sp}, \text{SDI}, \text{SI}, \bar{v}) \qquad \text{Function 3}$$

The first relationship was scrutinized for RPAIV, as well as for RTY at the stand and species level. The second and third relationships were analysed only for Scots pine as reference data for pure Norway spruce stands were not available. Thus, as the response variables y in Function 2 and 3 we used $\text{RPAIV}_{pi(sp)}$ and $\text{PAIV}_{pi(sp)}$, respectively.

An algebraic expression of our model is a simple linear model for Function 1 and 2:

$$Y_{ijt} = \beta_0 + \beta_1 \times X_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \qquad [5]$$

and multiple (linear) regression model in the case of Function 3:

$$Y_{ijt} = \beta_0 + \beta_1 \times X1_{ijt} + \beta_2 \times X2_{ijt} + {} + \beta_3 \times X3_{ijt} + \beta_4 \times X4_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \qquad [6]$$

In both equations, Y represents the stand variable of interest (RPAIV, RTY or PAIV), depending on predictor variables (X), *i.e.* stand age, Ma index, and m_{sp}, SDI, SI and $\bar{v}$. The indices i, j, and t represent the experiment the plots belong to, the plot representing a given experiment, and the time of a specific plot survey, respectively. The fixed effects parameters are $\beta_0 - \beta_4$, while b_i, and b_{ij} are random effects on experiment, and on plot level, respectively $b_i \sim N(0,\tau_1^2)$, $b_{ij} \sim N(0,\tau_2^2)$. With these random effects, we take care for the possible plot-specific and experiment-specific autocorrelation among the observations. Finally, ε_{ijt} stands for independent and identically distributed errors, $\varepsilon_{ijt} \sim N(0,\sigma^2)$. Thus, both equations represent a linear mixed regression model (*cf.* Zuur *et al.*, 2009).

For parameter estimation we applied the lme function from the R package nlme (Pinheiro *et al.*, 2013). Please notice also that the finally fitted model (Equation [6]) is the result of previous ranking processes based on Akaike's Information Criterion (AIC; Akaike, 1974), where also several interactions of the fixed effects (especially in view of m_{sp} and SDI, and SI) and random effects at different levels, as well as either untransformed or logarithmized values Y and X (depending on which option resulted in a better model fit) were tested. The final model only includes significant parameters and the residuals are normally distributed. As far as we know there is nothing such as an easily interpretable goodness of fit test for mixed models. Therefore, we provided only the basic fit statistics and took into account residual statistics during procedure of model fitting. All statistical evaluations were carried out with R 3.0.2 (R Core Team, 2014), namely the packages nlme (Pinheiro *et al.*, 2013).

Results

Development of whole stand and species characteristics over age

Before closer analysing the growth and yield of both species in mixed *versus* pure stands we contrast their development descriptively (Fig. 1 and Suppl. Fig. S2). In height as well as diameter growth Scots pine as an early successional species is ahead of Norway spruce in the early and middle stand age (see Fig. 1 and Suppl. Fig. S2, upper parts of graphs). However, Norway spruce as a late successional species catches up with Scots pine, and presently both species are more approaching in mean size. Notice that Norway spruce as a shade tolerant tree species occupies the upper but also lower storey of the canopy. Height and diameter growth of spruce varies stronger between the individual trees on a plot than for Scots pine, and the mean heights are lower. While Norway spruce remains rather unaffected in size growth by admixture of Scots pine, pine grows a bit faster in mixed compared with pure stands.

Stand density in terms of the number of trees remains on a much higher level in mixture compared with monocultures, especially in advanced stand development phases (Fig. 1, line 2.). Standing stand volume and total yield in the mixed stands as a whole considerably exceeds both pure stands (Fig. 1, lines 3. and 4.). A similar pattern, *i.e.* superiority of mixtures *versus* monocultures, is also underpinned by the higher total PAIV of Scots pine and Norway spruce in the mixed stands compared with the neighbouring pure stands and the yield tables, respectively (Suppl. Fig. S2, line 2.). In the last 100 years the PAIV of the mixed stands as a whole remained rather stable between 7 and 15 m^3 ha^{-1} yr^{-1} whereas it decreased gradually in both pure stands of pine and spruce. The main reason for the persistent development of PAIV in parallel to the x-axis in the mixed stands is the anti-cyclical trajectory of both species. The PAIV of Scots pine already decreases due to it species specific early culmination, while PAIV of Norway spruce still increases and compensates for the losses caused by Scots pine component. Latter we will discuss this finding as an example for temporal complementary of resource use in mixed stands.

Productivity gains by species mixture at species level and stand level

In Fig. 2 we contrast the productivity in mixture at the tree species and whole stand level with the reference values for the pure stands. For the comparisons at species level the observed productivities in mixture were scaled up to stand level (one hectare) by the species-specific mixing portions (see section *Quantification of mixing effects*). In case of pure Norway spruce stands, we used the predictions of the site specific yield tables by Schwappach (1943, site classes III and IV) as reference. Equality of growth in mixed and pure stands would be reflected by observations on or close to the bisector lines in Figure 2 (1.0-line). The lines above and below the bisector line represent overyielding, respectively underyielding at the level of 20% of mixed stands compared with the pure stands.

Fig. 2 reveals for both tree species, as well as for the mixed stand in total, considerable productivity gains by mixture. In case of Scots pine the gain amounts on average to +1.22 m^3 ha^{-1} yr^{-1} (Fig. 2, above, left) while it is even higher in the case of Norway spruce with +6.65 m^3 ha^{-1} yr^{-1} (Fig. 2, above, right). The mixed stand as a whole lies on average 2.92 m^3 ha^{-1} yr^{-1} above the monocultures of Scots pine (Fig. 2, below, left), and +2.39 m^3 ha^{-1} yr^{-1} above the weighted mean of both pure stands (Fig. 2, below, right). The finding that at the stand level over 90% of all observed cases lie above the reference 1.0-line makes obvious that overyielding is much more frequent than underyielding.

Fig. 3 underlines that both species contribute to the overyielding of the mixed species stands. In this graph the broken 1.0-lines (horizontal line refers to Norway spruce, vertical line to Scots pine) represent equality between mixed and pure stands. More than 65% of the observations lie over both the lines for Scots pine and Norway spruce. This observation and the fact that overyielding of Scots pine hardly correlate with the overyielding of Norway spruce indicates that the gain of one species is not on the expense of the other. Or in other words, that the overyielding of one tree species does not trigger underyielding of the other one. Thus, both species benefit from mixture as their species-specific traits may complement each other and improve their resource use due to reduced competitive stress or even some facilitation processes. On average productivity of Scots pine benefits from the mixture by 34% and Norway spruce by 83%. The calculated average mixing effect at stand level amounts to 41% and comes even to 65% in case when the productivity of mixed stands is only compared with monocultures of Scots pine.

Change of growth relationships between mixed and pure stands with advancing stand development

Fig. 4 shows the change of the growth relationship (RPAIV) between mixed and pure stand with proceeding stand development. Scots pine hardly benefits from the mixture in the early stand development phase, but draws more and more profit out of the association with Norway spruce since the age of 66 years (Fig. 4, above, left). If Scots pine would develop in parallel with the 1.0-line this would indicate a constant mixing effect, however, the increasing grey line with slope significantly higher than zero ($p < 0.001$, Table 3, line 1.) provides evidence of an increasing benefit of Scots pine from growing in mixture. A similar tendency shows

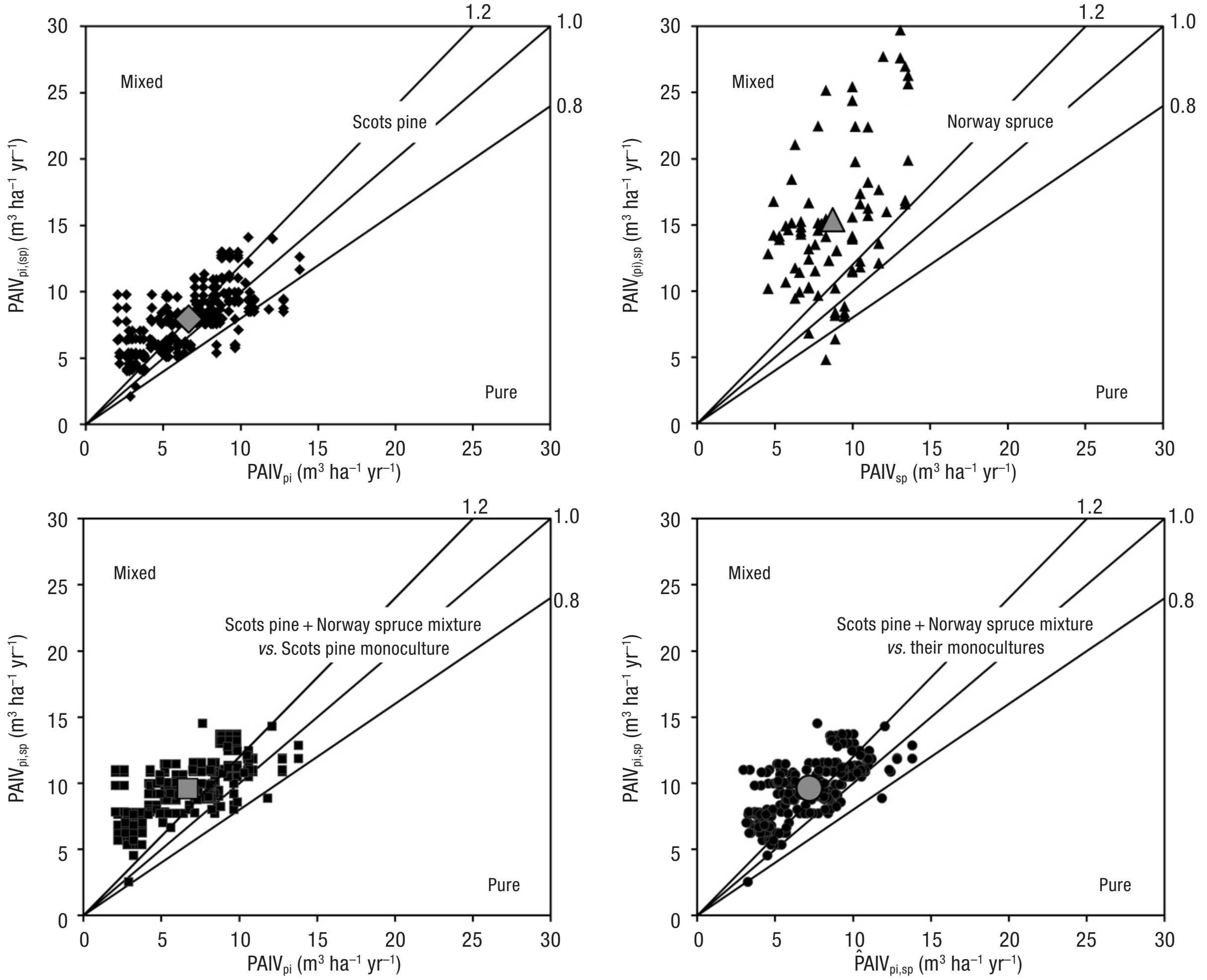

Figure 2. Comparison of periodic annual increment of volume (PAIV) in mixed stands *versus* pure stands at the species level (above) and stand level (below). The results at stand level include comparison of PAIV of mixed stands with corresponding pure stands of Scots pine (below, left) and with the weighted mean of both tree species in monocultures (below, right). Notice, that for Norway spruce the yield table by Schwappach (1943) was used as reference, as the respective pure stand plots were not available during the observation period of these long-term experiments.

Norway spruce, although the overyielding is visible from the beginning and the grey line starts at a higher level, as well as its slope is less steep (Fig. 4, above, right Table 3). The average values of RPAIV in mixed stand exceeds neutral mixing effects (1.0-line) at the age of around 60 years when compared with volume growth of Scots pine monocultures (Fig. 4, bottom, left). The same applies to the productivity of the mixed stands compared with the weighted means of the neighbouring pure stands and yield table, respectively (Fig. 4, bottom, right).

Fig. 5 shows the analogous evaluation for the relationship between the species and whole stand total yield (RTY) in the mixed *versus* pure stand. Of special interest is the mixing reaction at whole stand level (Fig. 5, below). In the mixed stand the increase of the total yield till the present age amounts to about 20% (Fig. 5, below, left and right). The species-specific analyses shown in Fig. 5 (above) suggest, that this whole stand reaction results from a moderate gain of Scots pine and a strong gain of Norway spruce (for the statistics results see Table 3). As Scots pine has an average mixing portion of 75% and Norway spruce only 25% during the considered stand development phase, the absolute effect of Norway spruce remains rather limited and probably would be much more pronounced in mixed stands with higher portions of Norway spruce. The average values of RTY in mixed stand exceeds neutral mixing effects around a stand age of 92 and 94 years. Fig. 5 underpins the very important fact, that the mixing

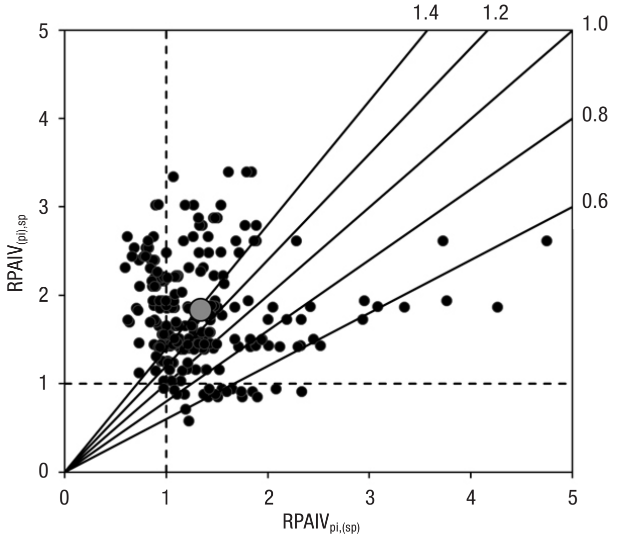

Figure 3. Relative productivity (RPAIV) of Scots pine and Norway spruce in mixture compared with pure stand (1.0-line). Large circle indicates mean values with RPAIV = 1.34 for pine and RPAIV = 1.83 for spruce. Pearson correlation: $r = -0.0068$, $p = 0.9152$. Notice, that for Norway spruce the yield table by Schwappach (1943) was used as reference, as the respective pure stand plots were not available during the observation period of these long-term experiments.

effects do not just modify stand growth temporarily, but modify and improve it continuously during long periods till the end of the rotation period. Notice that the increasing growth of mixed *versus* pure stands indicates a steady improvement of the growing conditions and productivity of both species when growing in mixture.

Effect of temporal growing conditions on the mixing reactions

In order to analyse the temporal variation of the mixing effects and any dependencies on the temporal growing conditions we used the following sets of variables. Firstly, we calculated the PAIV scaled up to 1 ha by mixing proportions for all available 4-5 years survey periods for the mixed and the neighbouring pure stand plots (Suppl. Fig. S1, above). Please notice that we excluded from this analysis one longer period because of missing data (1942-1958) related to World War II. The ratio between PAIV in mixed and pure stand gives the RPAIV-values which reflect any over- or underyielding of mixed *versus* pure stands. As observational values for pure stands were only accessible for Scots pine stands, we restricted the following analysis only to this tree species. Hence, we used the set of $RPAIV_{pi,(sp)}$ values for characterizing the periodic-specific mixing reactions. To analyse the dependency of $RPAIV_{pi,(sp)}$ on the temporal growing conditions, secondly we elaborated the long-term development of mean annual temperature and sum of annual precipitation (Suppl. Fig. S1, below). However, finally we focused on summer drought stress (see section *quantification of drought stress*). As the last step, we calculated for each survey periods the mean values of Martonne index and correlated them with corresponding $RPAIV_{pi,(sp)}$.

Fig. 6 shows graphically the decrease of overyielding with increasing values of Martonne index. The grey line results from linear model fitting to the relationship between the $RPAIV_{pi,(sp)}$ values and the Martonne index by a linear mixed model. The parameters in Table 3 reflect a significant decrease of the gains by mixing with increasing Martonne index. Obviously, the benefit of Scots pine from mixing is higher in years with scarce water supply compared to moist years under our investigated site conditions.

Mixing reactions depending on mixing portion and stand density

The observed values and model trajectories in cross diagrams according to Kelty (1992) (Fig. 7) show that even low mixing portions can cause strong mixing effects. In case of neutral mixing effects the growth of both species would lie close to the broken reference lines (increasing, decreasing, parallel to the x-axis, from left to right). The curves represent the observed average mixing reactions of each tree species and total stand according to nonlinear regression analysis based on the following model Equations [7] and [8].

$$RPAIV_{pi,\,(sp)} = m_{pi} \times (1 + a_1 \times m_{sp}), \qquad [7]$$

$a_1 = 1.4004\ (\pm 0.1337)$, $n = 250$, $R^2 = 0.004$, $p < 0.001$;

$$RPAIV_{(pi),\,sp} = m_{sp} \times (1 + a_2 \times m_{pi}), \qquad [8]$$

$a_2 = 1.1577\ (\pm 0.0546)$, $n = 250$, $R^2 = 0.468$, $p < 0.001$;

The graph shows that an admixture of 20-40 of Norway spruce to Scots pine stands can cause considerable losses but also gains in productivity (Fig. 7, left). In case of Norway spruce any admixture of Scots pine results in strong positive mixing effects and considerable gains in productivity (Fig. 7, middle). Consequently, in the cross diagrams for total stand behaviour (Fig. 7, right) nearly all observations lie above the re-

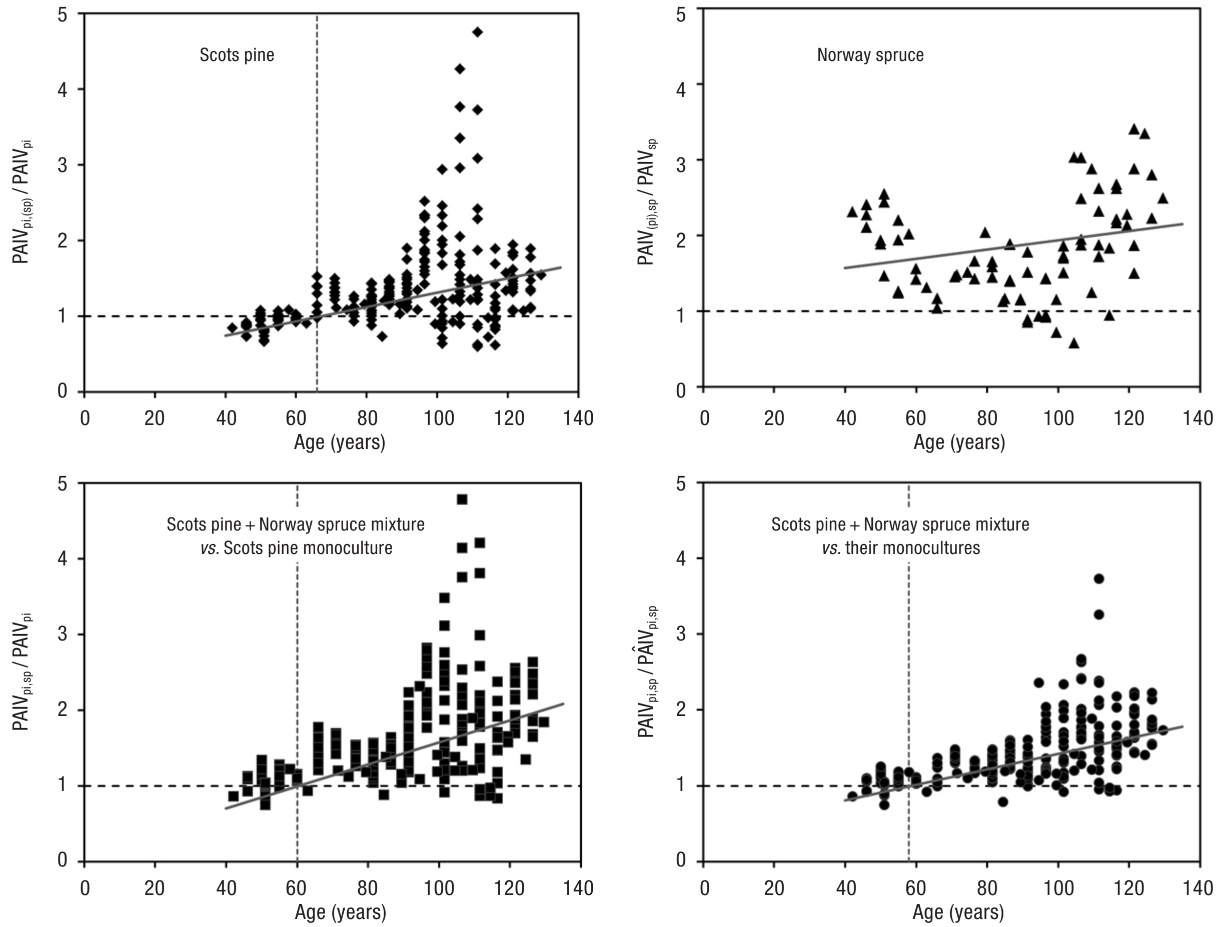

Figure 4. Changes of mixing effect at species-specific level: Scots pine (above, left), Norway spruce (above, right) and total mixed stand (below) expressed by relative productivity (RPAIV) over the stand age. The results at stand level include comparison of PAIV of mixed stands with corresponding pure stands of Scots pine (below, left) and the weighted mean of both tree species in monocultures (below, right). Broken horizontal lines indicate the productivity in pure stands (1.0-line) and vertical ones the age since the average values of RPAIV in mixed stand exceeds neutral mixing effects. Notice, that for Norway spruce the yield table by Schwappach (1943) was used as reference, as the respective pure stand plots were not available during the observation period of these long-term experiments.

ference line (1.0-line) for neutral mixing effects. Even low mixing proportions of Norway spruce cause strong overyielding at the stand level, which can even reach values of nearly 100%. This finding is underpinned by our regression model based on Equation [6] which confirms that volume growth of Scots pine strongly depends on admixture of Norway spruce and that there is an interaction between mixture proportion of this species and stand density (Table 3). The model further suggests that the positive effect of Norway spruce admixture on Scots pine volume growth is greater at higher stand density levels. Notice, that in case of our experiments in almost all cases SDI at the level of total stand is higher in mixtures than corresponding monocultures (Table 2).

Discussion

Species traits, niches, and hypothesized causes for overyielding

Ecological theory suggests a potential productivity advantage when stands contain more than one tree species (Kelty, 1992; Pretzsch, 2005, 2009). The basis for this advantage can be caused by complementary resource use, *i.e.* two or more species are able to use resources differently if they grow together and coexist on a site. Differential resource uptake among species suggests that the species in a mixture may utilize the resources of a site more completely than any single species would be able to do, leading to greater overall

Table 3. Results of the mixed model regressions for studied relationships (Equations [5] and [6])

Response variable Y	Predictor variable X_1	Predictor variable X_2	Predictor variable X_3	Fixed effects				Random effects		
				β_0	β_1	β_2	β_3	τ_1^2	τ_2^2	σ^2
$RPAIV_{pi,(sp)}$	age	—	—	0.3665* *0.0299*	0.0094*** *< 0.0001*	—	—	0.1630	0.0001	0.5205
$RPAIV_{(pi),sp}$	age	—	—	1.3283*** *< 0.0001*	0.0061*** *< 0.0001*	—	—	0.3749	0.1693	0.5963
$RPAIV_{pi,sp}$	age	—	—	0.3964** *0.0018*	0.0102*** *< 0.0001*	—	—	0.1506	0.0684	0.3170
$RPAIV'_{pi,sp}$	age	—	—	0.1241 *0.5817*	0.0145*** *< 0.0001*			0.2760	0.0001	0.5867
$RTY_{pi,(sp)}$	age	—	—	0.6145*** *< 0.0001*	0.0033*** *< 0.0001*	—	—	0.0333	0.0414	0.5194
$RTY_{(pi),sp}$	age	—	—	1.9916*** *< 0.0001*	*0.0001* *0.9934*	—	—	0.1695	0.1172	0.1727
$RTY_{pi,sp}$	age	—	—	0.5714*** *< 0.0001*	0.0045*** *< 0.0001*	—	—	0.1008	0.0471	0.0392
$RTY'_{pi,sp}$	age	—	—	0.5096*** *< 0.0001*	0.0053*** *< 0.0001*			0.1054	0.0678	0.0370
$RPAIV_{pi,(sp)}$	Ma	—	—	2.5786 *< 0.0001*	–0.1477*** *< 0.0001*	—	—	0.1348	0.0001	0.5602
$PAIV_{pi,(sp)}$	$\bar{v}$	mix_{sp}	$mix_{sp} \times SDI$	9.3302*** *< 0.0001*	–1.8904*** *< 0.0001*	–5.3053*** *< 0.0001*	0.0100*** *< 0.0001*	0.2515	0.3146	2.1370

PAIV: periodical annual volume increment. $\bar{v}$: mean tree volume. SDI: stand density index according to Reineke. mix_{sp}: mixing proportion of Norway spruce. Ma: Martonne index of aridity. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The respective *p*-values are given in italics below the parameter estimates. The number of observations used was 250 (RPAIV ~ age) 213 (RPAIV ~ Ma) and 172 (PAIV ~ $\bar{v}$, m_{sp}, $m_{sp} \times SDI$).

productivity. However, the link between differential resource use among species and greater total resource use does not necessarily apply to all kind of tree mixtures (Kelty, 1992; Pretzsch, 2009; Forrester, 2014).

In our study we found that on average mixed stand volume productivity of Scots pine and Norway spruce exceeds neighbouring pure stands of Scots pine, as well as the weighted mean of the growth and yield of neighbouring monocultures of both tree species. However, in the latter case, the results obtained should be treated with due caution as we employed instead of missing experimental data for pure Norway spruce stands the suitable yield tables by Schwappach (1943). Nevertheless, our findings are in line with other studies that were conducted based on mixed-species experiments of Scots pine and Norway spruce during initial stages of stand development (Brown, 1992; Jonsson, 2001; Lindén & Agestam, 2003; Mason & Connolly, 2014) or temporary established set of plots (Jonsson, 1962; Bruchwald *et al*., 1985; Pukkala *et al*., 1994).

For further explanation of the revealed mixing effects on stand productivity we discuss the different traits and niches of Scots pine and Norway spruce in face of niche complementary (Kelty, 1992; Pretzsch 2005; Forrester, 2014). Scots pine is a rather drought tolerant species while Norway spruce requires moist sites (Schmidt-Vogt, 1991; Modrzynski, 2007). Scots pine is a light demanding, early-successional species with low LAI (Bequet *et al.,* 2012), while Norway spruce is more shade tolerant, late successional-species (Brzeziecki & Kienast, 1994) with twice the LAI (Pokorny and Stojnič, 2012). Due to the double LAI, deposition is higher for Norway spruce than for Scots pine. Rubner (1960) reported that Norway spruce twigs with needles required at least 3-4% of full light to survive, whereas those of Scots pine need 10%. Scots pine sprouts earlier in spring than Norway spruce, whi-

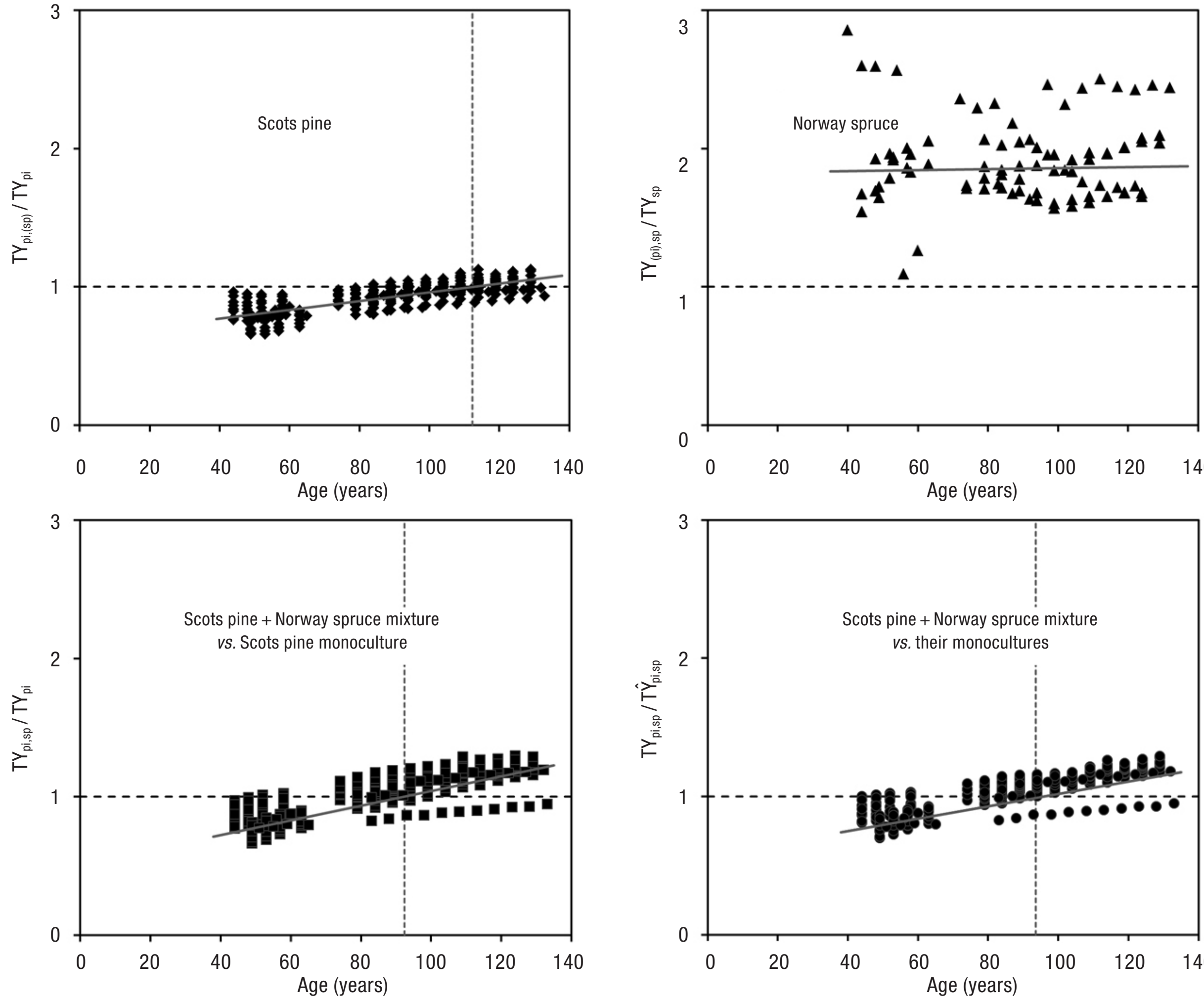

Figure 5. Effect of species mixing on the total yield over the stand age. The change are shown at species level for Scots pine (above, left) and Norway spruce (above, right). The change of total yield of the mixed stand in total is shown in relation to the pure stand of Scots pine (below, left) and to the weighted mean yield of both pure stands in monocultures (below, right). Broken horizontal lines indicate the productivity in pure stands (1.0-line) and vertical ones the age since the average values of RTY in mixed stand exceeds neutral mixing effects. Notice, that for Norway spruce the yield table by Schwappach (1943) was used as reference, as the respective pure stand plots were not available during the observation period of these long-term experiments.

le shoot length growth lasts longer in case of Norway spruce (Pretzsch, 2009). Scots pine is deep rooting and Norway spruce has rather shallow roots (Modrzynski, 2007). Nutrient contents in needles and litter decomposition of Scots pine is lower than for Norway spruce (Brown, 1992). Despite of these species-specific traits the ecological niches of both species overlap widely, *i.e.* both can be cultivated within a broad and similar range of sites in boreal and continental climate. However, when competing with each other Norway spruce dominates on the cool and wet sites and Scots pine on the warmer and dry sites. Their long-term coexistence is possible on sites moist enough for Scots pine to reach the upper canopy layer, but not so wet that Norway spruce becomes overwhelming dominant (see Pukkala *et al.,* 1994; Lindén & Agestam, 2003). This applies in Poland for sites with the annual precipitation around 600 mm yr^{-1} (Żybura, 1990). Our experimental plots represent exactly this precipitation condition, where both species can coexists without silvicultural interference, as none is overwhelmingly dominant. Scots pine mostly occupies the upper crown space, whereas Norway spruce is partly dominating and mostly lower.

This configuration enables the following niche complementary: Scots pine has the indispensable access to

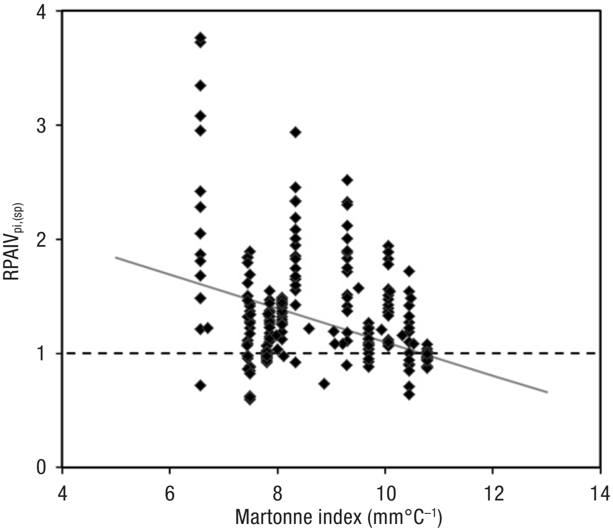

Figure 6. Stress reaction growth pattern for Scots pine in mixed *versus* pure stands. Mean relative productivity (RPAIV) of pine shown in dependence on the Martonne index. Regression line according to model Equation [5] (see Table 3). Broken line indicates the productivity in pure stand (1.0-line).

full sunlight but Norway spruce makes use of the light falling through the transparent crowns. Norway spruce enriches the rather poor litter in pure Scots pine stands and triggers a higher nutrient turn-over. The improved humus layer can mean a higher nutrient supply and water storage. Deep-rooting Scots pine contributes to an upward transport of water and nutrient from deeper soil layers and a mechanical stand stabilization against wind and storm damage (see also Kelty, 1992 and Pukkala *et al*., 1994). This hypotheses can be supported by Brown (1992) and Jones *et al*. (2005). In brief, they found improved nitrogen (N) status when Norway spruce was grown in mixture with Scots pine or common alder, which was linked to increased nitrogen (N) and phosphorus (P) availability in the mixed plots. The increased nutrient availability may also be due to mycorrhizal activity since fungi associated with Scots pine roots are known to contribute to the improved growth of Norway spruce in mixture on nutrient poor soils (Ryan and Alexander, 1992). Recent meta-analysis of species diversity productivity relationships in forests has indicated that the importance of complementarity increases with stand age (Zhang *et al*., 2012), what we also observed in our study. Finally the combination of early with late successional species means a combination of asynchronous growth rhythm with early culmination of Scots pine and late culminating Norway spruce. Latter means a longer maintenance of a rather high level of productivity, supported in the early state by Scots pine and in the late stand development phase by Norway spruce (see Figs. 4 and 5).

We hypothesize similarly to Mason and Connolly (2014), that the general trend towards overyielding of Scots pine in mixed *versus* pure stands results from a better nutrient supply due to improved deposition, litter decomposition triggered by the admixed Norway spruce (facilitation effects). The overyielding of Norway spruce probably results from an improved upwards

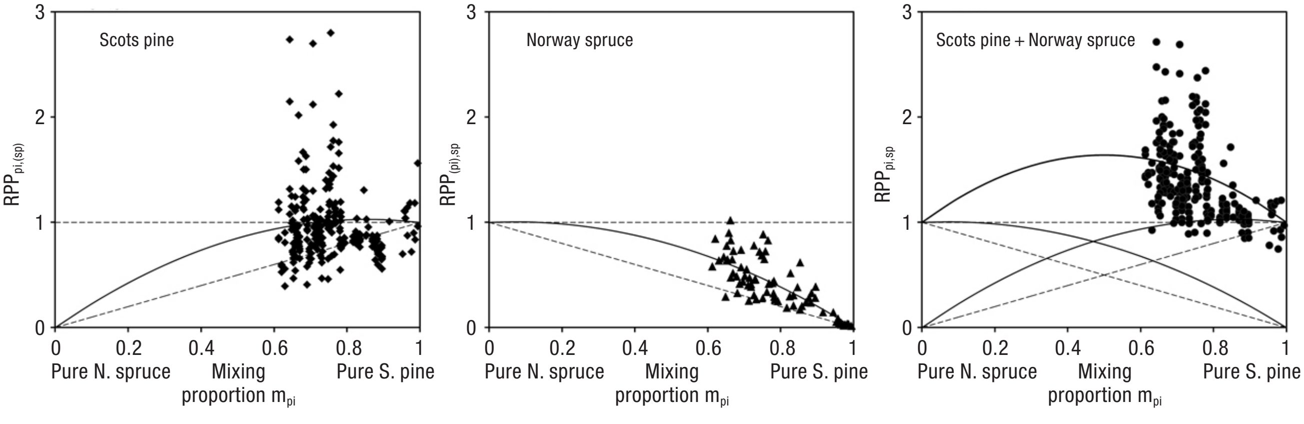

Figure 7. Relative productivity on the basis of the portions of volume growth of Scots pine (left), Norway spruce (centre) and the mixed stand in total (right) in relation to the productivity of the neighbouring pure stands. The points represent the observed relative volume productivity of mixed versus pure stands. The curves represent the average mixing reactions of Scots pine, Norway spruce and total stand according to fitted models based on Equations [7] and [8]. Notice, that for Norway spruce the yield table by Schwappach (1943) was used as reference, as the respective pure stand plots were not available during the observation period of these long-term experiments.

transport of water and nutrients caused by the deep rooting Scots pine. The increase of overyielding and stand density (standing volume) with progressing stand development indicates a continuous improvement of the sites quality due to the better resource supply, capture and use. The assumption that an increased resource supply and niche complementary is behind the overyielding is corroborated by the fact that the benefit of mixing is at maximum in years with scarce resource supply. In years with favourable growing conditions, the marginal utility of additional resource sequestration enabled by niche complementary becomes negligible (Pretzsch *et al*., 2013c; Forrester, 2014).

In cases when neighbouring pure stands of one or both species were missing Wiedemann (1942, 1951), as well as Pretzsch *et al*. (2010) used suitable yield tables as substitute. The outcomes of such comparison require that the underlying yield tables apply for the respective sites, nevertheless the results obtained should be treated with due caution. However, in many cases this is the only chance to exploit the valuable long-term information of mixed stand trials with one or even both pure stands missing or abandoned, *e.g.* because of damages such as bark beetle attack or windthrow. Using the yield tables as references is a makeshift which can be avoided by consequent establishment of triplets with mixed and pure stands of both combined species.

Conclusions

The following conclusions apply to the sites covered by our study, which are not wet enough for Norway spruce to dominate the upper canopy but sufficiently moist and cool for occasionally reach it. The analysed sites are rather warm and moist enough for a long-term dominance of Scots pine in the upper canopy in mixtures of Scots pine and Norway spruce. On sites with the species' height development on the same level or a superiority of Norway spruce the revealed niche complementary and overyielding *versus* pure stands cannot be expected. The obtained overyielding is relevant for forest management and a strong argument for establishment and tending of this species combination on the defined sites at the border between the boreal and continental climate. However, similar conditions can be found in the temperate climate in the Central European lowlands and hills, where Scots pine and Norway spruce are combined on south and west slopes with water supply restricting height growth of Norway spruce but sufficient for Scots pine to dominate. On such sites this species combination is highly productive in present and rather resistant against changing climate conditions in the future. Notice, that on the top of these advantages, the mixture of Scots pine and Norway spruce may contribute to a risk distribution concerning known biotic and abiotic disturbances and future risk due to climate change.

The long-term change of mixing effects during stand development and the short-term variability between survey periods with differing weather conditions underlines the indispensability of long-term experimental plots. Evaluations based on shorter phases of the stand development run the risk of premature statements with respect to mixing effects on productivity. Our evaluation provides evidence for significantly positive and practically relevant mixing effects on stand productivity. We hypothesize the long-term improvement of nutrient supply and water storage due to increase litter fall and improved humus decomposition as one cause for the overyielding. With increasing stand age and canopy stratification with Scots pine above and Norway spruce below complementary light usage becomes a second cause. Especially the long-term improvement of nutrient supply and water storage (facilitation effects) can be a generation overarching effect which improves the site fertility and silvicultural flexibility in the future.

Finally, the revealed overyielding of mixed compared with neighbouring pure stands, particularly under harsh weather conditions in case of Scots pine, substantiates the preferences of mixed Scots pine-Norway spruce stands regarding climate change.

Acknowledgements

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