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Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought

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Abstract Climate extremes are expected to increase in frequency and magnitude as a consequence of global warming, threatening the functioning, services and goods of forest ecosystems. Across Europe, the ecologically and economically important tree species *Fagus sylvatica* is expected to suffer particularly under such conditions. The regional introduction of provenances from drier and warmer climates is one option to adapt beech forest ecosystems to these adverse effects of climate change. Marginal populations from the drought-prone southern and north-eastern edges of the species' distribution come into focus in search of suitable candidates for Central European deciduous forests. Here, we test three marginal provenances (Spain, Bulgaria and Poland) and three provenances from the centre of the distribution range (Germany) for their response to drought in two different soil types (sand, loam) in a full factorial common garden experiment in Landau, Germany. Drought impacted all growth parameters negatively (leaf damage +22 % (percentage points), height −40 % and diameter increment −41 %), and the sandy substrate exacerbated this effect. However, provenances differed in their response to drought and soil type. Evidence for a local adaptation to summer drought was detected, especially in terms of mortality rates. The Bulgarian and Spanish provenance showed a stable performance under drought conditions (BG −27 % in diameter increment; ES −32 %), compared to the Polish (−48 %) or the most sensitive German provenances (−57 %), yet for Bulgaria on a low level of total increment. This may indicate a trade-off between drought tolerance and growth. Therefore, a sole focus on drought-resistant marginal provenances seems to not be conducive, as they might be less adapted to other climatic factors, e.g. frost, as well. However, intermixed with local Central European provenances, these may act as functional insurance in future drought-prone forest stands.

Keywords Extreme events · Local adaptation · Phenotypic plasticity · Plant–climate interactions · Provenance trial · Within-species diversity

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Introduction

Alongside an increase in average temperature, global warming is expected to trigger an increase in magnitude and frequency of climatic extremes such as prolonged drought events (IPCC 2012). This will especially affect the functioning of ecosystems with long-living organisms, such as forests, and may lead to a declining provision of forest goods and services (Allen et al. 2010; Lindner et al. 2010). The velocity of these changes in ecosystem functioning may exceed the natural dispersal rates of trees and the speed of evolutionary adaptation processes (Bertrand et al. 2011; Chen et al. 2011).

Fagus sylvatica is a naturally dominant and economically important, but drought-susceptible tree species in Central Europe that deserves special attention in the face of these changing conditions (Fotelli et al. 2009). Even though *F. sylvatica* is considered a high-risk species in the face of climate change (Ohlemuller et al. 2006; Scherrer et al. 2011), the area stocked with *F. sylvatica* constantly increases in Central Europe/Germany due to forest conversion from coniferous to mixed stands. According to Polley et al. (2009), beech is the species in Germany with the highest increase in stocked area between 2002 and 2007 (83,000 ha). Drought events most probably determine the southern edge of the distribution range (Jump et al. 2006). In particular at lower elevations, growth and distribution of *F. sylvatica* are expected to decline at its southern limits (Matyas et al. 2009; Hlasny et al. 2011; Jezik et al. 2011) and on xeric sites in Central Europe (Czucz et al. 2011). The observed recent decline in beech forest productivity in France could be linked to low water availability, especially in early summer (Lebourgeois et al. 2005; Charru et al. 2010). Furthermore, Piovesan et al. (2008) showed that basal area increment of European beech stands decreased with decreasing water availability in the Apennine Mountains in Italy. The exceptional 2003 drought period over Central Europe generated distinct negative effects on the performance of *F. sylvatica* (Czajkowski et al. 2005; Leuzinger et al. 2005; Betsch et al. 2011). Moreover, it seems that *F. sylvatica* loses its competitive advantage to less drought-sensitive species, e.g. *Quercus petraea*, under water-limited conditions in southern and south-eastern part of its distribution range (Bonn 2000; Fotelli et al. 2001; Friedrichs et al. 2009; Clark et al. 2011; Scharnweber et al. 2011), whereas positive impacts of climate change on competition may prevail on the northern distribution edge in Sweden (Bolte et al. 2010). Drought periods also increase pathogen and fungi susceptibilities of *F. sylvatica*, as shown by Jung (2009) for the post-2003 years in a Bavarian beech stand. Therefore, Rennenberg et al. (2004) and Gessler et al. (2007) consider the focus on *F. sylvatica* in the ongoing forest conversion as very risky.

However, *F. sylvatica*, with its wide geographic distribution, covers a broad range of climatic conditions (see Kölling 2007). The introduction of *F. sylvatica* provenances from warmer, more drought-prone regions, especially from the edges of its distribution range to Central Europe might therefore be one potential adaptation tool to dampen the adverse effects of future climatic environments (Bolte et al. 2009; Kreyling et al. 2011). The genetic composition of forest trees determines the phenotypic plasticity and with this their adaptive capacity to environmental stressors such as drought (Schaberg et al. 2008; Matyas et al. 2009). In Central Europe, *F. sylvatica* exhibits a high genetic diversity within populations

(Konnert 1995; Vornam et al. 2004), whereas on a continental scale, the genetic differentiation between populations becomes more distinct (Comps et al. 1990; Magri et al. 2006). These differences in genetic configuration between populations, most likely, display differences in adaptive capacity between provenances. In numerous provenance trials over the last decade, a contrasting performance of provenances from different geographic origins has been demonstrated (e.g. von Wuehlisch et al. 1995). Furthermore, it was shown that different provenances exhibit specific responses to abiotic stressors such as late frosts (Kreyling et al. 2012) or drought (Schraml and Rennenberg 2000; Peuke et al. 2006). In a European-wide provenance trial network, macroclimatic adaptation could be detected: the performance of different provenances was negatively correlated with climatic distance (absolute differences in certain climatic parameters) between test site and origin of the provenance (Matyas et al. 2009). Czajkowski and Bolte (2006) found a significantly higher transpiration and therefore higher water stress under drought conditions for German and West Polish provenances than for provenances from the more continental Central Polish eastern distribution edge of *F. sylvatica*. In the extraordinary dry year 2003, NW-Greek beech populations only experienced mild drought stress compared to the reported damages in beech forests in Central Europe, despite comparable climatic conditions (Fotelli et al. 2009), thereby indicating a local adaptation of Greek populations to water shortages. Therefore, such marginal populations from the dry edges of the current distribution range of *F. sylvatica* may come into focus in search of drought-resistant ecotypes (Rose et al. 2009; Kreyling et al. 2011) The susceptibility to climatic stressors such as drought, however, strongly depends on the interaction with additional biotic or abiotic factors (Messaoud and Chen 2011). The impact of drought and water stress on the performance of *F. sylvatica* depends on air ozone concentration (Pollastrini et al. 2010), carbon dioxide concentrations (Penuelas et al. 2008), light availability (Czajkowski et al. 2005; Lof et al. 2005) and soil chemistry (Weitner et al. 2007). Evidence suggests that, in general, drought reduces nutrient availability and uptake in forest soils (Rennenberg et al. 2009; Kreuzwieser and Gessler 2010). The interactive effects of soil nutrient balance and water availability on fine roots, microorganisms and soil nutrient cycling processes are poorly understood (Kreuzwieser and Gessler 2010). However, especially for *F. sylvatica* which grows on various soil types throughout its distribution range (Ellenberg and Leuschner 2010), the occurrence of drought conditions or water stress is a complex interactive mechanism between climatic and edaphic factors (Gaertner et al. 2008).

Considering the reported negative impacts of drought on the performance of *F. sylvatica* and the intraspecific

variability in drought response, it is important to know whether certain provenances of *F. sylvatica* are less susceptible to these negative effects and whether site factors such as soil type influence specific responses. This knowledge is crucial to assess the potential of selective transplanting of drought-resistant provenances as a tool to dampen negative impacts of such climate extremes in the course of climate change.

Here, seedlings of six provenances of *F. sylvatica*, three from the centre of its distribution range and three from the margins (SE, SW, NE), were exposed to drought in two different soil types (with contrasting nutrient availability and field capacity) in a full factorial common garden experiment. We hypothesized that (1) provenances differ in the extent of leaf damage, height and diameter growth and (2a) drought and (2b) sandy soil substrate negatively influence these performance indicators. We further assumed that (3) marginal populations are less drought sensitive, and we expected (4) that soil conditions and drought interactions significantly affect plant performance.

Materials and methods

Experimental site

The provenance trial (EVENT 3-Landau) is a subproject of the EVENT-Experiment series in Bayreuth, Germany (Beierkuhnlein et al. 2011). It was established in 2010 in the vicinity of the University of Koblenz-Landau, at the Julius Kühn-Institut (JKI), Federal Research Centre for Cultivated Plants, Siebeldingen (49°13′03″N, 8°02′47″E, 202 a.s.l.). The mean annual temperature at the site is 10.2 °C, and the mean annual precipitation is 643 mm, which is distributed bimodally with two major peaks in May/June and November/December (data: German Weather Service). Annual average temperature is expected to increase by 3.7 K by the end of the century (2080uxs compared to 1950–2000), and precipitation is projected to decrease by about 50 mm per year, with a major decrease in summer (JJA) precipitation (−60 mm), according to the A1B scenario of the MPI-ECHAM5-model (data: WorldClim).

Plant material

Seeds of six provenances of *F. sylvatica* were obtained in autumn 2009 and brought to germination at the *Bavarian Institute for Forest Seeding and* Planting (ASP) in Teisendorf, Germany, in spring 2010. All six provenances stem from autochthonous populations (Fig. 1; Table 1). The provenances were chosen to represent the centre of the distribution range (DE1, DE2, DE3) and the south-eastern (BG) and south-western (ES) edges, where drought limits

the distribution of the species, and the north-eastern edge (PL), where besides summer precipitation winter conditions and late frost are important limiting factors (Table 1; Fig. 1). In January 2011, the seedlings were transported to Siebeldingen and in March 2011, and they were planted in 12-litre pots with two different soil types. Individuals were selected randomly for each provenance and treatment from all living plants at planting date. Mean plant height at the start of the experiment was 22.1 cm (±6.6 cm SD), mean plant diameter 2 cm above the root collar 4.7 mm (4.4–5.3 mm) with a standard deviation of ±0.8 mm SD (0.6–0.8 mm).

Experimental set-up

The potted individuals were exposed to a fully crossed experimental design consisting of a precipitation treatment (drought and control) and two different soil types (sandy loam, loamy sand). Each treatment combination (drought with sandy loam, drought with loamy sand, control with sandy loam and control with loamy sand) was replicated with nine individuals. For two provenances (Spain, Poland), the number of replicates had to be reduced to 8 and 7, respectively, due to mice damage, resulting in 204 plants overall. The experiment was set up completely randomized in a concrete bed filled with sand. All pots were put on plastic saucers.

On April 13, the experiment was covered by a rainout shelter constructed of a steel frame (GlasMetall Riemer GmbH, Rahden-Sielhorst, Germany) and covered with a transparent polyethylene sheet (0.2 mm, SPR 5; Hermann Meyer KG, Rellingen, Germany). The lower edge of the rainout shelter was 80 cm above ground. The shelter permitted the penetration of nearly 90 % of the photosynthetically active radiation. Additionally, as seedlings of *F. sylvatica* are sensitive to direct radiation, a shading canvas (Quadra 105ME, 105 g, DM-Folien GmbH, Reutlingen, Germany) was attached to the inside of the polyethylene sheet, resulting in a penetration of about 55 % of the photosynthetically active radiation. As the shade-tolerant species European beech has shown to yield highest growth rates when exposed to medium light levels (e.g. Schall et al. 2012) most likely no limitation by light availability occurred in our experiment. From the planting date until the rainout shelter was set up, the plants received the ambient precipitation and were additionally watered with groundwater (March 14, 18, April 1, 4 8 and 11). After the rainout shelter was set up, and the plants were watered with groundwater on April the 18, 28 and 30, so that a sufficient water supply and root growth was guaranteed. From May 2, all plants were exposed to the control precipitation regime which simulated the local daily 40-year average precipitation. The application was done twice a week with groundwater.
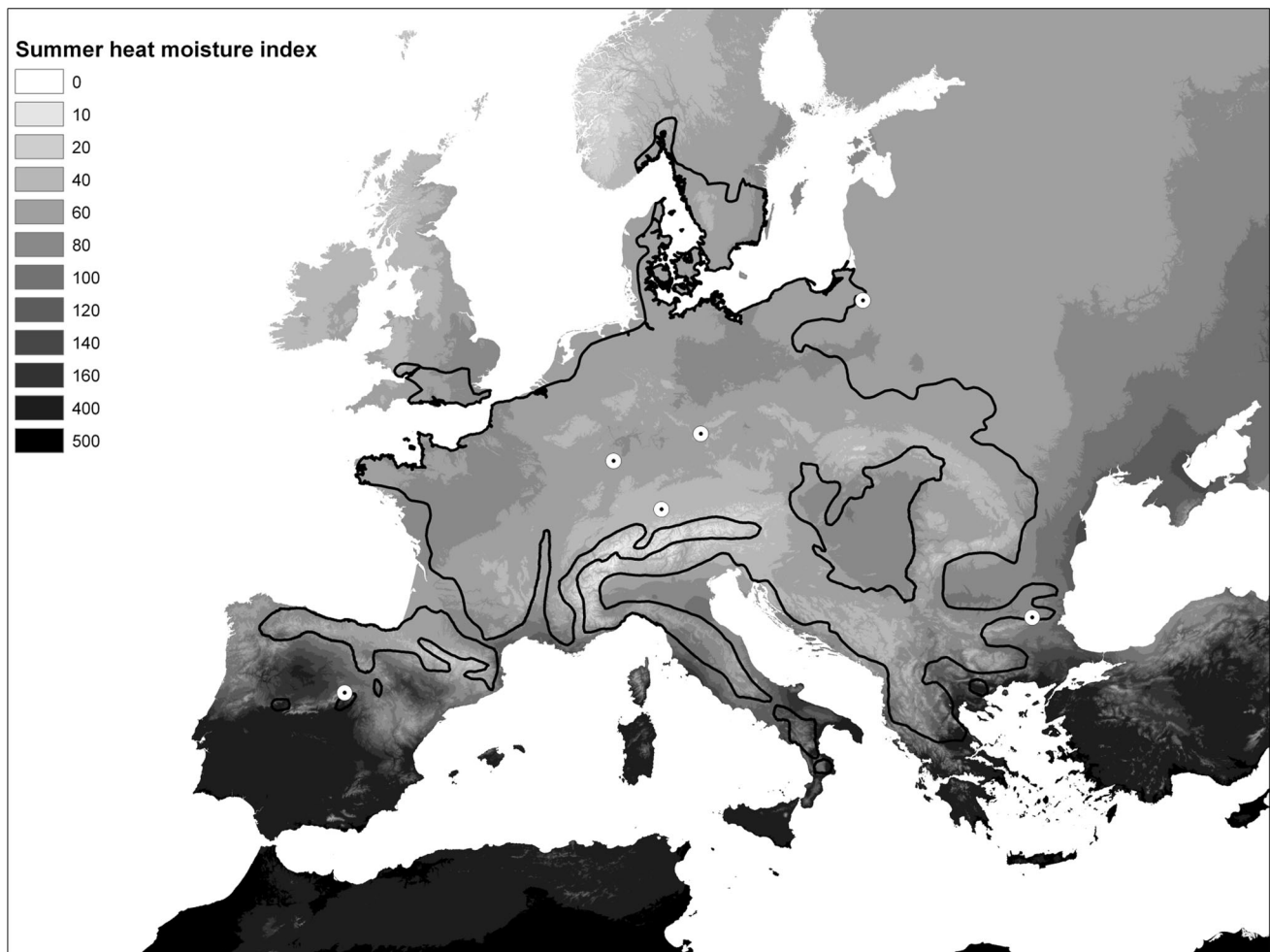
Fig. 1 Geographic origins of provenances used in the experiment. *Grey scales* display the Summer Heat Moisture index based on WorldClim data (Hijmans et al. 2005). Distribution range of *F. sylvatica* is outlined according to EUFORGEN

Table 1 Site information for the provenances used in the experiment

Code	Location	Country	Latitude	Longitude	Elevation (m a.s.l.)	SHMI	MWT (°C)	P(5–9) (mm)
BG	Kotel	Bulgaria	N42°51′59″	E26°26′40″	600	61	19.2	313
ES	Montejo de la Sierra	Spain	N41°07′12″	W03°30′36″	1,350	80	17.7	212
DE1	Hengstberg	Germany	N50°08′00″	E12°11′00″	569	47	15.9	341
DE2	Johanniskreuz	Germany	N49°18′00″	E07°50′00″	570	42	16.0	381
DE3	Kempten	Germany	N47°44′48″	E10°08′54″	803	26	15.3	580
PL	Mragowo	Polen	N53°52′00″	E21°20′00″	137	51	18.0	350

Mean temperature of the warmest month (MWT), summer precipitation (P(5–9)) and Summer Heat Moisture index derived from WorldClim (Hijmans et al. 2005)

The drought manipulation consisted of a 36-day period without irrigation. It started on May 9 and was completed when 20 % of the plants showed strong drought damage (76–100 % of the leaves damaged), on June 13. Approximately 12 days after the start of the treatment, soil moisture dropped below the permanent wilting point (pF = 4.2; Fig. 2) for the loamy sand substrate and about 1 week later for the sandy loam substrate. In the re-watering phase after the drought period, the plants were exposed to the control precipitation treatment again. Additionally they received the amount of water which was given to the control plants over the 36-day drought period, evenly distributed over

Fig. 2 Soil moisture for all four treatment combinations. The *light grey area* shows the artificial drought period, and the *dark grey area* shows the re-watering phase. The *two horizontal lines* depict the approximated permanent wilting points for the loamy (*black*) and the sandy substrate (*grey*)
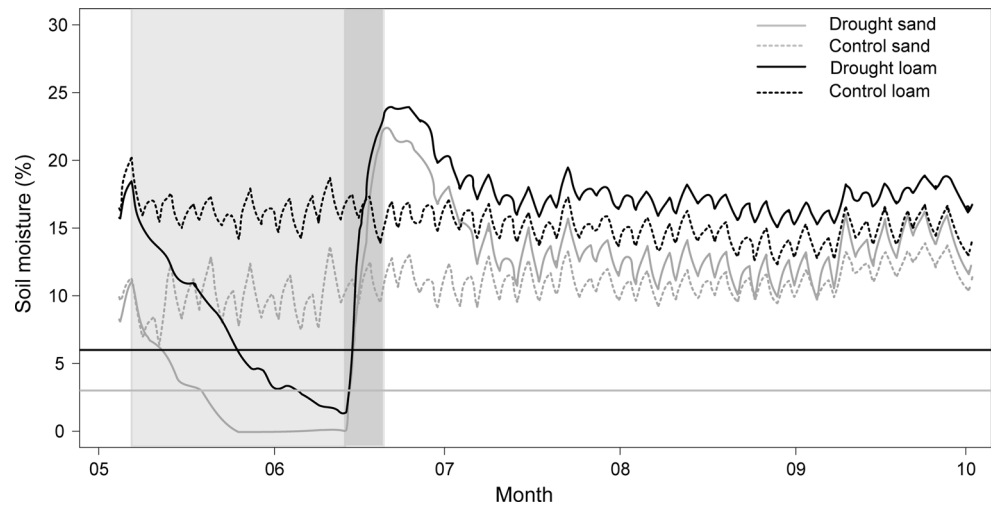

Table 2 Nutrient content and pH-values for the two soil types used in the experiment

	K (mg/kg)	Mg (mg/kg)	P (mg/kg)	NO_3 (mg/kg)	NH_4 (mg/kg)	$C_{org.}$ (%)	pH-$_{CAT}$	pH-$_{water}$	N (%)
Loamy sand	54.8	121	11.1	14.1	2.02	0.56	6.3	8.5	<
Sandy loam	118	267	48.3	31.0	3.98	1.92	4.7	7.6	0.14

1 week, so that at the end of the experiment, both the individuals in the control as well as in the drought treatment received the same amount of water.

The volumetric soil water content was measured with dielectric permittivity sensors (EC-5 soil water sensor, Decagon Devices, Inc., Pullman, USA). Altogether 10 sensors with two data loggers (ECH2O, Decagon Devices, Inc. Pullman, USA) were installed in the pots in 5–10 cm depth, three for the two soil types each in the drought treatment and two each in the control treatment.

The soil treatment consisted of two different soil types. The first one was a sandy loam substrate from a local forest topsoil dugout, from now on called *loam* or *loamy substrate*. The second soil type was a loamy sand substrate, consisting of a mixture between the loam and arenaceous quartz sand from a local sand pit (50 % each), from now on referred to as *sand* or *sandy substrate* (Table 2).

Response parameters

Short-term response to the treatments was determined by visual estimates by assigning the average percentage of damaged leaves per plant to six classes (0, 1–5, 6–25, 26–50, 51–75, 76–100 %). A leave was counted as "damaged", as soon as it exhibited necrotic tissue. The share of necrotic tissue of the whole leave was not taken into consideration. This assessment took place at the last day of the drought treatment. For each individual, midpoints of the six classes were used for further statistical analyses.

Long-term effects of the treatments were determined by measuring height and diameter shortly after planting time in April and after the growing period at the end of September. Increment was calculated by subtracting the initial values from the values at the end of the growing period. The statistic were conducted both for absolute and relative increment values. As the initial plant dimensions were very similar over the provenances and thus the relative values yielded similar results, we concentrate on absolute values in this study. Dead individuals were counted, and the percentage of dead individuals per treatment, soil type and provenance was calculated. Furthermore, the Summer Heat Moisture index (Wang et al. 2006) was calculated ((mean temperature of warmest month)/(mean annual summer (May–September) precipitation/1,000)) for each geographic origin of the provenances (data: WorldClim; Hijmans et al. 2005).

Statistics

Analyses of variance (ANOVA) combined with linear models was applied to test for the main and interactive effects of the three factors provenance, drought and soil on height and diameter increment and on leaf damage. Data were square root transformed in order to improve homogeneity of variance and normality of residuals prior to analysis if necessary. In case of significant effects, post hoc comparisons were run (Tukey's HSD).

To test for the long-term impacts of short-term damage, an ordinary least-squares regression was applied between
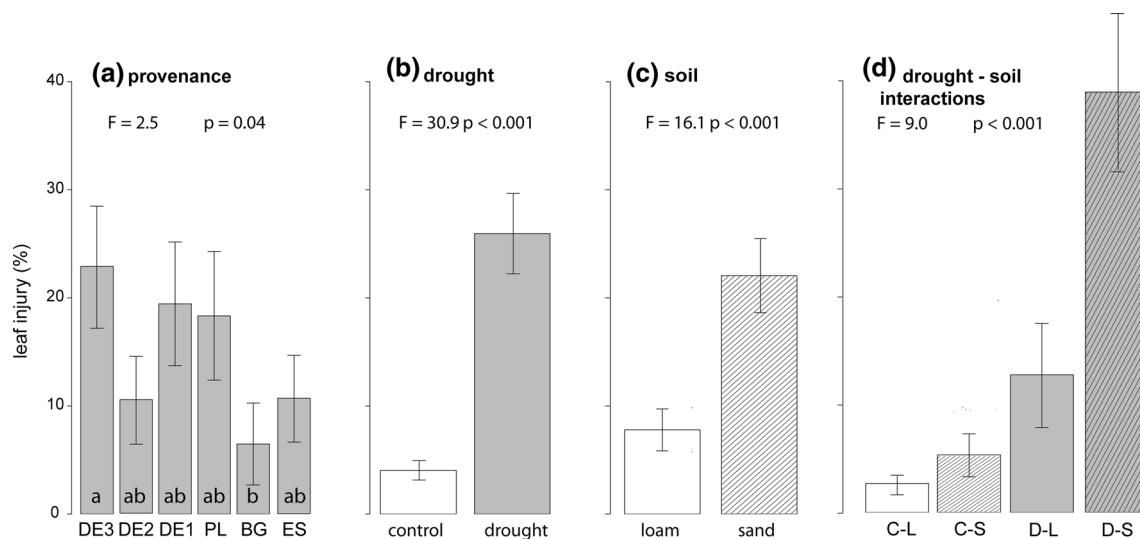
Fig. 3 Leaf damage of *F. sylvatica* at the end of the drought manipulation (June 13) in % in response to **a** provenance, **b** drought and **c** soil type. All significant main and interaction effects (**d**) of the three-factorial ANOVA are displayed. Provenances are arranged with increasing SHMI

the reduction in height and diameter increment in the drought treatment compared to control (in %) and the percentage of damaged leaves per plant averaged per provenance. Generalized linear models were used to determine the effects of treatment, soil and provenance on mortality, least-squares regressions to correlate mortality with increment rates.

Least-squares regressions were also used to assess the correlation between the Summer Heat Moisture index (SHM) at the geographic origins of the provenances and increment reduction (drought compared to control in %), leaf damage (%) and mortality (%) in order to detect local adaptations to drought events.

All statistical analyses were conducted with the software R.2.13.0 (R Development Core Team 2010).

Results

Leaf damage

The provenances differed in the percentage of damaged leaves per plant (ANOVA: $F = 2.5$, $p = 0.035$; Fig. 3a). The German provenance from Kempten (DE3) showed the highest share of damaged leaves (23 %), whereas the Bulgarian provenance exhibited a significantly lower percentage of damaged leaves (6.5 %). The drought treatment increased the percentage of damaged leaves significantly from 4 % in the control treatment to 26 % on average for plants under the drought treatment (ANOVA: $F = 30.9$, $p < 0.001$; Fig. 3b). Plants grown in sand showed a significantly higher share of damaged leaves (22.1 %) than

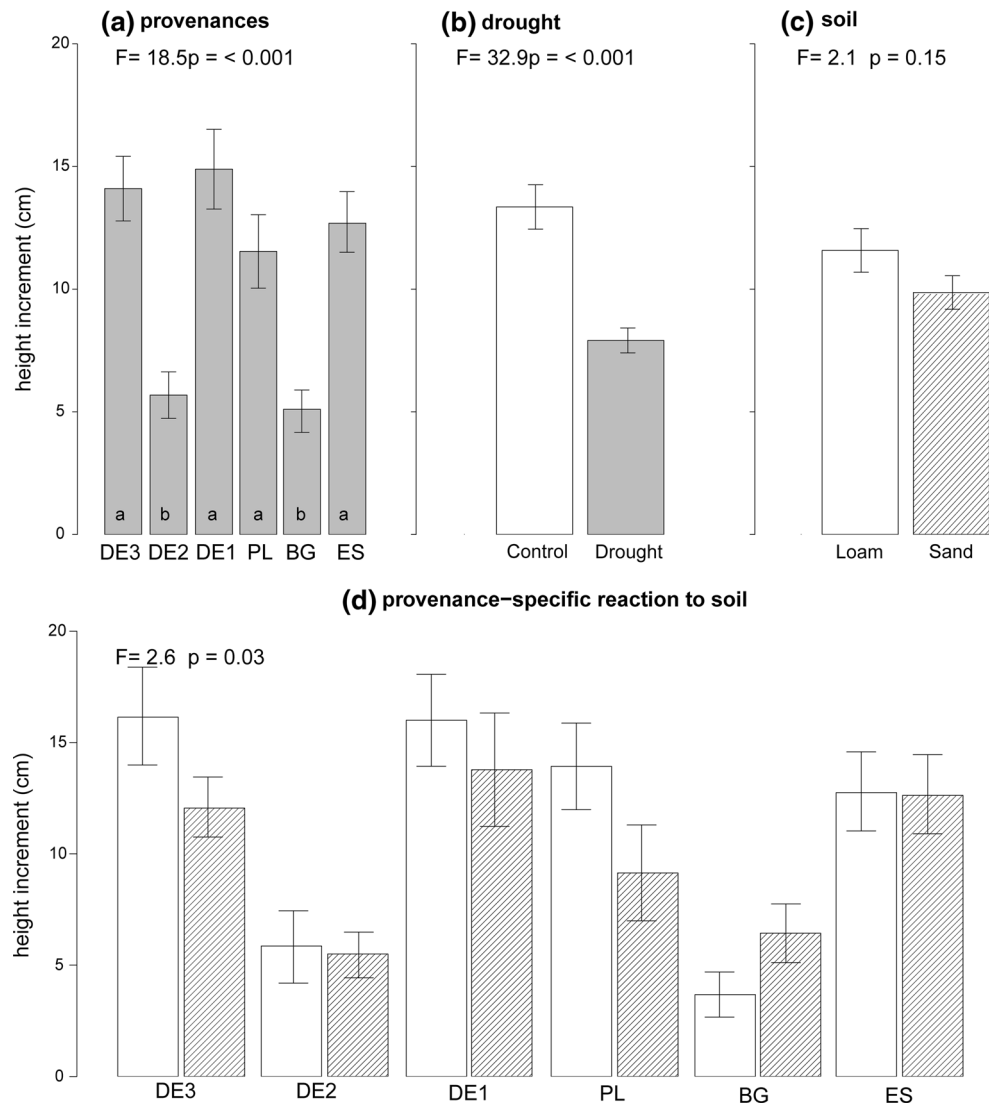plants in loam (7.8 %) (ANOVA: $F = 16.1$, $p < 0.001$; Fig. 3c).

Soil type significantly impacted the drought effect on leaf damage (ANOVA: soil × drought: $F = 9.0$, $p = 0.003$; Fig. 3d). In the loamy substrate, drought caused 4.7 times (D 12.8 %, C 2.7 %) more damage compared to control, whereas in sand, drought caused 7.2 times (D 39.1 %, C 5.4 %) more damage than the control treatment. Provenance-specific reactions to drought or soil type could not be detected (ANOVA: provenance × drought: $F = 1.3$, $p = 0.283$; provenance × soil: $F = 2.3$, $p = 0.128$).

Height increment

Provenances differed in terms of height increment (ANOVA: $F = 18.5$, $p < 0.001$; Fig. 4a). The Bulgarian and the German provenance from Johanniskreuz (DE2) showed significantly less increment than the other provenances (BG 5.1 cm, DE2 5.7 cm). The German provenance Hengstberg (DE1) performed best with 14.9 cm height increment. The drought treatment reduced the height increment significantly from 13.5 cm under control conditions to 8.1 cm on average for plants exposed to drought conditions (ANOVA: $F = 32.9$, $p < 0.001$; Fig. 4b). Soil did not influence increment in height (ANOVA: $F = 2.1$, $p = 0.149$; Fig. 4c).

The provenances showed different height increment patterns across the two soil types (ANOVA: provenance × soil: $F = 2.6$, $p = 0.026$; Fig. 4d). The Bulgarian provenance reacted positively to sandy soil, whereas all other provenances showed no or a negative reaction to the sand compared to the loam.

Fig. 4 Height increment of *F. sylvatica* in response to **a** provenance, **b** drought and **c** soil type. All significant main and interaction effects (**d**) of the three-factorial ANOVA are displayed. Provenances are arranged with increasing SHMI


(a) provenances F= 18.5 p = < 0.001

(b) drought F= 32.9 p = < 0.001

(c) soil F= 2.1 p = 0.15

(d) provenance-specific reaction to soil F= 2.6 p = 0.03

Provenance-specific reactions to drought or interactive effects of drought and soil could not be detected (ANOVA: provenance × drought: $F = 1.4$, $p = 0.235$; drought × soil: $F = 2.3$, $p = 0.132$).

Diameter increment

The Bulgarian provenance (BG) grew significantly worse (2.0 mm) than all other provenances in terms of diameter (ANOVA: $F = 3.1$, $p = 0.011$, Fig. 5a), while all others showed similar growth rates (2.6–2.9 mm). The drought treatment reduced the diameter increment significantly from 3.4 mm under control conditions to 2.0 mm on average for plants exposed to drought conditions (ANOVA: $F = 89.7$, $p > 0.001$, Fig. 5b). The sandy substrate also had negative impacts on secondary growth, reducing increment from 3.1 mm in loamy substrate to 2.2 mm in sandy substrate (ANOVA: $F = 37.3$, $p < 0.001$, Fig. 5c).

The two soil types triggered a provenance-specific reaction in terms of diameter increment (ANOVA: provenance × soil: $F = 2.6$, $p = 0.027$; Fig. 5d). The Bulgarian and Spanish provenances responded with a relatively stable diameter increment to sandy substrate compared to the loam, whereas all other provenances showed higher growth rates on loam. The German provenance Hengstberg (DE1) exhibited a notably strong decline in mean diameter increment on sand (even if not significantly different from reactions of other German and Polish provenances). Furthermore, the provenances showed a different tolerance to drought with regard to diameter increment (ANOVA: provenance × drought: $F = 2.7$, $p = 0.020$, Fig. 5e). Only a minor decrease could be detected for the Bulgarian provenance, while the German provenances Hengstberg (DE1) and Kempten (DE3) showed strong cutbacks in diameter increment in response to drought. Soil type significantly impacted diameter increment in response to drought (ANOVA: drought × soil: $F = 7.7$, $p = 0.006$).

Fig. 5 Diameter increment of
F. sylvatica in response to
a provenance, **b** drought and
c soil type. All significant main
and interaction effects (**d**–**f**) of
the three-factorial ANOVA are
displayed. Provenances are
arranged with increasing SHMI
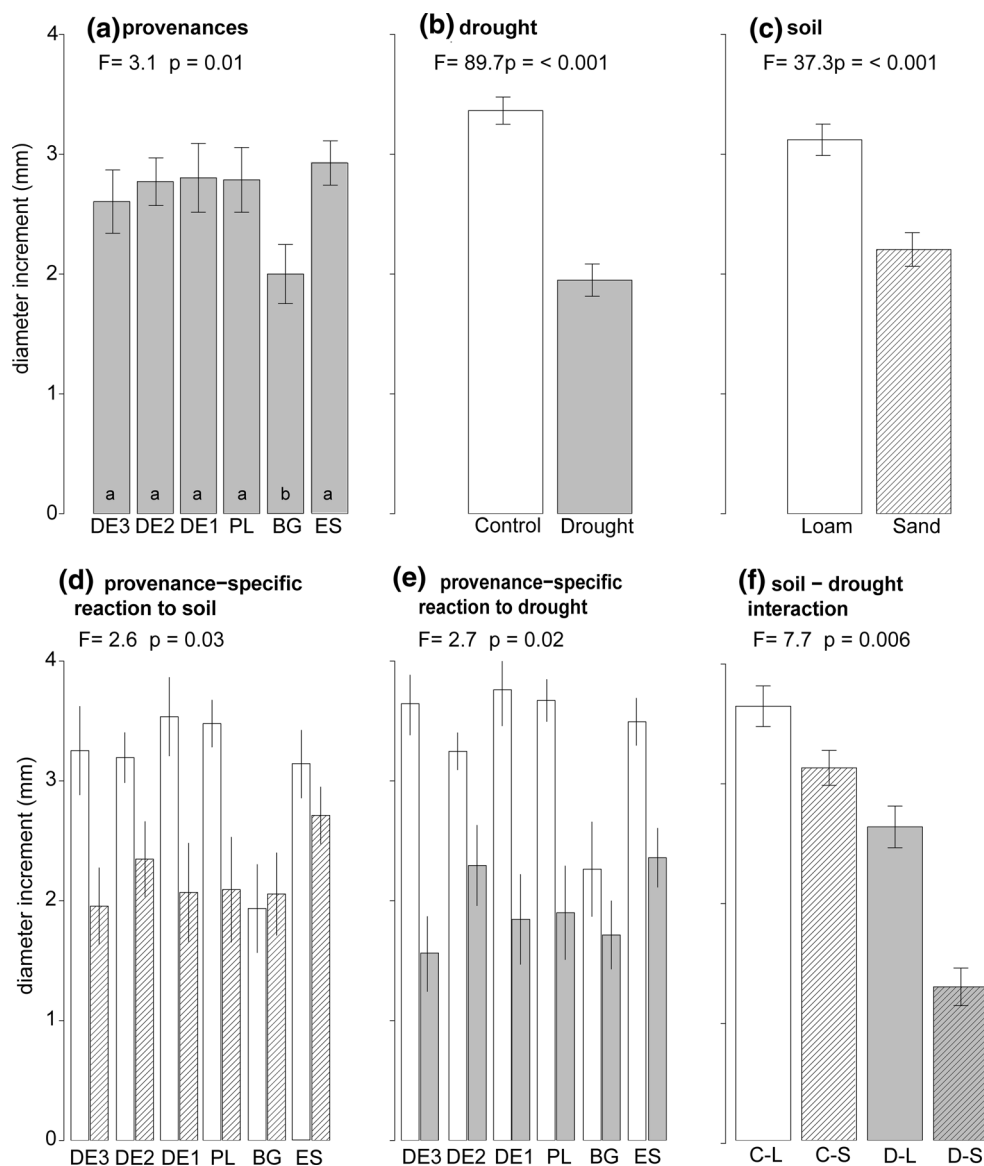
The sand fostered the negative impacts of the drought period on diameter increment (control 3.1 mm; drought 1.3 mm), whereas in the loamy soil, the drought impact was more moderate (control 3.6 mm; drought 2.6 mm).

Mortality

Mortality occurred solely within the drought treatment, and within the drought treatment mainly in the sandy substrate (drought/loam = 7.8 %, drought/sand = 25.5 %; ANOVA: $p = 0.012$). Provenance did not impact mortality significantly (ANOVA: $p = 0.097$), even though mortality correlated significantly with summer drought conditions at the places of origin of the provenances (see Results, Local adaptation). Mortality tended to increase (non-significantly) with diameter increment reduction (adjusted

$r^2 = 0.39$, $p = 0.110$) in the drought treatment compared to control.

Correlation of leaf damage with increment

The average percentage of damaged leaves per provenance was strongly correlated with a reduction in diameter increment (adjusted $r^2 = 0.99$, $p < 0.001$). The reduction in height increment exhibited a non-significant trend towards an increasing reduction with increasing leaf damage (adjusted $r^2 = 0.42$, $p = 0.097$).

Local adaptation

The SHM at the geographic origin of the provenances did not influence the reaction to drought with regard to height

Fig. 6 Correlation between the Summer Heat Moisture index at the origin of the provenances and the mean reduction in **a** height and **b** diameter increment, **c** mean leaf damage per provenance and **d** mortality per provenance
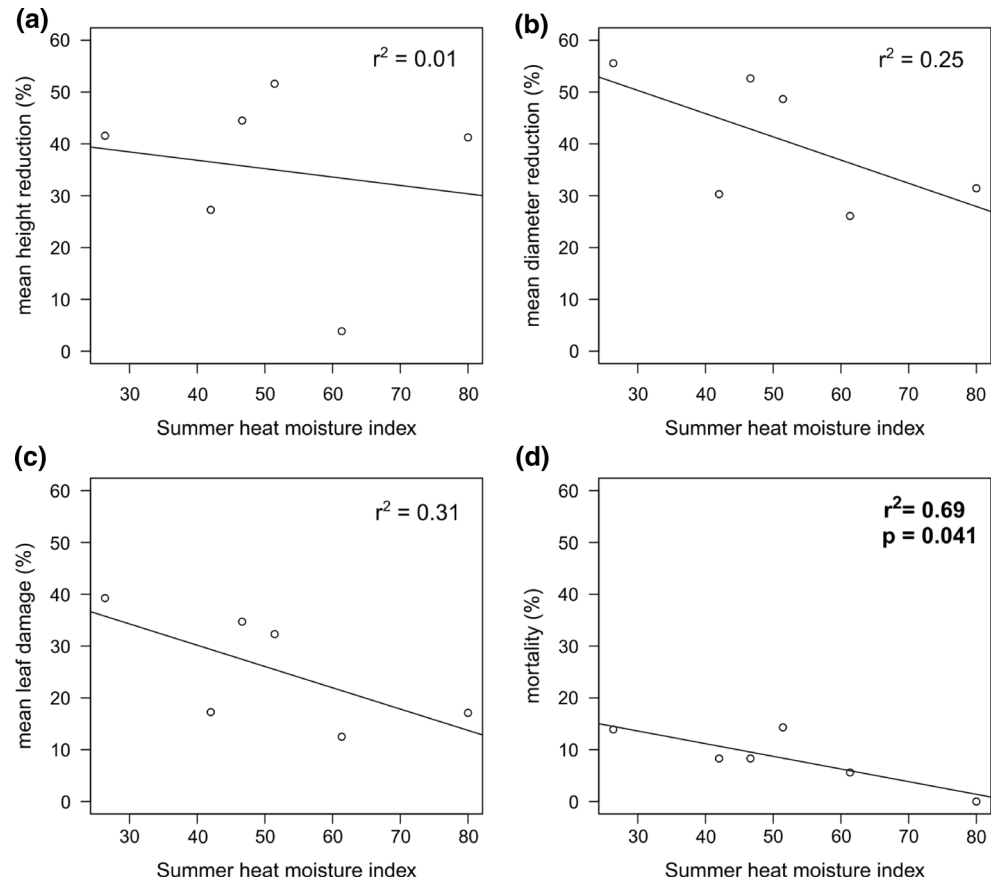
increment (adjusted $r^2 = 0.01$, Fig. 6a). However, even if non-significant, provenances from origins which are more prone to summer drought events (higher SHM) tended to be more drought tolerant in terms of diameter increment and leaf damage, as SMH at the geographic origins explained 25 % of the variance in diameter increment reduction (Fig. 6b), 31 % of the variance in leaf damage (Fig. 6c). A significant correlation ($p = 0.041$) could be detected between the SMH index and mortality (Fig. 6d). Here the Summer Heat Moisture index at the geographic origin explains 69 % of the variance in mortality.

Discussion

Intra-specific variation

The current distribution of *F. sylvatica* is a result of multiple glacial periods. *Fagus sylvatica* survived the last glacial maximum in several refuge areas in Europe (Magri et al. 2006). Most probably, refuge areas in the southwestern and Dinaric Alps played an important role in the re-colonization of Central and Western Europe, whereas the Mediterranean populations seem to have survived in several geographically distinct refuges on the Iberian and

Italian peninsulas and in the Balkan (Magri et al. 2006; Magri 2008; Brus 2010). In particular, the Balkan (and Italian) populations are genetically distinct from the other European populations (Magri 2008). This post-glacial migration pattern and genetic differentiation, most probably, also resulted in phenotypic variation between provenances. Distinct performances of European beech provenances grown in common garden experiments are well known and often demonstrated (e.g. von Wuehlisch et al. 1995; Nielsen and Jorgensen 2003; Giannini and von Wühlisch 2009). The differences between provenances in all of the examined parameters in this study are consistent with these previous findings and likely express the differences in genetic make-up.

In particular, the Bulgarian provenance showed a distinct performance in all parameters. Bulgarian beech populations are genetically distinct from Central European populations (Magri et al. 2006), which may explain the significantly lower increment. Surprisingly, one German provenance (DE2) performed significantly worse in terms of height increment than the other two German provenances (DE1, DE3), despite a most likely similar postglacial history and assumingly comparable genetic make-up. Yet, in Central Europe, genetic diversity is higher within populations than between populations (Konnert

1995). Furthermore, the silvicultural history of particular beech stands is often hard to be reconstructed. In addition, local soil conditions and small-scale rainfall patterns may be also responsible.

Effects of drought and soil on tree performance

Drought adversely impacted all measured parameter significantly: it increased the amount of leaf damage and decreased height and diameter increment. This is in compliance with numerous studies reporting on the drought sensitivity of *F. sylvatica* (Rennenberg et al. 2004; Lebourgeois et al. 2005; Jump et al. 2006; Piovesan et al. 2008; Friedrichs et al. 2009; Betsch et al. 2011; Hlasny et al. 2011; Jezik et al. 2011; Scherrer et al. 2011).

As expected, the sandy substrate with lower nutrient availability and water storage capacity resulted in more severe negative impacts on the performance of plants, compared with loamy substrate. The drought impact on leaf injury rates and diameter increment was more severe for plants grown in the sandy substrate, which shows the importance of the interaction between precipitation rates and soil properties (Gaertner et al. 2008). The soil moisture in the sandy substrate dropped below the approximated permanent wilting point 1 week before this point was reached in the loamy substrate. Plants in the sandy substrate therefore experienced $\sim$24 days of water stress, whereas plants grown in the loamy substrate only $\sim$17 days. The reduced nutrient uptake due to lacking water absorption during the drought might furthermore have weaker impacts in nutrient-richer soils than in poorer soils. Apart from nutrient uptake, evidence suggests that also nutrient availability of the soil is reduced due to drought conditions (Rennenberg et al. 2009; Kreuzwieser and Gessler 2010).

In this study, we did not investigate biomass allocation to above- and belowground components of the tree seedlings. In particular, at a seedling age, the ability of European beech to plastically react to environmental/drought conditions in terms of reallocation of resources is quite high, as Schall et al. (2012) demonstrated. European beech seedlings increased the investment into belowground biomass as a reaction to drought. According to the balanced-growth hypothesis (Hunt 1975; Shipley and Meziane 2002), plants reallocate resources to the organ that exploits the limiting resource, in our case the root system. Such potential reallocation effect of a drought treatment might lead to overestimation of growth reduction, as it might mask a constant biomass production, when just observing above ground growth. When trees get older, this morphological plasticity decreases and physiological acclimatization processes becomes more important (Schall et al. 2012). Therefore, a transfer of results from seedlings to mature trees should be backed by more research, e.g. in long-term provenance trials.

Provenance-specific reactions and local adaptation to drought and soil

Drought sensitivity in terms of diameter increment varied between the provenances in our experiment. The Bulgarian provenance (BG) showed a weak performance under the control treatment, yet the smallest reduction in diameter increment due to the drought treatment. The increment reduction between drought and control in other provenances (DE1, DE3, PL) amounted to 50 %. However, their absolute increment values under drought conditions were still higher than for the BG provenance. This behaviour of provenances correlates strongly with leaf injury rates ($r^2 = 0.99$). The interactive effect of provenance and drought treatment was not significant in this case, yet this is due to the fact that leaf injury almost exclusively occurred under the drought treatment. Given the relatively small number of provenances in our trial, significant correlations between the drought response of increment and leaf damage with the climate at the origin of the provenances could not be established. Yet, the reactions of both parameters tended towards a correlation with the long-term Summer Heat Moisture index at the origin of the provenances. This trend is supported by previous findings by Czajkowski and Bolte (2006) who demonstrate a correlation between the drier, continental climate at the origin of a beech provenance from central Poland with low water stress sensitivity and the moister climate of provenances from Germany and West Poland with higher drought stress sensitivity. It is further in compliance with the results of Nielsen and Jorgensen (2003) who found a significant interaction between soil water content and diameter increment for 14 provenances in a common garden experiment in Denmark. However, these authors found a greater adaptability of southern provenances to changing water conditions. In our experiment, the Bulgarian provenance showed a low but stable increment over the treatments while most northern provenances (except DE2 Johanniskreuz) performed at similar low levels under drought conditions but showed a much more positive response to favourable conditions than the Bulgarian one. Similar to the Bulgarian provenance, the Spanish one is not very responsive to drought in terms of leaf damage under dry conditions and showed the lowest mortality rates, however, in contrast to the Bulgarian provenance on a higher increment level and more notable reductions in increment. Surprisingly, the performance of the German provenance from Johanniskreuz (DE2) resembles more the southern provenances (than the other two German and the Polish provenances, which are geographically closer) with low leaf injury rates, low height

growth and lower drought-induced growth reductions. Nielsen and Jorgensen (2003) show in their study that northern provenances display a low but stable growth level and southern ones a more plastic response.

The results of our study and the results of Nielsen and Jorgensen might be superficially interpreted as inconsistent. On closer inspection, however, the mere geographic division of provenances into north and south might not reflect the actual climatic, and site condition populations were exposed to in past and present at their places of origin. The southern provenances used by Nielsen and Jorgensen (2003) do not stem from the very edges of the distribution range, except one from Mount Etna, Sicily (IT), and the places of origin of these southern provenances have relatively high precipitation rates, whereas the northern provenances come from regions with relatively continental climate with low precipitation sums (e.g. eastern Germany and Central Poland). They might be even more exposed to dry conditions at their origins. The same might be applicable for the concept of geographically marginal and central populations, as this concept excludes micro- and meso-climatic effects, and small-scale differences in soil and site conditions. Even in the centre of the distribution range, very unfavourable and "marginal" sites can be found, whereas on the geographic margins, favourable growth conditions can occur on small scale, e.g. at the windward side of small mountain ranges with orographic rainfall patterns.

In this study, the Summer Heat Moisture index of the ES provenance is even higher than for BG, still the drought tolerance in terms of stable growth is not as high as in BG, which may be due to edaphic reasons (Gaertner et al. 2008). This could mean that the actual drought severity, derived from precipitation and soil characteristics, might be lower at the origin of the Spanish provenance (ES). The behaviour of the German provenance (DE2) is also similar to the marginal provenance from BG, although it stems from the centre of the distribution range with climatic conditions comparable to the other German provenances. DE2 stems from the Palatinate Forest, a German mountain range with lower Triassic sandstone formations. The sandy soil there might create much drier conditions than what the other two German provenances experience at their point of origin. Furthermore, information on slope, exposition, soil depth and substrate at the exact location of seed sampling (i.e. of single mother trees) might improve explanatory power in future analyses.

Additionally, these intricate findings might indicate a complex pattern of within and between population variations, developed from the interplay of post-glacial history, local climatic adaptation, local growing conditions and human silvicultural practices. Herbette et al. (2010) and Wortemann et al. (2011) claim that phenotypic variability

in drought tolerance, here measured in cavitation resistance, is mainly caused by phenotypic plasticity and not by genotypic differences between populations. Yet, our data point towards some degree of inherited local adaptation to climate conditions at the origins of the provenances even when considering our small selection of provenances. Accordingly, marginal beech populations which face more adverse conditions are under stronger genetic selection (Wortemann et al. 2011) than populations on favourable sites. In our study, the Bulgarian provenance (BG) shows the most distinct provenance effect and provenance-specific reaction. It stems from the very south-eastern distribution edge of *F. sylvatica*, where summer drought is most probably the range-limiting factor (Jump et al. 2006). This again emphasizes the importance of marginal beech populations in the search of drought-resistant ecotypes (Rose et al. 2009).

A trade-off between survival under drought conditions and high increment under favourable conditions has been shown for four broad-leaved species in Kenya (Kondoh et al. 2006). Accordingly, *F. sylvatica* displays the lowest mortality under shade, yet the lowest growth rate under light compared to other deciduous trees (Petritan et al. 2007). Likewise, a continental and a Mediterranean *Pinus sylvestris* provenance did not differ under dry conditions, whereas under wetter conditions, the continental provenance showed higher root biomass allocation and seedling recruitment rates (Richter et al. 2012). This confirms previous findings that high phenotypic plasticity appears beneficial in highly variable environments.

The drought manipulation in our experiment can be considered as relatively mild. Only few individuals died due to the treatment. Provenance did not impact the mortality rate significantly in general. However, there is a clear and significant correlation between summer drought and mortality, with lower mortality rates of the southern marginal provenances due to drought treatment (BG = 11.1 %, ES = 0 %, all provenances 15.3 %), providing evidence for an adaptation to local climate conditions. Given the above-mentioned potential trade-off mechanisms, this slight trend towards higher mortality with stronger diameter growth reduction could point towards higher survival rates of less plastically responding provenances. A stronger genetic selection in drought-prone ecotypes (Wortemann et al. 2011) could lead to lower genetic diversity (Kawecki 2008) and thus low phenotypic plasticity (Schaberg et al. 2008; Matyas et al. 2009), though Kawecki (2008) also reports that for some marginal species, no genetic depauperation for ecologically relevant traits could be detected. Therefore, marginal populations could potentially secure ecosystem persistence under very extreme climatic events, yet might increase the risk of lower growth rates under favourable conditions.

Furthermore, the Bulgarian, Spanish and the German provenance from Johanniskreuz (DE2) showed relatively stable responses in height and diameter increment in the sandy substrate compared to the loamy substrate. This might indicate that these provenances are not able to exploit the improved water and nutrient condition in the loam. It could also indicate a local adaptation to certain soil characteristics, which was, e.g. found for *Pinus nigra* (Varelides et al. 2001). Still, such a potential trade-off between stress-tolerance and high performance under more favourable conditions is yet to be supported by more evidence in future provenance trials.

At the north-eastern edge of the distribution range, the SHM is not as high as at the southern edge. The Polish provenance (PL) originates from the ecotone between beech dominated forest and boreal forests. Beech dominates on moraine loamy soil, while Scots pine dominates on drier and sandier soils (Bolte et al. 2007). In particular, at the north-eastern margin where continental climate conditions are becoming more prevailing, correlations with single macro-climatic factors fail to explain distribution margins of *F. sylvatica* (Bolte et al. 2007). There, winter conditions and frost are at least as important as drought. Giving the clear response to drought in our experiment, it seems that a strong selection towards drought-resistant ecotypes does not take place.

As mentioned above, below-ground biomass production was not determined in this study, yet there might be differences in plasticity of biomass allocation between the provenances (Richter et al. 2012), which deserve more attention in future studies.

Conclusion and implications for research and forest management

Provenances of *F. sylvatica* differ in increment and exhibit differences in their sensitivity to drought. This intraspecific variability can probably be used to adapt forest ecosystems to future climate conditions. Yet, the impact of the interplay between climatic and soil and site characteristics on the emergence of drought conditions have to be accounted for as provenances react specifically to contrasting soil types. Therefore, the concept of marginality should be extended from a geographic to a more site-related concept; yet, especially marginal populations from the drought-prone southern edges of the distribution range are potential targets in the search for drought-resistant ecotypes. However, a potential trade-off between high phenotypic plasticity with high performance rates under favourable conditions, and stress-tolerance and survival under drought conditions and its impact on forest growth requires future research. Long-term provenance trials with a greater

number of central and marginal (maybe also from "marginal" sites in the centre of the distribution range) provenances, where the performance of trees can be monitored beyond the seedling age, could contribute in approaching these open questions. Differing from existing trials, a hypothesis-based selection of provenances and the option for climate manipulations in later ontogenetic stages should be applied. Furthermore, a single drought manipulation does not reflect a change in long-term mean values and changes in frequency of extreme events and there long-term impacts. Therefore, a network of several climatically different trial sites, including marginal sites, is needed.

Furthermore, more multi-factorial experiments could address the problem that resistance to one abiotic factor such as drought does not necessarily imply resistance to other climatic or abiotic factors such as frost (Kreyling et al. 2012) or forest pests. However, the establishment of multi-factorial, multi-site and long-term trials and experiments will take longer than there is time to start adaptive actions in forest management with regard to the velocity of climate change. Evidence suggests that the selection of a single best drought-adapted provenance for transplantations is not reasonable, considering the limited knowledge of the long-term effects. Nonetheless, marginal and drought-adapted ecotypes might be intermixed, together with local provenances and ecotypes adapted to other abiotic factors, in order to secure yield and stability under more extreme climatic conditions in the future. Forest management should therefore aim at increasing the genetic diversity of forest stands to secure populations against breakdown due to climatic extremes.

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