

## RESEARCH PAPER

# Resistance of European tree species to drought stress in mixed *versus* pure forests: evidence of stress release by inter-specific facilitation

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**Keywords**

Anisohydric species; drought resilience; hydraulic lift; isohydric species; overyielding; recovery; underyielding.

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**ABSTRACT**

While previous studies focused on tree growth in pure stands, we reveal that tree resistance and resilience to drought stress can be modified distinctly through species mixing. Our study is based on tree ring measurement on cores from increment boring of 559 trees of Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* [L.]) and sessile oak (*Quercus petraea* (Matt.) Liebl.) in South Germany, with half sampled in pure, respectively, mixed stands. Indices for resistance, recovery and resilience were applied for quantifying the tree growth reaction on the episodic drought stress in 1976 and 2003. The following general reaction patterns were found. (i) In pure stands, spruce has the lowest resistance, but the quickest recovery; oak and beech were more resistant, but recover was much slower and they are less resilient. (ii) In mixture, spruce and oak perform as in pure stands, but beech was significantly more resistant and resilient than in monoculture. (iii) Especially when mixed with oak, beech is facilitated. We hypothesise that the revealed water stress release of beech emerges in mixture because of the asynchronous stress reaction pattern of beech and oak and a facilitation of beech by hydraulic lift of water by oak. This facilitation of beech in mixture with oak means a contribution to the frequently reported overyield of beech in mixed *versus* pure stands. We discuss the far-reaching implications that these differences in stress response under intra- and inter-specific environments have for forest ecosystem dynamics and management under climate change.

**INTRODUCTION**

Drought events coupled with water or nutrient limitation and low-growth episodes of trees are widely held to increase when the climate changes (IPCC 2007). Drought stress is considered as highly relevant for forest ecosystem dynamics (Rennenberg *et al.* 2004, 2006; Bréda *et al.* 2006) as it can modify tree allometry (Pretzsch *et al.* 2012a), reduce tree and stand growth (Hartmann 2010; Pretzsch & Dieler 2011) or even cause trees or stands to die off (McDowell *et al.* 2008; Allen *et al.* 2009; Griess & Knoke 2011). Resistance, recovery and resilience of trees to drought stress in terms of growth performance depends, among other factors, on species (Zang *et al.* 2011), competitive status of the tree within the stand (Zang *et al.* 2012), age and size (Lloret *et al.* 2011) and site conditions (Pretzsch & Dieler 2011). How mixing of species modifies tree growth under drought stress compared with their performance in a monospecific environment is still unresolved (Pretzsch *et al.* 2010, 2012b; Richards *et al.* 2010), although it is essential for understanding, forecasting and management of mixed species stands.

Studies of Kelty (1992), Pretzsch (2012) and Richards *et al.* (2010) provide evidence that species mixing frequently improves resource supply, resource uptake, resource use efficiency and, as a result, also tree and stand growth. The main

cause is considered to be niche complementarity, which can reduce the competition for resources in mixed *versus* pure stands (Morin *et al.* 2011). For example, in homogenous pure stands of the rather shallow rooting Norway spruce, roots and water uptake concentrate in the upper soil layers. In mixture with the deeper rooting European beech, competition is less severe as the two species differ in their strategies of space occupation (Wiedemann 1942). A second cause for advantages of species mixing is that two plants, or two populations of plants, can interact in such a way that one exerts a positive effect and facilitates the other (Vandermeer 1989). Examples of facilitation are the phenomena of atmospheric N fixation (Kelty 1992), or hydraulic lift (Dawson 1993) by one species with a benefit of N to water supply of the other. The benefit of species mixing is widely held to be more pronounced on nutrient-poor and dry sites than on rich sites (Pretzsch 2012). The stress-gradient hypothesis predicts that facilitation prevails on poor sites, while on rich sites competition prevails (Callaway & Walker 1997). The above findings on the kind and extent of intra- and inter-specific interactions and their dependency on site conditions are mostly based on the 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, which improve mixed

versus pure stand performance, especially on poor sites, in the long term can be assumed to also be effective and relevant for plant and stand performance in the short term, e.g. in dry years. For example, available water might be better stored and used in mixed stands due to a more water receptive humus layer and more extensive root system when shallow and deep rooters are combined. One might argue 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, as in such years the benefit of mixture in terms of growth gain should be most pronounced.

In order to improve knowledge of growth reactions of European tree species to drought stress in mixed versus pure stands, we will address the following questions:

- 1 Do Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* [L.]) and sessile oak (*Quercus petraea* (Matt.) Liebl.) in pure stands differ in their resistance, resilience, or recovery to episodic drought stress?
- 2 Is the resistance, resilience or recovery after episodic drought stress of these three species in mixed stands different from their performance in pure stands?
- 3 Does the resistance, resilience or recovery of a species in mixed stands depend on the admixed species?

Our study objects were mature trees in even-aged and mono-layer pure and mixed stands in temperate forests. The chosen species are relevant for forest ecology and management and make up about two-thirds of forest cover in Central Europe.

## MATERIAL AND METHODS

For comparing the performance of trees with intra- and inter-specific environment under episodic drought stress, we apply indices for resistance, recovery and resilience ( $R_t$ ,  $R_c$  and  $R_s$ , respectively) introduced and explained in detail in

Lloret *et al.* (2011). The three indices were calculated individually on the basis of the annual basal area increment ( $\text{cm}^2\cdot\text{year}^{-1}$ ) for 559 sample trees. Basic components of all three indices are the following annual or periodic mean values of the basal area increment:

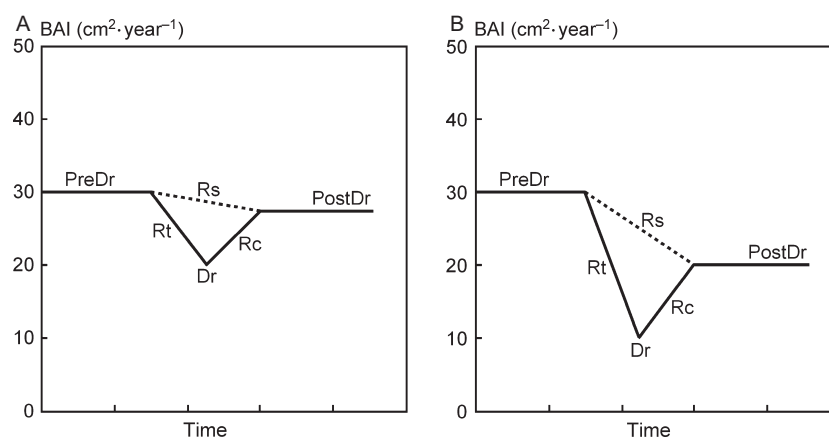
PreDr is the mean basal area increment in a period of the  $n_{\text{PreDr}}$  years before the drought period;

Dr is the mean basal area increment in a period of  $n_{\text{Dr}}$  years during the drought period; and

PostDr is the mean basal area increment in a period of  $n_{\text{PostDr}}$  years after the drought period.

The resistance,  $R_t = \text{Dr}/\text{PreDr}$ , quantifies the decrease from the pre-drought period to the drought period;  $R_t = 1$  is complete resistance; the further the value falls below  $R_t = 1$ , the lower the resistance. Recovery,  $R_c = \text{PostDr}/\text{Dr}$ , describes the growth reaction after the drought period.  $R_c = 1$  indicates persistence of a low growth level even after the drought period;  $R_c < 1$  indicates a further decline, and  $R_c > 1$  indicates recovery from the level reached during the drought period. Resilience,  $R_s = \text{PostDr}/\text{PreDr}$ , represents the ratio between post-drought and pre-drought increment;  $R_s \geq 1$  indicates full recovery or even an increase after the episodic stress, while  $R_s < 1$  indicates growth decline and low resilience.

In order to clarify the indices  $R_t$ ,  $R_c$  and  $R_s$ , Fig. 1 shows the courses of basal area growth for a tree (A) with a moderate reaction to episodic stress, and (B) with a strong growth reduction after stress and the corresponding stress indices. In the caption of Fig. 1, we show how to calculate  $R_t$ ,  $R_c$  and  $R_s$  for the two stress response patterns (A) and (B). For more details on the indices and their ecological foundation, see Lloret *et al.* (2011). The identification of the three indices with the slopes  $R_t$ ,  $R_c$  and  $R_s$ , as in Lloret *et al.* (2011: 3; Fig. 1A) is misleading. For example, the slope  $R_t$  in terms of the slope of a straight line would yield  $R_t = (\text{Dr} - \text{PreDr})/(2 - 1) \neq \text{Dr}/\text{PreDr}$ . Therefore, in the following we avoid the term 'slope' when we



**Fig. 1.** Course of growth in two different stress events characterised by growth in the period before drought (PreDr) growth in the drought period (Dr) and growth after the drought period (PostDr) (modified after Lloret *et al.* 2011). Indices for resistance,  $R_t = \text{Dr}/\text{PreDr}$ , recovery,  $R_c = \text{PostDr}/\text{Dr}$ , and resilience,  $R_s = \text{PostDr}/\text{PreDr}$ , are used to characterize the stress response patterns. (A) Tree with low growth decrease by drought (PreDr = 30, Dr = 20, PostDr = 27.5; unit of BAI is  $\text{cm}^2\cdot\text{year}^{-1}$ ) indicated by high resistance,  $R_t = \text{Dr}/\text{PreDr} = 20/30 = 0.67$ , and resilience,  $R_s = \text{PostDr}/\text{PreDr} = 27.5/30 = 0.92$ , and medium recovery,  $R_c = \text{PostDr}/\text{Dr} = 27.5/20 = 1.38$ . (B) Tree with strong growth decline (PreDr = 30, Dr = 10, PostDr = 20; unit of BAI is  $\text{cm}^2\cdot\text{year}^{-1}$ ) indicated by low resistance,  $R_t = \text{Dr}/\text{PreDr} = 10/30 = 0.33$ , considerable recovery  $R_c = \text{PostDr}/\text{Dr} = 20/10 = 2.00$ , which results in a medium resilience,  $R_s = \text{PostDr}/\text{PreDr} = 20/30 = 0.67$ . In the graphs  $R_t$ ,  $R_c$  and  $R_s$  are represented by the gradient of decline from PostDr to Dr, the increase from Dr to PostDr, and the difference in level of PreDr and PostDr, respectively.

interpret and discuss the indices. Note for the later discussion that  $R_s = R_t \times R_c$ .

For analysing the drought response in 1976, we used the mean annual basal increment in the 3 years before the drought period, the basal area increment in the dry year, and the mean annual basal increment in the 3 years after the drought period ( $n_{PreDr} = 3$ ,  $n_{Dr} = 1$ ,  $n_{PostDr} = 3$ ). The year 2003 was similarly analysed. The 1-year length of the drought period ( $n_{Dr} = 1$ ) is justified as both 1976 and 2003 were extremely dry, but shortly before and after these years the water supply was much better. For the reference periods before and after the dry years, we finally used a 3-year length ( $n_{PreDr} = 3$ ,  $n_{PostDr} = 3$ ); however, evaluations on the basis of periods with a length of 3, 4, 5 and 6 years yielded equivalent results.

All included trees belong to late-successional species, whose slow ontogenetic drift produces a rather broad saddle in the basal area increment curve (Kramer 1988). As we choose rather mature trees, aged 59–123 years (Table 1), both drought periods 1976 and 2003 lie on the broad saddle of the unimodal growth curve (Fig. 4). Within this middle-aged phase the growth course is fairly parallel to the abscissa, and elimination of any age trend (transformation by detrending and indexing of the growth rates) is unnecessary. An additional justification for using absolute and untransformed data was that the analysed periods comprise just 7 years, which is sufficiently short to avoid effects of long-term age trends. In order to stay as close as possible to the original data and to imply as few model assumptions as necessary, we performed the analysis on the basis of the untransformed annual basal area records.

#### Study area, sites and forest stands

We took our samples along an ecological gradient through South Germany, reaching from nutrient-poor and dry sites to nutrient-rich and moist sites. An additional criterion for the selection of sample areas was the availability of pure and mixed stands of the species with similar age, site conditions, stand density and equal silvicultural treatment in close proximity. For the species combinations spruce/beech and oak/beech we finally found four suitable sample areas each, where the species are present in pure and mixed stands. The sample

areas include the long-term experiments Nordhalben (NOR 811), Arnstein (ARN 851), Freising (FRE 813) and Schongau (SON 814) in spruce and beech, and Rothenbuch (ROT 801), Rimpfing (RIM 102), Kelheim (KEH 804) and Illertissen (ILL 38) in oak and beech (Fig. 2 from north to south). All eight long-term experiments are series of mixed stands of spruce/beech and oak/beech. Most of these experiments were already subjects of other studies described elsewhere (see e.g. Pretzsch 2009; Pretzsch *et al.* 2010). In close proximity to these existing mixed stand plots, we sampled trees in pure stands for the comparison between tree performance in mixed *versus* pure stands.

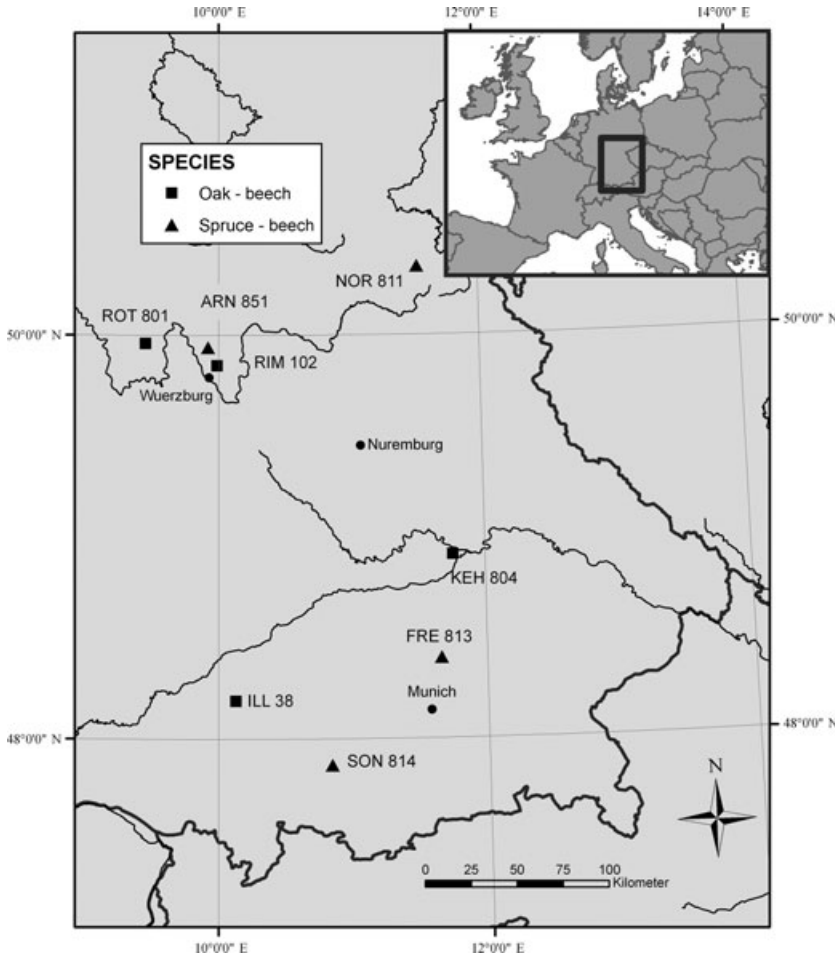
The eight experimental areas are spread from north to south Bavaria, and cover the following six eco-regions (from north to south): eco-regions '2 red sandstone Spessart', '4 Franconian limestone', '6 Franconian Alp and Upper Palatinate Jurassic', '8 granite region of Franconian Forest', '12 Tertiary prealpine lowlands', '14 Swabian-Bavarian young moraine and molasse prealpine lowlands'. The sample sites lie between 9°26'–11°48' E and 47°52'–50°20' N, at 290–785 m a.s.l. The geology of the basic soil material is granite, sandstone in the north, limestone, Jurassic and chalkstone material in the centre, and tertiary, moraine and molasses material in the south of the study region. Soils vary between brown soil and parabraun soil. The substrate is mainly loam and silt, and the water conditions range from dry to moist. The mean annual precipitation ranges from 660 to 1114 mm, with 330–648 mm in the vegetation period. The mean annual temperature is 5.5–8.5, and 12.5–16.5 °C in the vegetation period (mean values for 1951–1980). The sites lie within the natural distribution area of oak and beech. Spruce would occur naturally only in the most northeastern part (Czech–German border mountains) and southern part (prealpine mountains) of the region, but not in the lowlands between (see Fig. 2).

The climate diagram for the long-term mean from 1951 to 1980 in northern Bavaria (Fig. 3A) show the unimodal annual course, with peak temperature and precipitation in summer, characteristic for the Central European temperate climate. The course of temperature and precipitation in 1976 and 2003 shows periods with above average temperatures and below average precipitation during the vegetation period

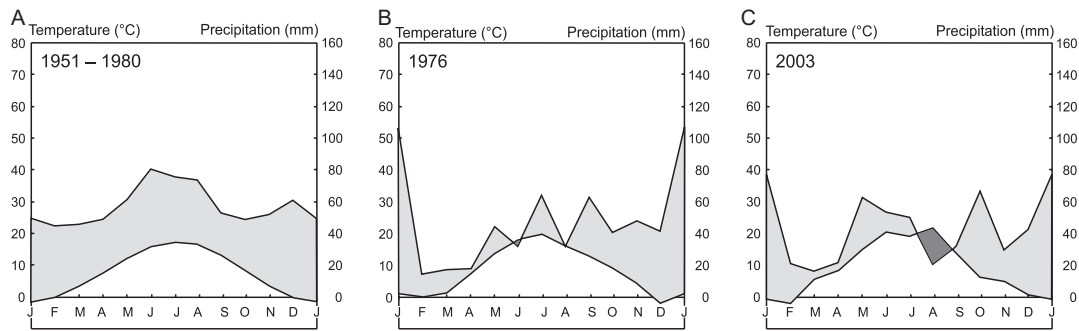
**Table 1.** Characteristics of the 559 sample trees, of the stands in which they grow, and of the site conditions (means and SD). The sample comprises Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* [L.]) and sessile oak (*Quercus petraea* (Matt.) Liebl.).

species	composition	n	age (years)		dbh (cm)		BA (m <sup>2</sup> ·ha <sup>-1</sup> )		site index (m)	
			mean	SD	mean	SD	mean	SD	mean	SD
Norway spruce/European beech										
Norway spruce	Pure	73	59	6	31.1	3.7	59.7	15.4	36.5	1.5
Norway spruce	Mixed	70	59	6	35.6	5.0	42.8	12.9	37.5	1.5
European beech	Pure	79	70	9	32.3	5.0	37.7	12.0	36.6	1.3
European beech	Mixed	79	70	9	31.3	1.0	43.4	12.5	36.5	2.2
sessile oak/European beech										
sessile oak	Pure	67	123	17	41.9	5.6	42.4	13.8	28.0	3.1
sessile oak	Mixed	62	123	17	42.5	8.8	37.7	9.5	28.1	2.9
European beech	Pure	65	111	20	49.0	1.2	37.6	13.1	31.0	3.2
European beech	Mixed	64	111	20	42.7	10.4	35.0	9.8	30.6	4.1

n, sample size; age, stand age in years; DBH, diameter at breast height in cm; BA, stand basal area in m<sup>2</sup>·ha<sup>-1</sup>; site index, site fertility quantified by mean tree height in m at stand age 100 years.



**Fig. 2.** Location of the eight sampling areas for trees in pure and mixed forest stands. Trees in pure and mixed stands of Norway spruce and European beech (black triangles) were sampled in NOR 811, ARN 851, FRE 813 and SON 814. Trees in pure and mixed stands of European beech and sessile oak (black squares) were sampled in ROT 801, RIM 102, KEH 804 and ILL 38 (from north to south).



**Fig. 3.** Climate diagrams for the long-term mean temperature and precipitation in northern Bavaria in 1951–1980 (A), for the drought year 1976 (B), and the drought year 2003 (C).

(Fig. 3B and C). This long-term climate diagram for 1951–1980 and for the years 1976 and 2003 is based on datasets from 16 climate stations in northern Bavaria (Amberg, Bamberg, Hof, Kahl, Kissingen, Kronach, Nürnberg, Oberviechtach, Regensburg, Reimlingen, Rothenburg T., Schlüsselfeld, Teuschnitz, Weiden, Weissenburg, Würzburg). Analogous evaluations for six stations in southern Bavaria (not shown) gave similar patterns, with slightly higher precipitation and lower temperature (not shown).

The summer heat and drought in 1976 and 2003 were the most severe in Europe’s recent climate history. The tempera-

tures from May to August were 5–6 °C above the long-term mean, and precipitation from February to April and in summer from July to September were 50% below the normal level. In 1976, the drought started in spring and continued to late summer (Fig. 3B). In 2003, it also started in spring and became more severe in late summer (see arid phase in August), but eased temporarily, with a rather moist period from May to June. Schär *et al.* (2004) discuss such extreme conditions as typical for future climate conditions, with both higher mean temperature and higher variability of temperature.

For characterising average water supply of the sampled stands we calculated the index  $Ma$  of Martonne de (1926) on the basis of the annual precipitation ( $Pa$  in mm) and mean annual temperature ( $Ta$  in °C),  $Ma = Pa/(Ta + 10)$ . We used the recordings in the 30-year period 1971–2000 in order to obtain stable mean values. The monthly long-term average temperature and precipitation values for the forest sites were taken from the climate raster maps of South Germany, with a spatial resolution of 50 m × 50 m (LfU 2012). The index  $Ma$  ranged between 31.1 mm·°C<sup>-1</sup> in the rather dry and warm north (experimental plot RIM 102) and 62.8 mm·°C<sup>-1</sup> in the moist and cool south (experimental plot SON 814) of South Germany.  $Ma$  values of the sites in the centre of Bavaria lie in between ( $Ma = 37.7$ – $56.5$  mm·°C<sup>-1</sup>).

The drought events of 1976 and 2003 have in common that in both years the temperature, precipitation, and consequently the  $Ma$  value, was reduced to 60–70% of the long-term mean. However, the drought events of 1976 and 2003 differ to the conditions in the 3 years before and after (PreDr, PostDr): in the 3 years before and after 1976 the  $Ma$  was rather similar to the long-term mean, *i.e.* the drought of 1976 was a short and abrupt event; in contrast, in the years before 2003 the  $Ma$  values were 10% above the long-term mean and in the 3 years after 2003 the  $Ma$  it was still only 90% of the mean, *i.e.* the initial conditions before the drought event of 2003 were better than 1976, but the drought stress lasted longer.

#### Sampling procedure and field measurements

Fieldwork took place in autumn 2010 and spring 2011. When we sampled trees of species A in pure stands, we included only trees with all six nearest neighbours belonging to the same species. When we sampled trees of species A in mixed stands (of species A and B), we included only trees where at least 50% of the six nearest neighbours belong to species B. As the trees in pure and mixed stands of each sample area served for comparison in terms of growth response to drought, we always started with the existing mixed stands in the long-term experiments and chose pure stands of the respective species of similar age, site index, soil conditions and a distance of <1 km from the mixed stand in order to keep the climate conditions comparable. The setup of eight sample areas, two species combinations, sampling in pure and mixed stands, and about 20 sample trees per stand resulted in a total of 559 sample trees (Table 1). In each stand, we selected about 20 dominant trees at a distance of >20 m from each other in order to guarantee that they were independent of each other.

All sampled trees had live crown ratios of nearly 50%, thus representing typical trees in the upper canopy of the stands. Diameter at breast height (DBH) was measured in mm using a girth tape. Tree height ( $h$ ) and height of the crown base ( $h_{cb}$ ; base of the lowest crown primary branch) were measured ( $h$  and  $h_{cb}$  in 1/10 m) using the Vertex III ultrasonic hypsometer (Haglöf, Sweden).

We built upon standard techniques of increment measurement using increment boring (Pretzsch 2009). One increment core was taken at breast height on each sample tree stem in N and E direction in order to obtain medium representative increment records. Due to the main wind direction from

SW, this is also the direction with the widest diameter of the oval stem cross-section. Boring from N and E is at 45° to this maximum diameter and yields more representative tree ring widths. Cores were taken back to the pith in order to ensure a radial boring direction and enable counting of the ring number to estimate tree age (tree age  $\cong$  number of tree rings at height 1.10 m + 5 years). The increment cores were taken with the borer MORA CORETAX (Haglöf).

For assessing neighbourhood conditions of every sample tree, we applied the angle count method of Bitterlich (1952), which delivers the basal area through a Spiegel relascope application. The resulting stand basal area (m<sup>2</sup>·ha<sup>-1</sup>) in the tree vicinity is widely used as an indicator of tree competitive status (Pretzsch 2009: 298). For a detailed description of this method, routinely applied in forest ecology, see Prodan (1951) and Avery & Burkhardt (1975).

Around our trees the stand basal area varies between 35.0 and 59.7 m<sup>2</sup>·ha<sup>-1</sup> (Table 1), reflecting medium to high stand densities. Note that in Central European stands, which are similarly middle-aged to ours, a stand basal area of 25 m<sup>2</sup>·ha<sup>-1</sup> reflects a rather low density and competition, while 100 m<sup>2</sup>·ha<sup>-1</sup> represents maximum density. Site index in terms of mean tree height (m) at age 100 years was assessed using standard methods (Pretzsch 2009: 433–434) with the yield tables of Assmann & Franz (1965) for Norway spruce, Schober (1975) for European beech and Jüttner (1955) for sessile oak. Tree and stand characteristics, such as tree diameter, height, crown cross-section area, stand basal area and site index, represent potential covariates for the scrutiny of any differences between stress response patterns of trees in mixed *versus* pure stands.

#### Sample and data preparation

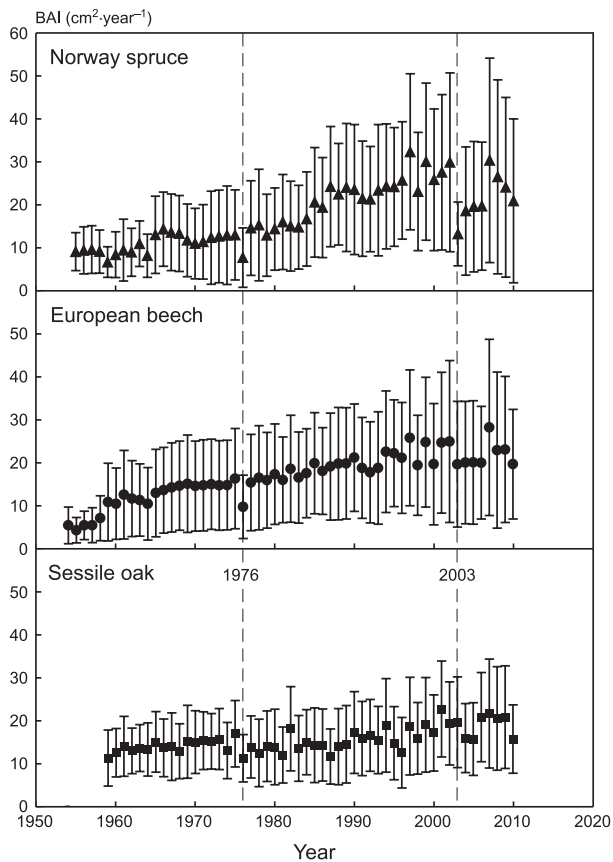
The increment cores were glued on wooden slides, ground and polished on a sanding machine using paper with 120 grit, cleaned with compressed air and analysed to the nearest 1/100 mm using a digital positioning table (Kutschenreiter and Johann; Digitalpositionimeter, Biritz and Hatzl GmbH, Austria). For cross-dating and synchronisation, the extremely narrow rings in 1976 and 2003 were most helpful. The radial increments ( $ir$ ) of the two cores of a tree ( $ir_1$ ,  $ir_2$ ) were added to obtain a representative time series of aboveground diameter increment ( $id$ ) for each tree ( $id = ir_1 + ir_2$ ). The basal area increment in year  $n$ ,  $n-1$  ...  $n-k$ , on which the subsequent evaluation was based, resulted from the diameter series as follows:

$$BAI_n = (d_n^2 \times \pi)/4 - (d_{n-1}^2 \times \pi)/4 = (d_n^2 - d_{n-1}^2) \times \pi/4,$$

$$BAI_{n-1} = (d_{n-1}^2 - d_{n-2}^2) \times \pi/4,$$

and analogously for all years in retrospect.

In total, we sampled 559 trees; 284 in pure stands of spruce, beech and oak, and 275 in mixed stands (Table 1). The range of diameters and tree ages confirms that we sampled only rather mature trees. The range of stand basal areas between  $BA = 35.0$ – $59.7$  m<sup>2</sup>·ha<sup>-1</sup> indicates medium to high stand density, and the site index between  $SI = 28.1$ – $37.5$  m mean height at age 100 years indicates medium site quality. The mean Martonne index was  $Ma = 49.6$  mm·°C<sup>-1</sup> on sites stocked with spruce and beech and  $Ma = 42.5$  mm·°C<sup>-1</sup> for oak and beech.



**Fig. 4.** Course of the annual basal area increment of Norway spruce ( $n = 143$ ), European beech ( $n = 287$ ) and sessile oak ( $n = 129$ ) in pure and mixed stands in South Germany from the mid-1950s to 2010. From each of the  $n = 559$  trees we sampled two cores in order to obtain a reliable basal area increment per tree. Mean and SD display a strong growth reduction in the drought years 1976 and 2003 for spruce and beech, while oak reacts less distinctly.

#### Data analysis

Basis for scrutiny of questions (1)–(3) is the 559 measures of the annual basal area growth in pure and mixed stands from the mid-1950s to 2010. The mean measures ( $\pm$ SD) for all trees sampled in pure and mixed stands (Fig. 4) show the stress reaction during and after the drought years 1976 and 2003, which are the focus of the following analysis. The statistical analysis further uses tree, stand and environmental attributes as covariates (Table 1).

Question (1) asks whether the three species differ in  $R_t$ ,  $R_c$  and  $R_s$  in pure stands. For that purpose we fitted a generalised linear mixed model (GLMM) with a random effect for controlling any site effects and a Wald test for *post-hoc* analysis of differences between marginal means. The respective dataset comprised the indices  $R_t$ ,  $R_c$  and  $R_s$  derived from the 284 increment cores sampled in pure stands (73 for spruce, 144 for beech, 67 for oak) for the drought periods 1976 and 2003. The species groups were dummy-coded with Norway spruce as the reference group. Covariates (quantitative predictors) were tree diameter, basal area, tree age, site index and Martonne aridity index. We kept only those covariates in

the analyses that contributed to the model with  $P$ -values  $< 0.10$ . Dashes in the output (Tables S1–S3A, see Supporting Information) indicate omitted covariates with  $P \geq 0.10$ . We used the Akaike information criterion (AIC) as fitting criterion and report AIC values for both the full model (including all covariates) and the actual model (including only covariates with  $P < 0.10$ ; see bottom of Tables S1–S3). As no transformations of the dependent variables were necessary for ensuring normal distribution and variance heterogeneity, the model parameters (Tables S1–S3) directly reflect the effect of the dummy variables and covariates on the stress response variables  $R_t$ ,  $R_c$  and  $R_s$ . The marginal means adjusted by the covariates represent the group means (and SE) of  $R_t$ ,  $R_c$  and  $R_s$ , and partly show significant differences. In the Tables S1–S3, significant variables and covariates ( $P < 0.05$ ) are printed in bold. Significant differences between cell means ( $P < 0.05$ ) are marked with arrows between the respective groups (Tables S1–S3B).

Question (2) was scrutinized analogously with GLMM. However, in this case we analysed species-by-species whether the indices  $R_t$ ,  $R_c$  and  $R_s$  in 1976 and 2003 differed in mixed *versus* pure stands. This analysis was based on 284 trees in pure stands and 275 trees in mixed stands. We applied a dummy coding, with pure stands as the reference group.

Based on the same statistical method, question (3) addressed which species show differences in the stress response ( $R_t$ ,  $R_c$  and  $R_s$ ) between mixed and pure stands and whether their reaction patterns also depend on the admixed species. As beech differed in its response in mixed and pure stands, we asked whether the performance of beech in mixture with spruce ( $n = 79$ ) differed from its performance in mixture with oak ( $n = 64$ ). In this case, the mixture was dummy-coded using beech/spruce as reference.

All preconditions of the covariance analyses were given: with the  $\chi^2$  test we guaranteed that the independent variables  $R_t$ ,  $R_c$  and  $R_s$  are normally distributed within and above all treatment groups (grouping variables were species spruce, beech, oak; mixed, pure; mixture beech/oak, beech/spruce). Using the Bartlett test, we assured that variance homogeneity is given between the groups. The latter precondition was rather uncritical, as the sample size was equal and relatively high in all groups. As the sample trees were selected randomly in the pure as well as in the mixed forest stands, we could assume that the error components within and between the samples are independent from each other. The preliminary tests showed that a transformation of the dependent variables was not necessary, *i.e.* the resulting cell means and standard errors (Tables S1–S3) needed no re-transformation, but could be directly understood in terms of their relevance and ecological significance.

The fact that  $R_s = R_t \times R_c$  (as  $R_t = Dr/PreDr$ ,  $R_c = PostDr/Dr$  and  $R_s = PostDr/PreDr$ ) underlines that the three parameters are redundant, and we can concentrate on discussion of resistance and resilience without omitting any information (Lloret *et al.* 2011). The slight differences in the cell means (see Tables S1–S3B) between the evaluation of the inter-specific reactions in monocultures, addressed in question (1), and the intra-specific differences between pure and mixed stands, addressed in questions (2) and (3), result from the different set and slightly different effects of the covariates that were included in the respective models.

All statistical evaluations were carried out with PASW Statistics, Version 18.0 (SPSS Inc., New York, NY, USA).

## RESULTS

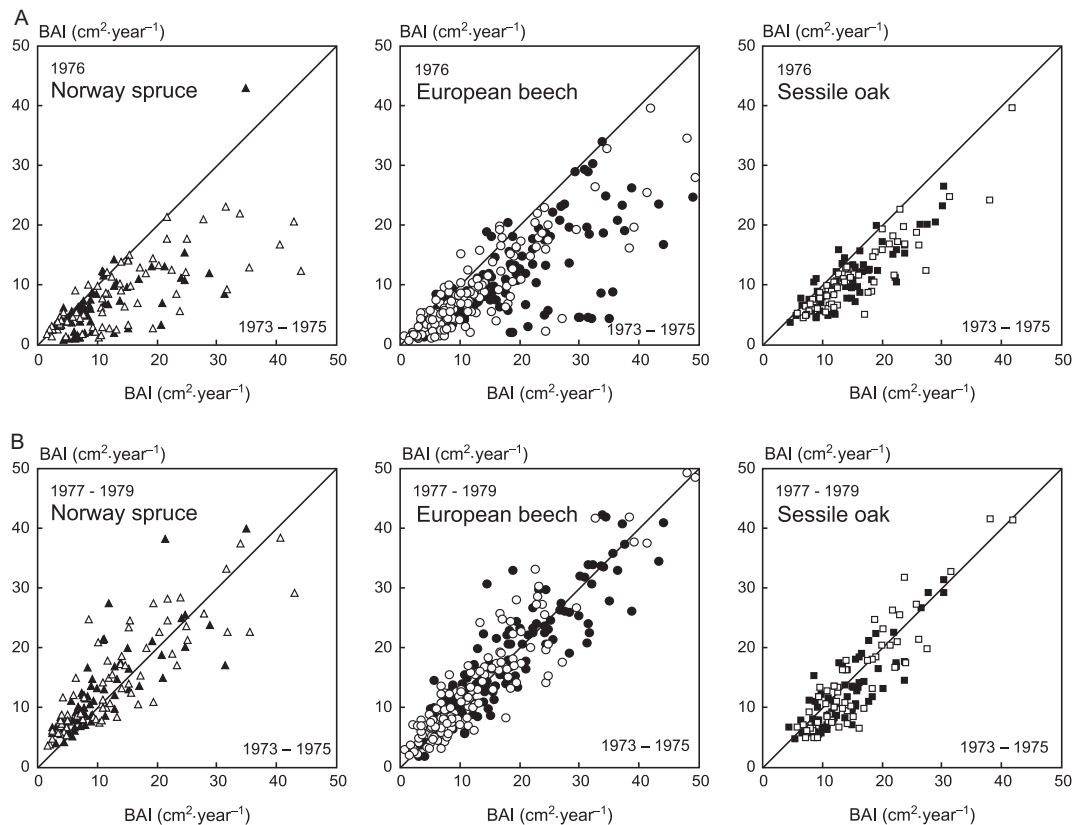
For a first overview of the stress reactions of the trees, we consider their resistance and resilience in 1976. In 2003 the stress reactions were similar in their basic patterns but less incisive. In Fig. 5A the annual basal area growth in 1976 is plotted over the mean growth in the respective reference period 1973–1975. The filled symbols represent trees in pure stands, unfilled symbols are trees in mixed stands. Suppose the drought did not affect the trees, the points would lie on or close to the bisector line and indicate perfect resistance. In the scattergrams for spruce, beech and oak most of the points lie below the bisector line, indicating drought-induced growth reductions, which are very distinct for spruce and beech and less obvious for oak. Figure 5B shows how the same trees overcome drought stress. The mean growth in the period after the drought of 1977–1979 was plotted over the mean growth in the reference period 1973–1975. Observations close to the bisector line indicate perfect resilience, symbols below the line indicate continuous growth reduction during the drought period, and symbols above the bisector line suggest that growth after the drought exceeded the level observed before the drought period. Any visually detected differences in Fig. 6 between spruce (triangles), beech (cir-

cles) and oak (squares) and between trees in mixed stands (unfilled symbols) and pure stands (filled symbols) are subsequently scrutinized more thoroughly using statistical analyses (Tables S1–S3).

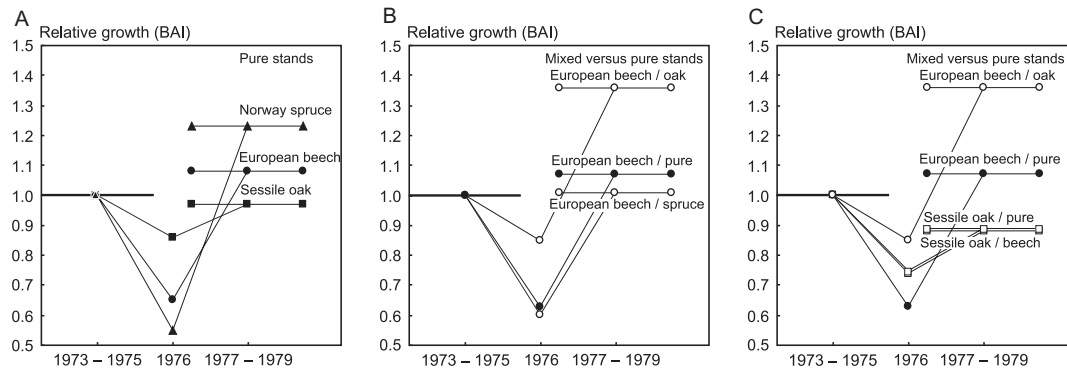
Using 1976 and 2003 for this analysis, we assumed that these years represent single and independent drought events, *i.e.* we assumed that, because of the 27 years in between, the drought in 1976 had no pronounced after-effect on the stress reaction in 2003. In case of significant exhaustion or strengthening triggered by 1976 and affecting growth in 2003, there should be a distinct negative or positive correlation between the indices in the 2 years. However, Pearson correlation between the values  $R_t$ ,  $R_c$  and  $R_s$  in 1976 and 2003 yielded rather inconsistent results. In the case of Norway spruce the correlation was sometimes slightly negative. For European beech and sessile oak we found slightly positive correlations for  $R_t$ , slightly negative correlations for  $R_c$ , and no correlations for all for  $R_s$ . Due to this inconsistent pattern and the 27-year period in between the 2 years we subsequently consider these years as single and independent drought events.

### Species-specific differences in $R_t$ , $R_c$ or $R_s$

The covariance analyses showed clear species-specific differences in  $R_t$ ,  $R_c$  and  $R_s$  in 1976 and 2003 (Table S1A). In all cases the species effect on  $R_t$ ,  $R_c$  and  $R_s$  was significant. The better the water supply, as indicated by the Martonne index



**Fig. 5.** Resistance (A) and resilience (B) of Norway spruce, European beech and sessile oak in graphical representation for the year of drought stress 1976. (A) Relationship between annual growth (BAI in  $\text{cm}^2\cdot\text{year}^{-1}$ ) in 1976 and in the 3-year reference period before 1976. (B) Relationship between annual growth in the 3-year period after 1976 (BAI in  $\text{cm}^2\cdot\text{year}^{-1}$ ) and growth in the 3-year reference period before the drought stress year 1976. The filled symbols represent individuals in pure stands, the unfilled symbols are individuals in mixed stands.



**Fig. 6.** Species-specific stress reactions caused by the drought year 1976 shown in relation to mean growth level in the 3-year period 1973–1975 before the drought stress (reference line = 1.0). (A) Norway spruce, European beech and sessile oak in pure stands. (B) European beech in pure and mixed stands. (C) European beech and sessile oak in pure and mixed stands. The courses represent growth in the dry year 1976, and in the recovery period (period mean of 1977–1979) in relationship to growth in the reference period (period mean of 1973–1975).

( $M_a$ ), the higher the resistance and resilience and the lower the recovery effect. Other covariates did not show consistent effects on the stress indices in 1976 and 2003.

The cell means for the resistance of spruce, beech and oak in 1976 ( $R_t = 0.55$ ,  $0.65$  and  $0.86$ , respectively) reflect that the drought reduced growth to 55%, 65% and 86% of the preceding reference period (Table S1B). The drought in 2003 caused a growth reduction of 38%, 15% and 4% in pure stands of spruce, beech and oak ( $R_t = 0.62$ ,  $0.85$  and  $0.96$ , respectively). The cell means of  $R_c$  reflect that spruce recovered more rapidly from the drought stress. In the period after the drought year 1976, growth achieved was 307% ( $R_c = 3.07$ ) and after 2003 140% ( $R_c = 1.40$ ) of that in the low growth years. Compared to this rather rapid recovery of spruce, the beech and oak recovered much slower or even stay at the level of  $R_c < 1$ . The cell means of  $R_s$  revealed that after 1976, the growth level was rather similar to that before the stress event ( $R_s = 1.23$ ,  $1.08$  and  $0.97$ , respectively). After 2003, spruce and beech needed a little longer to recover; however, 3 years after the drought stress the growth level was again similar to the level before the stress ( $R_s = 0.78$ ,  $0.80$  and  $0.96$ , respectively).

#### Differences in $R_t$ , $R_c$ or $R_s$ between mixed and pure stands

Scrutiny of  $R_t$ ,  $R_c$  and  $R_s$  in mixed *versus* pure stands revealed no differences for spruce and oak but significant stress release through mixture in case of beech. Table S2A shows the results for beech, where covariance analyses revealed clear advantages in mixed *versus* pure stands. Except for the index  $M_a$ , all other included covariates showed no general pattern in their effect on  $R_t$ ,  $R_c$  and  $R_s$ . The finding that  $M_a$  had a positive effect on  $R_t$  and  $R_s$ , but a negative influence on  $R_c$ , underlines that the better the water supply, the higher was the growth level during the drought period, and capacity of the tree to come undamaged out of the drought period.

Comparison of the adjusted cell means for beech in 1976 showed that in pure stands growth was reduced to 63% ( $R_t = 0.63$ ) of the reference period, but only 72% ( $R_t = 0.72$ ) in mixture (Table S2B). Cell means for resilience showed that in both mixed and pure stands growth was higher after the

drought period of 1976 than before ( $R_s = 1.17$  and  $R_s = 1.07$ , respectively). However in mixture beech emerged from the stress period about 10% better than beech in monoculture ( $R_s = 1.17$  in mixed stands,  $R_s = 1.07$  in monoculture). Analogous comparison for 2003 showed much better recovery and resilience of beech in mixed *versus* pure stands.

#### Dependence of $R_t$ , $R_c$ or $R_s$ in mixture from the admixed species

After the above revelation that beech significantly benefits from species mixing, we scrutinized whether the beech benefit depends on the kind of species with which it is admixed. Covariance analyses showed that with respect to drought stress release, admixture with oak was much more beneficial for beech than admixture with spruce (Table S3A). Comparison of adjusted cell means underlined that  $R_t$  and  $R_s$  values in 1976 and 2003 were significantly higher when beech was mixed with oak rather than spruce (Table S3B). In the drought year 1976, growth of beech was reduced to 60% ( $R_t = 0.60$ ) when mixed with spruce, but 85% ( $R_t = 0.85$ ) when mixed with oak. The beneficial effect of mixing for beech in terms of resistance was even more obvious in 2003, with  $R_t = 0.74$  in mixture with spruce *versus*  $R_t = 1.03$  in mixture with oak. Resilience of beech was also significantly higher in mixed compared with pure stands (Table S3B).

#### Generic stress response patterns

Figure 6A summarizes the species-specific reaction patterns in pure stands for 1976. In 2003 the species-specific stress reactions were similar in their basic patterns but less pronounced. In comparison to beech and oak, the growth of spruce was less drought resistant and fell most distinctly from 1973–1975 to 1976. However, the deeper the drop in growth of a species, the stronger its recovery from 1976 to 1977–1979. The ranking of the species growth level after the drought period (oak < beech < spruce) is opposite to the ranking within the drought period (spruce < beech < oak; Fig. 6A). This reversed ranking of the species performance within and after the drought period means that the species temporal reaction pattern in pure stands is much more pronounced to



species overall growth reduction by drought. Scrutiny of any differences between the species performance in mixed *versus* pure stands revealed characteristic differences only for beech (Fig. 6B). Figure 6C highlights the remarkable finding that drought stress in beech is released through mixture with oak. However, oak performed equally in mixed and pure stands.

## DISCUSSION

The basal area increment (BAI) at breast height is used as an indicator for tree stress response, as any growth decline measured at breast height clearly indicates stress events and losses of aboveground productivity. But equating losses of BAI with total tree growth would probably overemphasise the stress response, as trees can reduce their diameter growth in the lower stem parts, where increment cores are normally taken, while they hardly reduce their growth in the upper stem parts and the crown. Both in dry years and on xeric sites trees reduce or even interrupt their growth primarily in the lower parts of the stem close to breast height (Kramer 1988) and may favour root growth at the expense of shoot growth (Comeau & Kimmins 1989; Pretzsch *et al.* 2012a). Suppose species differ in their allocation pattern under stress, then the comparability of their stress reactions based on BAI would be questionable.

Stress response patterns may change with tree age and tree size (Carrer & Urbinati 2004; Rozas 2005; Rossi *et al.* 2008). Basal area increment seems to be more sensitive to limiting climatic conditions, including extreme drought events, in older and taller trees (Candel-Pérez *et al.* 2012); however, changes in the response patterns with ontogeny are reported to be species-specific (Rozas *et al.* 2009; Linares & Tiscar 2010). In our samples all three species, beech, spruce and oak, were in a rather mature development phase (Table 1, Fig. 4). It is not surprising that the covariance analyses (Tables S1–S3) showed no consistent effect of age or size on the stress response variables, as our sample covered only rather mature trees and a limited range of tree size. The reaction patterns for younger trees in terms of  $R_t$ ,  $R_c$  and  $R_s$  might be less distinct, as in our sample stands.

The revealed stress response patterns are well substantiated because of the far-reaching study area, the large number of sampled trees and the extensive additional measurements of the sampled tree and stand attributes, such as tree size, competitive status and stand density (see Table 1). However, additional physiological or hydrological measurements at the individual tree level in pure and mixed stands were not possible in this study. Therefore our causal explanations for the species-specific and mixing-specific stress response patterns remain speculative.

The growth reactions indicated by  $R_t$ ,  $R_c$  and  $R_s$  immediately during or after the stress events in 1976 and 2003 can be understood as primary physiological stress responses. In particular, for pure conifer stands it is well known that primary disturbance by drought can pave the way for secondary damage by insects, fungi or windthrow (Griess & Knoke 2011). Mixing can mitigate the susceptibility to such secondary stress effects (Jactel & Brockerhoff 2007). That means that on top of any positive effects of mixing on stress release and growth of trees, the reported avoidance or mitigation of secondary stress effects by species mixing can further improve

the performance of mixed compared with pure stands (Scherer-Lorenzen *et al.* 2005).

Notice that both 1976 and 2003 represent two single drought events with an interval of 27 years between them. We assume that due to the long period between the two events, the second stress reaction is not affected by the previous intervals, as prognosticated in climate change scenarios (IPCC 2007), the performance of the species in pure and mixed stands is probably lower compared with single stress events. This tendency is reflected to some extent by the stress reaction pattern of 2003 compared with 1976. The year 1976 represents a short and abrupt drought, the growth decrease was abrupt, and the upward trend started immediately after 1976. In 2003 the severity of the drought was similar to that of 1976, but on top of that the following years were drier than average. This does not change the ranking between the species and the differences between mixed and pure stands, but it explains why the recovery and resilience in 2003 is generally somewhat lower than in 1976 (Tables S1–S3B).

### Species-specific stress reaction patterns in pure stands

The study revealed clear species-specific differences among trees when coping with drought stress in pure stands: spruce falls back but also recovers quickly, oak is most resistant but recovers most slowly, and the beech reaction pattern lies in between (Fig. 6A). The different species-specific reactions in pure stands can be explained from the isohydric character and low drought resistance of spruce, the more anisohydric behaviour of beech, and the strongly anisohydric character and high drought resistance of oak (Zang *et al.* 2011, 2012). Isohydric species reduce water consumption and growth already in the early phase of drought stress through stomata closure. Using such a preventive strategy might leave resources to neighbouring other species. But especially in short drought periods, they can avoid stress damage (losses of leaves and fine roots) and therefore recover very quickly and forage for accumulated nutrients unexploited during the survived drought period (Hartmann 2010). Anisohydric species such as beech and oak behave differently: they keep on transpiring and growing despite drought stress until the water runs out. Therefore they slump less in growth, but risk morphological changes or losses of fine roots and leaves due to previous cavitation of water conducting pipes due to drought stress. The latter means a slower recovery after the drought stress, as growth can only be accelerated again after cavitation of xylem tissue and organ losses are overcome (Leuschner 1998). The leaves shed by anisohydric species may provide isohydric species with additional nutrients when both species occur closely associated in mixed stands.

The response patterns in Fig. 6A reveal that the more a species growth is reduced during the drought period, the more it regrows after the drought. Following Körner (2002), we hypothesise that low growth in short drought periods (as in 1976 and 2003) is mainly induced by scarce nutrient supply due to reduced decomposition and mineralisation, which are both dependent on moisture. The lower the consumption of nutrients during the low-growth period, the better is the supply in the years thereafter. Both 1976 and 2003 represent two single drought events with a rather short duration but

high intensity of water stress. Therefore partial hydraulic failure (predicted for high intensities of water stress) rather than carbon starvation (predicted for long duration of water stress) may have contributed to the temporary growth decline (McDowell *et al.* 2008).

An additional reason for the remarkable change in the ranking concerning  $R_t$  and  $R_s$  (Fig. 5A) might be that in the low-growth periods, the less drought resistant species such as spruce and beech overweight biomass allocation into roots in order to improve access to water and nutrients. However, after the episodic stress, allocation might overweight above-ground growth to rebalance the allometric proportions between root and shoot biomass (McCarthy & Enquist 2007). Following the latter explanation, the species-specific stem growth reaction under drought stress would rather reflect the species-specific morphological root–shoot plasticity than the whole tree performance (Pretzsch *et al.* 2012a).

#### Modification of the stress reaction by inter-specific environment

For species mixtures growing under different degrees of chronic stress (*e.g.* located along ecological gradients), the stress-gradient hypothesis (SGH) predicts that facilitation occurs more on poor sites, while competition is more likely on rich sites (Callaway & Walker 1997). Recent findings that overyielding of mixed *versus* pure forest stands of spruce, beech and oak occurs mostly on poor sites, while neural mixing effects or even underyielding prevails on rich sites is in accordance with this hypothesis (Holmgren *et al.* 1997; Pretzsch 2012). Our results suggest that facilitation is not only triggered by permanently harsh environments, but can also emerge under episodic stress. Facilitation and competition always occur simultaneously (Vandermeer 1989), and the net effect in terms of over- or underyielding in relation to the species performance in pure stands reveals whether facilitation or competition prevails. Our findings that in drought periods, growth of beech in mixture with oak can be superior to its growth in pure stands indicate that under stress, facilitation prevails. The fact that not all mixtures behaved like this is in line with the more differentiated view on the SGH considering different species, abiotic and biotic factors (Holmgren & Scheffer 2010).

The finding that beech profits from the mixture but not at the expense of oak suggests a one-sided facilitation of beech by oak (Fig. 6C). A tempting explanation for the stress release of beech in mixture with oak might be an improvement of humus quality, which increases water storage, nutrient supply and, through this, the water use efficiency (Augusto *et al.* 2002; Binkley *et al.* 2004; Richards *et al.* 2010). However, such an improvement of site quality should benefit both species. Our findings that mainly beech profits from the mixture without causing any adverse effects to the other species, call this explanation into question. The stress release might also result from the mixed species complementary traits of coping with drought stress. Let us suppose species A is an isohydric species and mixed with an anisohydric species B. Species A already reduces water consumption in the early phase of drought stress through stomata closure, while species B keeps on transpiring and growing despite drought stress. Then in mixture the reduction of water consumption of species A can mean a benefit for species B. Notice

that in our mixed stands spruce plays the role of A (isohydric) and beech and oak the role of B (anisohydric). Following this argumentation, when mixed with spruce, beech should considerably benefit in stress resistance, but it does not. Furthermore, when the stress is over, the isohydric species recovers quicker than the anisohydric neighbour species, which can become an advantage for species A. Following this argument, spruce should recover quicker in mixed *versus* pure stands, but our observations do not reflect such behaviour. We conclude that an explanation simply through the complementarity of the species traits and niches is not sufficient.

That the beech release from drought stress was only observed in mixture with oak suggests that the deep-rooting oak facilitates the much more shallow-rooting beech through hydraulic lift of water. Caldwell *et al.* (1998) list *Quercus* among other genera that exhibit hydraulic lift in the field, and they stress that all deep-rooting plants with low resistance to water loss from roots might provide this facilitative feature. According to Dawson (1993), hydraulic lift is the passive movement of water from deep, moist soil layers through the root system upwards. Under extremely dry conditions, the water potential in upper soil layers is lower than in the root system, and the roots lose water to the soil. Shallower-rooting species like beech or spruce can benefit from this increase in soil moisture both directly, as their water supply increases, and indirectly, as nutrient availability increases with soil moisture. Körner (2002) stresses that the indirect effect of water surplus *via* nutrient availability on plant growth may be much more relevant as the direct effect. Oak not only increases resistance of beech during the drought years, but also causes a stronger recovery and resilience. So the level of beech growth in mixture with oak is higher in the years after compared with before the stress. The causes for that higher resilience in mixture with beech may be a better maintenance of the root system during the drought period compared to pure stands, where beech tends to suffer organ losses (Rennenberg *et al.* 2004). In addition, there might be a better availability of nutrients in mixture due to more continuous mineralization in both dry and moist years compared with the nutrient availability blocked by drought in the pure stands.

#### Relevance of successive drought events for over- and underyielding of mixed *versus* pure stands

Recent studies show that mixed spruce/beech forests (Pretzsch *et al.* 2010; Griess & Knoke 2011) and oak/beech forests (Pretzsch 2012) mostly out-yield pure stands of the same species by about 20%. Supposed reasons for the superior performance of mixed stands are competition reduction because of niche complementary (Kelty 1992) and facilitation of one species by the other (Vandermeer 1989; Holmgren *et al.* 1997). Our finding that beech copes better with drought stress when mixed with oak and that this advantage is not at the expense of oak suggests that stress release might contribute to the above stated overyielding of mixed *versus* pure stands. The following rough estimate shows that under the present frequency of drought events, this contribution is rather low, but it can increase when episodic drought stress increases, as prognosticated under climate change (IPCC 2007). Suppose a tree's long-term basal area growth under normal conditions amounts to

20 cm<sup>2</sup>·year<sup>-1</sup> (100%). If a drought episode occurs every 20 years and reduces growth in pure stands to 10 cm<sup>2</sup>·year<sup>-1</sup> (50%), this results in a reduction to  $(19 \times 20 + 1 \times 10) / (20 \times 20) = 97.5\%$  in the long term. A growth reduction in the mixture to only 15 cm<sup>2</sup>·year<sup>-1</sup> (75%) results in  $(19 \times 20 + 1 \times 15) / (20 \times 20) = 98.75\%$ . This means, in the long run, the benefit would only be 1.25%. However, when a similar drought stress occurs every 5 years, the same analysis would yield  $(4 \times 20 + 1 \times 15) / (5 \times 20) = 90\%$  for the pure and  $(4 \times 20 + 1 \times 15) / (5 \times 20) = 95\%$  for the mixed stand. This is equivalent to 5% plus of mixed *versus* pure stands due to better stress management. So, while under the present conditions the plus from stress effects is evident but not too relevant in terms of long-term productivity gains of mixed *versus* pure stands, it may become more relevant when stress frequency or the length of the stress periods increases.

### Implications for forest ecosystem dynamics and management

Presently, environmental policy and multifunctional forest practice frequently revive mixed species stands of spruce, beech or oak, as they fulfil forest functions and services such as productivity (Morin *et al.* 2011; Pretzsch *et al.* 2012b; Zhang *et al.* 2012b), environmental protection (Hector & Bagchi 2007; Griseb & Knoke 2011) and habitat conservation (Hector & Bagchi 2007; Jactel & Brockerhoff 2007) better than monocultures. In many cases beech is involved in the revival of close-to-nature stands, as without human interference beech would cover more than two-thirds of the Central European forest area. Humans, however, reduced beech mainly through clearing for agricultural land and replacement with faster and straighter growing species such as spruce or pine. Presently, beech covers 70 million ha, which is only 20% of its natural range, and the future role of beech in view of climate change is still open for debate (Zang *et al.* 2011, 2012). While Rennenberg *et al.* (2004) assume severe growth decline of beech under chronic or episodic stress, and even question the survival of beech under climate change in Central Europe, Ammer *et al.* (2005) and Bolte *et al.* (2009) credit beech with much more resilience and acclimation to drought stress. These and other works on the behaviour of beech under water stress within (Gärtner *et al.* 2008) or close to the border (Fotelli *et al.* 2008) of its natural range so far are based exclusively on observations or model scenarios for beech in pure stands. Our results underline that the performance of species in mixed stands can be significantly different from their behaviour in pure stands. However, mixed stands, especially mixed stands including beech, gain more and more importance.

Artificial pure spruce stands cultivated far beyond the species' natural range in the lowlands of Central Europe are presently being transformed to mixed stands of spruce and beech on a large scale. Retrospective analyses show that in the long term, mixed stands of spruce and beech produce on average 20% more biomass per unit area than monocultures of these two species (Pretzsch *et al.* 2010; Pretzsch 2012). But it is still questionable as to how stable this or other favoured mixtures will behave under stress events, which are projected to increase due to climate change. Our results show that the reactions of both species under drought stress are rather asynchronous, but are very similar in mixed and pure stands (Fig. 5). In terms of growth under drought stress, we should

not expect an overyielding of mixed *versus* pure stands. Although our findings are that neither spruce nor beech reduces growth in mixture in relation to pure stands. Obviously, over a broad range of site condition, both species can be mixed without severe destabilisation of their inter-specific competition and growth performance under drought stress.

In parts of the Central European beech region, oak and beech would occur in mixture. But beech is fit enough to dominate in most parts of the region and to out-compete oak except in dry sites, very moist sites and sites with extremely low temperatures in winter and spring (Leuschner 1998). Mixed stands of oak and beech naturally occur on sites where the combination either of drought and warmth or moistness and coldness restrict the competitiveness of beech to such an extent that oak can successfully compete with beech. The presently balanced competitiveness between oak and beech will react very sensitively to climate changes and may probably turn in favour of oak when temperature rises and precipitation becomes scarce in summer but ample in autumn and winter. Our finding that growth of beech in mixture with oak decreases less than under intra-specific conditions improves its competitive strength. Compared with oak, beech falls back less in size growth in dry years, and thus gains a better starting position than the admixed species in the competitive game after the drought phase. This stress release by mixing is an important emergent property that has been hardly considered so far. It means that the realized niche of beech in mixed stands may be wider than in pure stands. Species-specific climate envelopes, as long as they are based on pure stand conditions (Kölling & Zimmermann 2007), are of limited relevance when taking into account that a species growth and distribution is facilitated by mixture.

Of special ecological and silvicultural interest is that sessile oak combines a considerable resistance and resilience to episodic drought stress, a remarkable consistency in its low stress reaction in pure and mixed stands, and a facilitative effect on neighbouring beech without any disadvantages to its own performance. While oak's superior resistance and resilience to drought has been repeatedly reported (Bréda *et al.* 2006; Zang *et al.* 2011, 2012), its invariant and facilitative behaviour in mixed stands provide additional arguments for a preferential choice of this species as a stabilising component of ecosystems under climate change.

### Perspectives

As in many other parts of the world, wood-oriented forest practice in Europe has transformed most natural mixed species forests into artificial pure stands, and forest science has focused on pattern and processes in intra-specific plant environments. Our study stresses that tree behaviour in the inter-specific environment of mixed stands can be considerably different from what we know from pure stands. The shown facilitation of beech by oak is just one example of system properties that emerge in mixture and can increase stress resilience and productivity under drought. This and other positive or negative interactions that may emerge in mixture require further causal analysis, as they are the prerequisite for a better understanding, modelling, prognosis, establishment and management of mixed species stands. While in the past the focus was on inter-specific competi-

tion, further research into mixture of species, which often co-evolved, should rather address intra- and inter-specific interactions, including competition and facilitation. Experiments can surely contribute to analysing inter-specific interactions. However, in mature stands experiments are difficult to realize, even more difficult to repeat and their results hardly general. On the other hand, if such experiments are established in young stands, their results are hardly transferable to mature stands. This dilemma can be overcome by studies such as ours in mature forests under extreme events and along ecological gradients. Such *in situ* approaches utilise that in harsh environments or under episodic stress, trees disclose essential aspects of their interactions most obviously and can reveal system knowledge useful for better risk prevention.

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## SUPPORTING INFORMATION

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

**Table S1.** Covariance analysis results of the differences between Norway spruce, European beech and sessile oak regarding resistance (Rt), recovery (Rc) and resilience (Rs) in drought periods 1976 and 2003 in pure stands.

**Table S2.** Covariance analysis results of the differences in the stress reaction pattern (Rt, Rc, Rs) in the drought periods 1976 and 2003 for European beech in mixed versus pure stands.

**Table S3.** Covariance analysis results of the differences in the stress reaction pattern (Rt, Rc, Rs) in the drought periods 1976 and 2003 of beech in mixture with oak versus beech in mixture with spruce.

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