RESEARCH PAPER

Temporal variation of competition and facilitation in mixed species forests in Central Europe

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ABSTRACT

Facilitation, reduced competition or increased competition can arise in mixed stands and become essential to the performance of these stands when compared to pure stands. Facilitation and over-yielding are widely held to prevail on poor sites, whereas neutral interactions or competition, leading to under-yielding of mixed *versus* pure stands, can occur on fertile sites. While previous studies have focused on the spatial variation of mixing effects, we examine the temporal variation of facilitation and competition and its effect on growth. The study is based on tree ring measurement on cores from increment borings from 559 trees of Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* [L.]) and sessile oak (*Quercus petraea* (Matt.) Liebl.) in southern Germany, half of which were in pure stands and half in adjacent mixed stands. Mean basal area growth indices were calculated from tree ring measurements for pure and mixed stands for every species and site. The temporal variation, with positive correlations between species-specific growth indices during periods of low growth and neutral or negative correlations during periods of high growth, is more distinct in mixed than in neighbouring pure stands. We provide evidence that years with low growth trigger over-yielding of trees in mixed as opposed to pure stands, while years with high growth lead to under-yielding. We discuss the relevance of the results in terms of advancing our understanding and modelling of mixed stands, extension of the stress gradient hypothesis, and the performance of mixed *versus* pure stands in the face of climate change.

INTRODUCTION

Generally, the more the growing space of a plant is restricted by neighbours, the stronger the competition for resources relative to solitary growth. Living in association with neighbours, however, may also provide advantages over solitary growth, through facilitation. For example, neighbours may protect against windthrow (Dhôte 2005), improve water supply through hydraulic lift (Dawson 1993) or protect neighbours from sun scorch of bark (Assmann 1970). Competition and facilitation (negative and positive interactions) between neighbouring plants occur simultaneously and are difficult to separate (Callaway & Walker 1997). Instead, their net effect on plant performance in terms of growth rate, survival or reproduction is used to indicate the balance between competition and facilitation. The benefits derived from living in association are widely held to be higher in harsh environments, where facilitation gains the upper hand, and less in mild, fertile environments where competition overshadows facilitation (Bertness & Callaway 1994; Callaway & Walker 1997). This conceptual model, formalised as the 'stress gradient hypothesis' (SGH), has been actively tested and debated over the last decade and has been extended to take into consideration the nature of the species, type of stress and temporal variation (Holzapfel *et al.* 2006; Lortie &

Callaway 2006; Sthultz *et al.* 2007; Maestre *et al.* 2009; Holmgren & Scheffer 2010).

In forests, these patterns of interaction, in terms of tree growth rates depending on site conditions, apply for pure stands but can become even more obvious and pronounced in mixed stands, where niche complementarity can additionally modify the competition for resources (Morin *et al.* 2011), and facilitation can exert further facilitative effects (Forrester *et al.* 2006). Hence, over-yielding has frequently been found in mixed stands (Amoroso & Turnblom 2006; Erskine *et al.* 2006; Pretzsch & Schütze 2009). However, few studies have explored the SGH from the perspective of species interactions in terms of growth in mixed forests (Callaway 1998; Pretzsch *et al.* 2010; Gómez-Aparicio *et al.* 2011).

Findings with regard to type and extent of intra- and inter-specific interactions and their dependence on site conditions are mostly based on the net long-term performance of plants or populations analysed along ecological gradients (*e.g.* gradients from nutrient-rich to -poor sites or from moist to dry sites). However, niche complementarity and facilitation that improve the performance of mixed *versus* pure stands in the long term, especially on poor sites, can also be assumed to be relevant and effective for both plant and stand performance in the short term, *e.g.* in dry years. Pretzsch *et al.* (2012) provide evidence of drought stress release through inter-specific

facilitation in mixed stands of European tree species. While trees in mixed and pure stands performed similarly in years with average growing conditions in terms of mean temperature and precipitation, trees in mixed stands outperformed trees of the same species in neighbouring pure stands in drought years, such as 1976 and 2003. This finding of positive mixing effects and improved resilience and resistance in harsh years raises the question of whether the effects of facilitation and competition on growth vary temporally with annual growing conditions, as they do spatially along ecological gradients.

Various studies have examined temporal variability in plant interactions, but the time period considered in most of them was limited to a few years (Callaway 1998; Tielbörger & Kadmon 2000; Sthultz *et al.* 2007). This kind of temporal approach may be of great interest where the objective is to determine the role of facilitation and competition in tree regeneration (Gasque & García-Fayos 2004; Nuñez *et al.* 2009), in short-lived perennial plants (Soliveres *et al.* 2010) or in response to extreme climatic conditions (Pretzsch *et al.* 2012). However, a longer time interval is more appropriate for studying temporal variability in growth associated with between-tree interactions in mature stands.

In this study, we hypothesise that the modification of inter-specific interactions (*i.e.* competition and facilitation) as a result of temporal growing conditions is similar to that associated with the spatial variation of growing conditions along ecological gradients. We use the term 'facilitation' to mean a reduction of competition in terms of tree growth, which can be caused by niche complementarity and/or through a direct support effect of one species by another. We base our study on tree ring measurement on cores from increment borings of 559 Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* [L.]) and sessile oak (*Quercus petraea* (Matt.) Liebl.) trees in southern Germany, half of which were in pure stands and half in mixed stands. In order to reveal any temporal variability in tree species interactions, the study draws attention to (i) correlations between species-specific tree growth indices in pure and mixed stands in periods of low growth *versus* high growth, and (ii) the extent of facilitation *versus* competition depending on the annual growing conditions.

MATERIAL AND METHODS

Study area and target species compositions

The study was conducted in Bavaria in Germany. The three species Norway spruce (44%), European beech (14%) and sessile oak (6%) were chosen as they cover more than 64% of the total forest area in Germany; 50% of this presence being in mixed species stands. For each of the two species compositions, beech–oak and beech–spruce, four sites were chosen from long-term experiments in mixed stands in which it was possible to find adjacent pure stands of the respective species with similar site conditions, age, stand density and silvicultural treatments (Fig. 1).

The eight selected sites lie between 9°26′ and 11°48′ E and 47°52′ and 50°20′ N at 290–785 m a.s.l. Mean annual precipitation ranges from 596 to 1343 mm and mean temperature from 6.5 to 9.3 °C (Table 1). The geology of the basic soil material is granite, sandstone in the north, limestone Jurassic and chalk-stone material in the centre, and tertiary moraine and molasse material in the south of the study region. Soils vary between brown and parabrown. The substrate is mainly loam and silt, and the water conditions range from dry to moist. More details of the study area and the long-term experimental sites can be found in Pretzsch *et al.* (2012).

Data collection

At each of the long-term experimental sites, around 20 dominant trees of each species were chosen as sample trees to represent tree growth in mixed stands. In order to adequately reflect the growth performance of each species in mixed stands, the selected individuals had to satisfy the criteria of having at least 50% of the six nearest neighbours belonging to the other species. Trees with similar dendrometric characteristics as the sample trees in the mixed stands were then selected in nearby pure stands. In all cases, these pure stands were <1 km from the mixed experimental sites and had similar site conditions, age, stand density and silviculture; thus growth performance could be compared between the sample trees in each stand type.

Sample trees in mixed and pure stands were selected considering that the minimum distance between trees was 20 m to ensure that they were growing independently of each other. Tree diameter at breast height (DBH), total height, height of the crown base and eight crown radius (to estimate the cross-sectional crown area) measurements were recorded to characterise the sample trees. Additionally, the characteristics of the stand surrounding each sample tree were described as the basal area and the site index (Tables 1 and 2). Basal area was estimated through the angle count method according to Bitterlich (1952), and site index from mean tree height (m) at age 100 years using the yield tables of Assmann & Franz (1965) for Norway spruce, Schober (1975) for European beech and Jüttner (1955) for sessile oak.
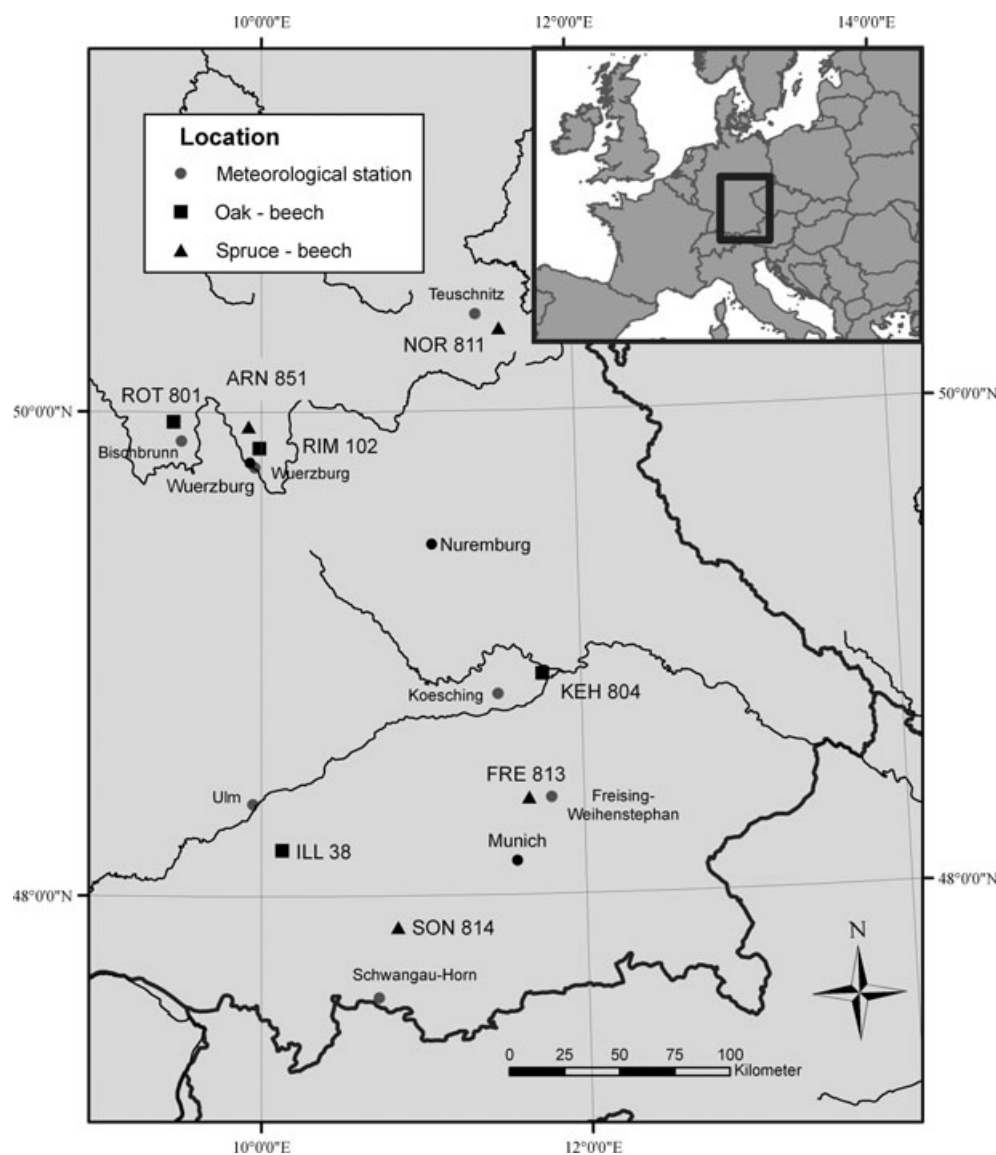
For each sample tree, two cores were taken close to breast height (1.3 m) from the north- and east-facing aspects to obtain representative tree ring widths, since the maximum diameter frequently corresponds to the southwest-facing aspect, as the dominant winds are from that direction. Cores were extracted to the central pith in order to ensure a radial boring direction and to enable tree age to be estimated from a ring count (adding 5 years to the age at breast height). All measurements were taken in autumn 2010 and spring 2011.

Climatic data were obtained from the meteorological stations located nearest to the study areas. From north to south, the meteorological stations used for the study sites were: Teuschnitz for NOR_811, Bischbrunn for ROT_801, Wuerzburg for ARN_851 and RIM_102, Koesching for KEH_804, Freising-Weihenstephan for FRE_813, Ulm for ILL_38 and Schwangau-Horn for SON_814 (Fig. 1).

Basal area growth data

The increment cores were glued onto wooden slides, ground and polished on a sanding machine using 120-grit sandpaper, cleaned using compressed air and analysed to the nearest 1/100 mm using a digital positioning table (Kutschenreiter & Johann; Digitalpositiometer, Britz & Hatzl, Austria). Where the cores had not been taken perpendicular to the tree rings, the distances between consecutive tree rings were corrected

Fig. 1. Location of the eight study sites and corresponding meteorological stations.

Table 1. Main site and climate characteristics.

oak-beech	altitude m a.s.l.	longitude	latitude	age$_{oak}$ years	age$_{beech}$ years	SI$_{oak}$ m	SI$_{beech}$ m	P mm	T °C
ROT_801	415	9°26′24″	49°57′36″	135	135	24.7	26.2	972	7.9
RIM_102	290	9°59′24″	49°51′0″	100	100	28.5	29.5	596	9.3
KEH_804	490	11°48′36″	48°54′36″	120	120	31.8	33.9	715	8.2
ILL_38	555	10°7′48″	48°11′24″	135	90	27.0	33.3	745	8.1

spruce-beech	altitude	longitude	latitude	age$_{spruce}$ years	age$_{beech}$ years	SI$_{spruce}$ m	SI$_{beech}$ m	P mm	T °C
ARN_851	312	9°26′24″	49°54′0″	60	76	35.8	34.2	596	9.3
FRE_813	500	11°39′36″	48°24′0″	52	57	36.8	37.9	800	7.9
NOR_811	560	11°31′48″	50°20′24″	66	78	38.7	36.2	995	6.5
SON_814	785	10°50′24″	47°52′12″	57	69	36.6	37.7	1343	7.1

SI = site index estimated as the mean height in m at age 100 years of the selected dominant trees; P = annual precipitation; T = mean annual temperature.

Table 2. Characteristics of sample trees and mean tree basal area growth of corresponding sample cores for each species growing in pure or mixed stands by site (mean values with SD in parentheses).

		pure					mixed				
oak-beech	species	N	DBH cm	H m	G m² ha⁻¹	BAI cm² per year	N	DBH cm	H m	G m² ha⁻¹	BAI cm² per year
ROT_801	Oak	18	38.5 (5.4)	32.4 (3.8)	37.4 (6.1)	13.4 (3.6)	18	35.4 (4.2)	35.6 (4.1)	43.5 (6.3)	11.3 (2.5)
	Beech	17	49.7 (10.6)	36.6 (3.9)	32.2 (6.8)	24.3 (4.7)	19	37.9 (8.4)	32.6 (4.9)	35.5 (5.9)	15.7 (3.0)
RIM_102	Oak	16	36.8 (4.4)	33.3 (2.6)	37.3 (6.2)	14.2 (3.7)	16	38.1 (5.7)	32.8 (4.3)	33.8 (4.7)	15.0 (3.4)
	Beech	17	47.7 (7.8)	38.3 (3.7)	51.8 (9.0)	24.4 (6.6)	15	34.0 (7.2)	31.4 (5.6)	32.9 (5.7)	14.5 (5.9)
KEH_804	Oak	15	41.6 (7.3)	38.1 (3.3)	33.3 (6.7)	16.5 (3.7)	16	40.2 (6.5)	35.3 (3.5)	30.9 (6.5)	13.9 (3.5)
	Beech	15	47.2 (10.5)	39.0 (4.0)	23.1 (6.7)	23.2 (3.5)	15	37.8 (11.2)	34.3 (6.3)	28.9 (6.3)	17.4 (7.4)
ILL_38	Oak	18	48.9 (8.9)	34.7 (6.7)	59.6 (14.4)	16.8 (3.3)	15	54.4 (10.3)	37.1 (6.3)	43.3 (12.2)	23.4 (4.6)
	Beech	16	48.0 (7.6)	36.1 (6.0)	42.0 (8.4)	26.0 (5.7)	15	55.9 (16.3)	33.8 (6.8)	42.7 (14.6)	31.5 (12.7)
spruce-beech											
ARN_851	Spruce	15	30.4 (5.8)	25.5 (1.6)	44.4 (6.9)	16.6 (7.8)	19	36.9 (8.9)	27.7 (2.8)	29.9 (7.5)	25.9 (10.5)
	Beech	20	32.7 (4.4)	29.1 (2.4)	26.9 (6.3)	16.6 (9.4)	20	29.6 (4.9)	27.3 (3.3)	20.4 (7.9)	13.7 (7.8)
FRE_813	Spruce	18	31.1 (3.0)	24.9 (1.2)	58.7 (9.8)	21.2 (10.3)	15	25.5 (4.5)	23.2 (3.0)	45.2 (11.5)	17.1 (8.5)
	Beech	19	24.7 (6.7)	24.4 (2.3)	51.4 (11.7)	10.5 (1.8)	19	31.2 (9.7)	26.5 (3.8)	42.2 (6.4)	17.0 (2.6)
NOR_811	Spruce	20	35.3 (5.8)	30.0 (2.0)	52.2 (6.6)	20.3 (5.2)	20	39.8 (5.3)	32.0 (1.8)	44.8 (7.6)	24.8 (7.4)
	Beech	20	33.8 (7.0)	30.8 (3.5)	39.5 (8.3)	13.3 (3.2)	20	30.7 (5.2)	30.5 (2.4)	44.2 (9.4)	11.9 (2.9)
SON_814	Spruce	20	26.8 (3.5)	25.4 (1.5)	79.5 (9.2)	14.2 (4.1)	16	35.7 (8.7)	27.2 (2.3)	53.4 (12.6)	24.5 (5.8)
	Beech	20	36.2 (4.8)	29.1 (2.8)	33.9 (5.7)	23.3 (5.9)	20	31.3 (5.9)	29.5 (2.5)	56.6 (9.8)	17.6 (3.1)

N = number of sample trees; DBH = diameter at breast height; H = total height; G = basal area of the stand in which they grow; BAI = annual basal area growth.

using a cosine function. The tree ring series were visually cross-dated and synchronised using extreme years, such as 1976 and 2003 (which had narrow rings), for a previous study on tree species resistance to drought in pure and mixed stands (Pretzsch *et al.* 2012). For the purposes of the present study, radial growth series from 1953 to 2010 were used in order to cover a broad range of annual growing conditions including low-growth periods, such as the mid-1970s, and high-growth periods, such as the late 1990s.

Tree ring widths were transformed to basal area increments (BAI), the latter being more closely related to biomass increment and less age-related, thus avoiding the need for age detrending (Biondi 1999). To estimate the BAI series for each tree, first a diameter increment time series was calculated by adding the radial increments of the two cores of a tree. Then, using the diameter of the tree in the sampling year as starting point, the respective diameters for previous years were calculated by subtracting the annual diameter growth for each year to obtain a diameter time series. Finally, from the corresponding tree basal area series, the basal area increments were estimated.

In spite of the efforts made to find similar trees growing in mixed and pure stands, some differences were found between the two types of tree (Table 2). Minor disturbances, which may have influenced individual tree growth, along with the high variability between trees normally found in this kind of forest (Zang *et al.* 2011), cannot be controlled through *a posteriori* tree selection for the purpose of comparison. Hence, the tree samples for mixed and pure stands might not satisfy *ceteris paribus* conditions. To overcome this shortcoming, particularly bearing in mind that the main objective was to study the variability in tree growth, a filter was applied in order to obtain comparable basal area growth indices. These indices were obtained by dividing the basal area increment of the year i (BAI_i) by the moving average of the basal area increments for 10 years (BAI_{i-5}, BAI_{i-4},….BAI_{i+4}). This filter mitigates the possible effects of small differences among tree sizes in year-to-year variability, while maintaining the series close to the real basal area growth data (see Fig. S1). Basal area growth index series were calculated for all trees and then a mean series (IBAI) was obtained for each species and type of stand (mixed/pure) at each of the study sites. Possible temporal autocorrelation between growth indices of the same series was considered when fitting the models (see following sections).

Interaction index

Plant interactions and possible shifts from competition to facilitation at temporal and spatial scales are usually explored using the relative interaction index (RII; Armas *et al.* 2004). This index represents plant interactions as a continuum from competition to facilitation. If interaction is measured in terms of growth and it is evaluated comparing pure and mixed stands, the expression of the relative interaction index for the year i would be:

$$RII_i = \frac{Gm_i - Gp_i}{Gm_i + Gp_i} \qquad (1)$$

where Gm_i and Gp_i are the growth in mixed and pure stands, respectively, during year i. This index presents the advantages that it is symmetrical, it is continuous and it is relative (Armas *et al.* 2004). In our study, one possibility was to apply it directly using the basal area increments (BAI_i) of mixed and pure series, since size differences among trees would be mitigated *via* the denominator. However, due to the uncontrolled factors associated with the samples in mixed and pure stands, it is not

possible to compare the growth rates from each stand type directly nor, consequently, to evaluate the net interaction effect. Since our main objective was to determine whether inter-annual variability in tree growth differs between trees of the same species growing in pure and mixed stands, we used mean values of the calculated basal area growth indices ($IBAI_i$) of both types of stand. In the basal area growth indices, the size effect had already been removed, since the basal area increments were divided by the moving average, thus yielding a dimensionless index. Therefore, we used the difference between mean values of basal area growth indices in mixed and pure stands as an interaction index (II), whose expression for the year i is:

$$II_i = IBAIm_i - IBAIp_i \qquad (2)$$

where $IBAIm_i$ and $IBAIp_i$ are mean basal area growth index values for mixed and pure stands, respectively, in year i. This index is symmetrical (positive and negative values around zero), it is continuous and it is also relative, since the two populations are comparable. The index value is positive when the growth index is higher in mixed than in pure stands, expressing an interaction between species of facilitation or complementarity, while when it is negative this indicates that competition dominates the between-species interaction.

Determination of the stress gradient

Different stress gradients were explored to test whether temporal variability in species interactions varies according to these gradients, in the same way as stated in the SGH. First, we explored the use of climate variables as expressions of the stress gradient. In order to select the climate variables that have the greatest influence on basal area growth for each species and site, correlations between climate variables and growth indices in pure stands were analysed. Monthly temperatures and precipitations, the corresponding seasonal and annual values, as well as other aggregated values were considered. However, the correlations detected were in general low and did not reveal a clear stress factor for each species or site (see Table S1).

Therefore, it was decided to use an indicator of productivity. According to Grime (1977), stress can be defined as those environmental conditions that limit the rate of dry matter production in all or part of the plant; hence the stress gradient can be defined in terms of growth (Lortie & Callaway 2006). The use of basal area growth as an indicator of productivity has the advantages of being highly correlated with biomass production and that it is easily measured. Consequently, we chose the gradient of basal area growth indices as surrogate for the stress gradient. It was assumed that the main stress factors affecting the growth of a given species were similar in mixed and pure stands, so the basal area growth indices of pure stands were chosen ($IBAIp$). Years with high $IBAIp$ were considered benign years for the species, while those with low growth indices were assumed to be high stress years.

Analysis

In order to better understand the relationships between species in terms of tree growth in mixed stands, we analysed correlations between the mean basal growth indices of the species

(A and B) comprising the mixture ($IBAIm_A$, $IBAIm_B$) and compared these to the corresponding correlations in pure stands ($IBAIp_A$, $IBAIp_B$). These correlations were calculated for years with high-growth/low-stress levels ($IBAIp > 1$) as well as for low-growth/high-stress years ($IBAIp < 1$) to detect possible variability within the stress gradient. If the correlation between the growth indices of two species growing in pure stands at a particular site is very high (similar year-to-year variation), this indicates that both species have similar environmental requirements; whereas if there is low correlation, this suggests that the growth of each individual species is influenced by different environmental conditions. Changes among the correlations in pure and mixed stands might indicate that species interactions modify the way in which environmental conditions influence tree growth.

To test whether there were inter-annual shifts between species interactions along stress gradients, linear models relating the interaction index (II) to stress factors were fitted for each species and site. As growth indices are temporal series in which there may be temporal autocorrelation, an autoregressive component of order one was included in all models to avoid such autocorrelation.

As mentioned previously, we explored both climate variables and IBAI as stress factors. Where IBAI in pure stands ($IBAIp$) is used as a surrogate of stress factors, the model is as follows:

$$II_i = a_0 + a_1 \cdot IBAIp_i + AR(1) + \varepsilon_i \qquad (3)$$

II_i being the interaction index in the year i, a_0 and a_1 parameters to be estimated, $IBAIp_i$ is the mean basal area growth index in a pure stand in the year i, AR(1) is the autoregressive component of order one, and ε_i is a random error term. If the slope a_1 is not significantly different from zero, this indicates that there is no trend towards temporal shifts in species interaction with the stress gradient; the temporal variation being similar in mixed and pure stands. If the slope a_1 is negative and the intercept a_0 is positive, this indicates a positive interaction in years with low values of $IBAIp$ (note that as regards growth or productivity, low values are related to high stress) and lower values (negative) of II in years with high $IBAIp$ (low stress). If the slope is positive, it reflects an opposite trend to the stress gradient.

RESULTS

Relationships between species-specific growth indices

In oak–beech sites, the correlation between basal area growth indices of the two species growing in pure stands was positive and significant for three sites (Table 3). When dividing data by low-growth and high-growth years in pure stands ($IBAIp$), correlations were only significant for two sites in high-growth years for oak, indicating that the two species share only part of the inter-annual growth variability.

When comparing these correlations with those in mixed stands, it can be seen that the correlations were lower or even negative in mixed stands. However, the small size of the sample meant that only some of the correlations were statistically significant when dividing data by high- and low-growth years. It is interesting to note the change in the correlations between pure and mixed stands in high-growth years, varying from being positive in pure stands to negative or close to zero in

Table 3. Simple correlation coefficients between mean basal growth indices of the two species that form each mixture growing in mixed or pure stands (in parentheses, number of data collected).

mixture/site	all years		$IBAIp_{oak} < 1$		$IBAIp_{oak} \geq 1$	
oak-beech	mixed stands	pure stands	mixed stands	pure stands	mixed stands	pure stands
ROT_801	**0.422** (38)	**0.428** (38)	0.014 (18)	0.019 (18)	−0.055 (20)	0.186 (20)
RIM_102	−0.123 (41)	0.245 (41)	−0.042 (20)	0.402 (20)	−0.242 (21)	0.303 (21)
KEH_804	0.120 (44)	**0.344** (44)	0.145 (21)	0.363 (21)	0.289 (23)	**0.441** (23)
ILL_38	**0.516** (42)	**0.597** (42)	**0.424 (23)**	0.379 (23)	0.335 (19)	**0.518** (19)
			$IBAIp_{beech} < 1$		$IBAIp_{beech} \geq 1$	
ROT_801			0.264 (21)	0.178 (21)	0.300 (17)	0.204 (17)
RIM_102			0.149 (19)	0.412 (19)	**−0.543** (22)	−0.032 (22)
KEH_804			0.136 (20)	0.387 (20)	−0.149 (24)	0.403 (24)
ILL_38			0.321 (20)	−0.359 (20)	0.214 (22)	0.358 (22)
beech-spruce	all years		$IBAIp_{beech} < 1$		$IBAIp_{beech} \geq 1$	
ARN_851	**0.681** (33)	**0.763** (33)	**0.721** (17)	**0.851** (17)	0.208 (16)	0.455 (16)
FRE_813	0.279 (33)	**0.490** (33)	0.178 (14)	0.393 (14)	0.155 (19)	0.438 (19)
NOR_811	**0.669** (38)	**0.586** (38)	**0.557** (21)	**0.554** (21)	0.433 (17)	**0.554** (17)
SON_814	0.040 (31)	0.318 (31)	−0.009 (15)	0.124 (15)	0.205 (16)	0.384 (16)
			$IBAIp_{spruce} < 1$		$IBAIp_{spruce} \geq 1$	
ARN_851			**0.746** (17)	**0.719** (17)	0.139 (16)	0.437 (16)
FRE_813			0.233 (18)	0.396 (18)	0.199 (15)	0.492 (15)
NOR_811			**0.747** (19)	**0.641** (19)	**0.592** (19)	0.347 (19)
SON_814			0.082 (18)	0.231 (18)	−0.206 (13)	**0.713** (13)

Correlations were calculated for all years and by dividing the series according to the basal area growth index in pure stands (IBAIp higher and lower than 1) of the three target species. Statistically significant coefficients in bold.

mixed stands. This is particularly remarkable in site RIM_102 (Fig. 2), where the correlation in high-growth years for beech ($IBAIp_{beech} \geq 1$) in mixed stands reached a value −0.54.

The correlations between the basal area growth indices of beech and spruce growing in pure stands were, in general, higher than those between beech and oak (Table 3). In the case of the former species, for high-growth years, there was a similar change in correlations to beech–oak, with a decrease in correlation coefficients in mixed stands, except for site NOR_811 in high-growth years for the pure spruce stand ($IBAIp_{spruce} \geq 1$).

Annual shifts between facilitation and competition

In accordance with our main hypothesis, we found that inter-annual variability in basal area growth was associated with shifts in the inter-specific interactions of the two studied mixtures, although the results varied among species and sites. The species that presented the smallest differences in basal area growth indices between mixed and pure stands was oak. For this species, only at two sites was the slope of the relationship between the interaction index and the mean basal area growth index in pure stands statistically different from zero (Table 4). At these two sites, the slope was small and negative, indicating a weak positive interaction or facilitation in years with low-growth indices and negative interaction or competition in good years with high-growth indices.

A similar pattern of interaction shifts was found for the other two species (Table 4). For beech growing with oak, the

slope was negative and statistically different from zero at three sites, in all cases being steeper than for oak (from −0.23 to −0.42). In the case of beech growing with spruce, the model fitted was also significant for three sites, with slopes that ranged from −0.24 to −0.43. These high values reflect a more pronounced mixing effect on growth variability in beech. For spruce, the range in slope varied from −0.26 to −0.36; where the model is significant at three of the four sites.
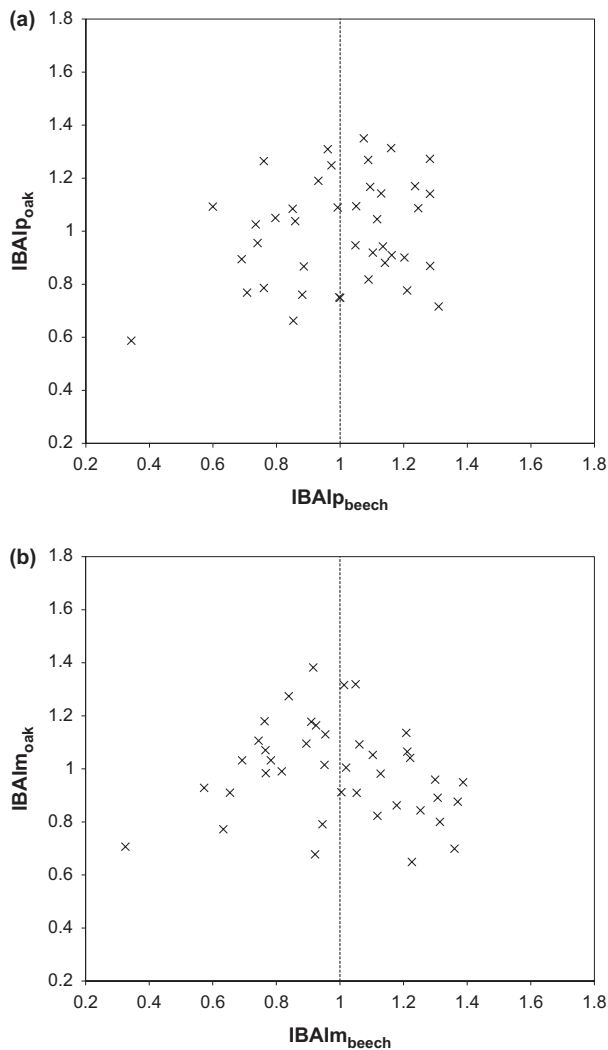
It is important to note that for some sites, the fitted models (equation 3) did not explain much of the variability of the interaction index, making the results less reliable. For instance, the coefficient of determination for beech at site ILL_38 was only 0.12. However, in the other significant models the values were higher, reaching as much as 0.6, which is high considering the characteristics of the data.

DISCUSSION

Temporal variations in relationships between species-specific growth indices

The variations observed in correlations between the basal area growth indices of oak and beech growing in pure and mixed stands highlights the importance of plant interactions in the mechanisms underlying the growth response of trees to environmental variability. The lower values of correlations in mixed stands than in pure oak or beech stands in years with high-growth indices might be due to a prevalence of competition

Fig. 2. Relationships between mean basal area growth indices of oak and beech growing in pure (a) or mixed (b) stands in the study site RIM_102. IBAI: mean basal area growth index for pure (p) or mixed (m) stands.

precipitation over the course of the year for both of the above species (Zang *et al.* 2011), although oak was found to be more resistant and less resilient to drought than beech (Pretzsch *et al.* 2012). The lower dependence of oak on climate factors might explain the higher competition between these two species in high-growth years, when likely climatic conditions are not the limiting factor, and not very high correlations between the two species in low-growth years, suggesting a certain degree of niche complementarity (Pretzsch *et al.* 2012).

In the case of the spruce–beech mixture, the correlations between the growth indices of these two species were higher than for oak–beech mixtures, and were similar for pure and mixed stands. This fact suggests that most of the year-to-year variability was driven by similar climate factors for both the species and stand types (Table S1), as previously reported in other studies concerning climate–growth relationships in pure stands in the region (Zang *et al.* 2011). However, this does not mean that the intensity of the effects of climate factors is equal in pure and mixed stands, as revealed in our results concerning shifts in inter-specific interactions.

Temporal variation in inter-specific interactions

The results from the fitted models, relating the interaction index and the growth index in pure stands as an indicator of the temporal stress gradient, showed that annual variations in abiotic factors lead to shifts in the balance between facilitation and competition in inter-specific interactions on tree growth, with a facilitation effect in low-growth years and a competition effect in high-growth years (Table 4). These frequent shifts demonstrate that facilitative and competitive mechanisms do not act in isolation from each other in nature, but co-occur within the same community and even between the same individuals at varying intensities, producing complex and variable effects (Callaway & Walker 1997; Callaway 1998). Other studies have reported changes in tree inter-specific interactions when exploring the effects of annual climate conditions in specific years (Callaway 1998; Pretzsch *et al.* 2012). However, our results confirm that the annual net effects of interaction are 'snapshots' of a continuous long-term mechanism.

The possible benefits associated with mixed stands of oak and beech, as opposed to pure stands, in low-growth years, when competition for belowground resources are expected to be higher than for light (Pretzsch & Dieler 2011), may include: an increase in supply of resources due to increased litter deposition resulting from a higher leaf area index (LAI) in mixed stands (André *et al.* 2008); increased leaf nutrient content and leaf litter decomposition, as found previously for the oak–beech mixture (Jonard *et al.* 2008); or improved mineralisation due to changes in root depths, mycorrhiza and soil chemistry. However, the nutritional interactions in mixed forests are difficult to generalise due to the limited number of studies (Rothe & Binkley 2001).

Based on the findings of Caldwell *et al.* (1998), we hypothesise that the deep-rooting oak facilitates the much more shallow-rooting beech (Pretzsch *et al.* 2012). Resource uptake might be higher as a result of improved temporal and spatial positioning of the two species from spring to autumn and from the canopy to the root space. Moreover, resource-use efficiency may be increased due to improved resource supply, or less respiratory losses, and leaf size class distribution. Pretzsch & Dieler (2012) found that the allometric crown plasticity of

between the two species when growth conditions are favourable. A number of studies concerning oak–beech mixtures have documented the competitive superiority of beech, both aboveground and belowground (Leuschner et al. 2001; Hein & Dhôte 2006; Rewald & Leuschner 2009), which may result in a negative influence of beech admixture on oak, particularly where the environmental conditions are more favourable for beech. However, in years with low-growth indices in beech, the competition may be lower, resulting in positive correlations. This supports the results of Pretzsch *et al.* (2012), who identified a clear facilitative effect of oak on beech in years of extreme drought, using the same tree sample as used in the present study.

Climate–growth correlations in our data were not significant for oak at three sites, whereas for beech, winter and spring temperatures and annual precipitation correlations were low but significant (Table S1), probably because the indirect effects of climate factors on nutrient supply through modification of decomposition and mineralisation rates are of more importance (Körner 2002). Other studies conducted in the same region have reported similar dependence on temperature and

Table 4. Parameter estimates (SD in parentheses) and fitting statistics for the models relating the interaction index (II) to mean basal area growth indices in pure stands (IBAIp) fitted by species and site (equation 3).

species/site	n	a_0 (intercept)	a_1 (slope)	AR(1)	MSE	R^2
oak with beech						
ROT_801	38	0.080 (0.037)	−0.080 (0.035)	0.387 (0.156)	0.0019	0.18
RIM_102	41	0.177 (0.058)	−0.185 (0.057)	n.s.	0.0052	0.21
KEH_804	44	n.s.	n.s.	n.s.	–	–
ILL_38	42	n.s.	n.s.	n.s.	–	–
beech with oak						
ROT_801	38	0.419 (0.067)	−0.418 (0.065)	0.439 (0.158)	0.0062	0.59
RIM_102	41	0.249 (0.113)	−0.231 (0.105)	0.504 (0.142)	0.0229	0.28
KEH_804	44	n.s.	n.s.	0.560 (0.139)	0.0123	0.28
ILL_38	42	0.326 (0.141)	−0.327 (0.140)	n.s.	0.0173	0.12
beech with spruce						
ARN_851	33	n.s.	n.s.	n.s.	–	–
FRE_813	33	0.435 (0.083)	−0.428 (0.084)	n.s.	0.0038	0.46
NOR_811	38	0.420 (0.057)	−0.422 (0.056)	0.392 (0.163)	0.0054	0.67
SON_814	31	0.238 (0.051)	−0.236 (0.051)	n.s.	0.0018	0.42
spruce with beech						
ARN_851	33	0.255 (0.070)	−0.261 (0.061)	0.490 (0.169)	0.0121	0.49
FRE_813	33	0.305 (0.066)	−0.307 (0.066)	n.s.	0.0071	0.41
NOR_811	38	n.s.	n.s.	n.s.	–	–
SON_814	31	0.359 (0.166)	−0.384 (0.167)	0.433 (0.194)	0.0149	0.27

n = data number (years); a_0 and a_1 = parameters of the models; AR(1) = autoregressive component; MSE = mean square error; R^2 = coefficient of determination; n.s. = not significant.

beech is much higher than that of oak, so that the beech might assure more shading and water storage above the ground and better access to all the different soil layers below the ground. In years with poor water supply, productivity is restricted by belowground resources rather than by light, leading to less competitive advantage for beech. However, the better the supply of water and nutrients, the higher the competition for light, which therefore dominates in years with ample resource supply (Maestre *et al.* 2009). As we did not measure the resource supply, resource uptake or resource-use efficiency, the considerations discussed remain speculative.

The common pattern of the relationships identified in the interaction index models for spruce–beech when studying temporal variation is in accordance with the results of Pretzsch *et al.* (2010), when comparing productivity in pure and mixed stands along a spatial ecological gradient. They found that over-yielding was common on poor sites, where facilitation by beech offset nutrient limitations in spruce (Augusto *et al.* 2002), whereas on rich sites over-yielding was less frequent and appeared to be related to a reduction in the severe intra-specific competition that is common in pure beech stands (Pretzsch & Biber 2005).

Since the data used in this study do not satisfy strict *ceteris paribus* conditions, it is not possible to study the net effect of mixing on radial growth. However, two of the spruce–beech sites (FRE_813 and SON_814) belong to an age series of pure and mixed stands, where a positive mixing net effect on mean tree size and on aboveground biomass was reported for both species (Pretzsch & Schütze 2009). At these two sites we identified temporal shifts between facilitation and competition. These temporal shifts seem to be associated with a trend towards a net facilitation effect, while a lack of shifts (similar interannual variation in mixed and pure stands) may reflect a neutral or positive competition effect (similar or higher competition in mixed than in pure stands). It could be speculated that poor sites are created *inter alia* by a high frequency of unfavourable years, and that the abovementioned long-term effect of mixing on growth should be even more visible in unfavourable years, when the benefit of mixture in terms of growth should be most pronounced.

Extension of the stress gradient hypothesis

The stress gradient hypothesis (SGH) predicts that net competitive effects will be more important under benign environmental conditions, whereas facilitation will dominate under harsher conditions (Bertness & Callaway 1994). The SGH has been extended in recent years to predict different responses depending on the life history of the interacting species, the type of stress factor (driven or not driven by resource limitations; Michalet *et al.* 2006; Maestre *et al.* 2009; Holmgren & Scheffer 2010), as well as plant ontogeny (Soliveres *et al.* 2010). However, it is not yet possible to generalise this conceptual model due to a lack of empirical evidence. Our results highlight the fact that temporal scale is an important factor when analysing plant interactions along stress gradients (Michalet 2007; Sthultz *et al.* 2007). The general trend revealed from the results agrees with the SGH: facilitation in high-stress years and competition in benign years, although the observed differences among species, mixtures and sites confirm the need to consider these factors in the conceptual model.

Temporal shifts in plant interactions in the context of SGH have previously been addressed in a number of studies, mainly in relation to herbaceous plants and shrubs and in short to medium temporal windows (Sthultz *et al.* 2007; Soliveres *et al.* 2010). Our study, however, considers a longer time span and examines long-lived plants in the mature stage, where inter-specific interactions have an important effect on tree growth (Oliver & Larson 1996). The importance of annual climatic conditions on tree species interactions was previously reported (Callaway 1998), comparing the growth of *Abies lasiocarpa* trees before and after the death of *Pinus albicaulis* neighbours, although only 2 years were analysed. More recently, Wong (2012) extended this study to cover a larger time span and also highlighted the importance of a long-term approach when analysing tree interactions under different stress gradients. In this regard, our study also confirms the usefulness of an annual secondary growth series (Soliveres *et al.* 2010), which can be easily obtained from trees through non-destructive stem coring.

Concerning the use of a productivity gradient as a stress gradient, it is important to note that the variation in productivity from one site to another (expressed as site index) differed between species. The best site for one species is not necessarily the best for another, as revealed in our sample sites (Table 1). These differences in site productivity among species point to the existence of corresponding differences in species susceptibility to environmental stress, which is usually a consequence of multiple environmental factors operating simultaneously (Kawai & Tokeshi 2007). This allows us to define the stress gradient through a productivity gradient, instead of environmental stress gradients (Grime 1977; Lortie & Callaway 2006). This fact is well illustrated when comparing the patterns of the interaction index along the stress gradient using both a climate stress factor and an indicator of productivity (Fig. S2). By expressing the stress gradient using basal area growth indices in pure stands, the models explained more temporal variability of the interaction index than by using the climate variables most strongly correlated with growth indices (Table S1). However, these differences are expected to be higher in temperate ecosystems than in other types of ecosystem, such us boreal, Mediterranean or desert ecosystems, which are more influenced by one clear stress factor.

Implications for forest growth modelling

Forest growth models have frequently been used to study inter-specific interactions and their impact on stand growth (Porté & Bartelink 2002; Pretzsch 2002), and recently they have also been used to determine the role of abiotic stress in plant–plant interactions (Gómez-Aparicio *et al.* 2011; Kunstler *et al.* 2011). The temporal variability identified in between-species interactions has two important implications for growth modelling. First, it highlights the importance of the time span of data used to develop growth models. The temporal range of data used to build forest growth models can vary greatly, from short time spans (frequently covering a single growth period; *e.g.* Kunstler *et al.* 2011), to long time spans associated with long-term permanent plots (*e.g.* Pretzsch 2002). Growth models based on data from a single growth period may be influenced to a certain extent by the abiotic conditions present during the period assessed, resulting in misleading interpretations of the inter-specific interactions, which must be viewed from the perspective of a longer time scale. Second, it

underlines the need to consider the interplay between abiotic conditions and plant–plant interactions. The prevalent approach for including between-tree interactions in forest growth models is the use of competition factors or indices based on the distribution, size and abundance of neighbouring trees (*e.g.* Daniels *et al.* 1986; Biging & Dobbertin 1995; Canham *et al.* 2004). However, this competition factor is rarely modified to include climate conditions in order to take into account the shifts in inter-specific interactions along spatio-temporal environmental gradients (Gómez-Aparicio *et al.* 2011; Kunstler *et al.* 2011).

Implications for forest management adaptation to climate change

To define measures for adapting forest management to climate change it is first necessary to assess the vulnerability of forests to this change, and the possible impacts in the medium to long term (Spittlehouse & Stewart 2003). Most of the studies concerning impacts of climate change on forest growth that are based on empirical data focus on mono-species stands, with few considering mixed stands (*e.g.* Linares *et al.* 2011). Fewer still have attempted to compare tree response to climate in pure and mixed stands (Pretzsch *et al.* 2012). Our results reveal that inter-annual growth variability in a given species can vary between pure and mixed stands, suggesting that the influence of climate conditions on tree growth is modulated by species interactions. Moreover, the different behaviour found in the two studied mixtures, as well as that associated with site characteristics, highlights the importance of considering these factors when evaluating forest vulnerability to climate change in terms of tree growth.

The differences in variability in the growth index between pure and mixed stands suggests that mixing might improve forest resilience, buffering the effect of inter-annual climate variation through shifts between competition in good years and facilitation in high stress years. As the frequency of years with harsh climate conditions is expected to increase with climate change, the effect of mixing on growth should become even more visible in the future. Consequently, the promotion of mixed stands could contribute significantly towards reducing the impact of climate change on forest growth, besides the other potential benefits of mixed stands (Griess & Knoke 2011).

CONCLUSIONS

Our results evidenced the presence of significant temporal shifts between competition and facilitation in mixed forests of beech–oak and beech–spruce in Central Europe. In high-growth years there was an increase in between-species competition in mixed stands, while in low-growth years inter-specific interactions tended towards facilitation or/and complementarity, resulting in lower growth reduction than in the respective pure stands. These shifts agree with the general pattern predicted in the 'stress gradient hypothesis', but using a temporal stress gradient instead a spatial one. This fact highlights the importance of considering temporal variation when analysing plant interactions. Seemingly contradictory reports on over-yielding or under-yielding of mixed species *versus* pure stands may go back to differences in the temporally or locally

prevailing environmental conditions, and become consistent when they are considered. Although temporal variations have been previously confirmed in other studies, we explored a longer temporal window necessary for studying long-lived plants, with our target being tree species.

The results of our study have direct implications for forest growth modelling and for adapting forest management to climate change. Climate envelopes used as guidelines for species cultivation under climate change may be misleading if they are based on species performance in pure stands. Where facilitation becomes particularly relevant under harsh conditions, species mixing may foster species occurrence beyond conventional climate envelopes. Given the buffer effect of tree mixing on temporal variability of growth indices compared to mono-species stands, the promotion of mixed stands in forest management can improve forest resilience in terms of growth in the face of climate change. On the other hand, forest growth models may be based on long-term data, which would adequately represent the temporal variability in environmental conditions and may consider the influence of this variability on inter-specific interactions in order to correctly predict the effect of these interactions on tree growth. Models that are presently applied for all kinds of stand are mainly parameterised with pure stand data; however, shifts between competition and facilitation described here demonstrated extremely relevant emerging properties of mixed stands and need to be integrated into future models.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Correlations between basal area growth indices and seasonal and annual climate variables (only significant correlations).

Figure S1. Example of the detrending of basal area growth series.

Figure S2. Relationships between the interaction index (II) and the stress gradient for spruce and beech in FRE_813, expressing the stress gradient with the summer temperature (a), and the mean basal area growth indices in pure stands (IBAIp) (b).

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