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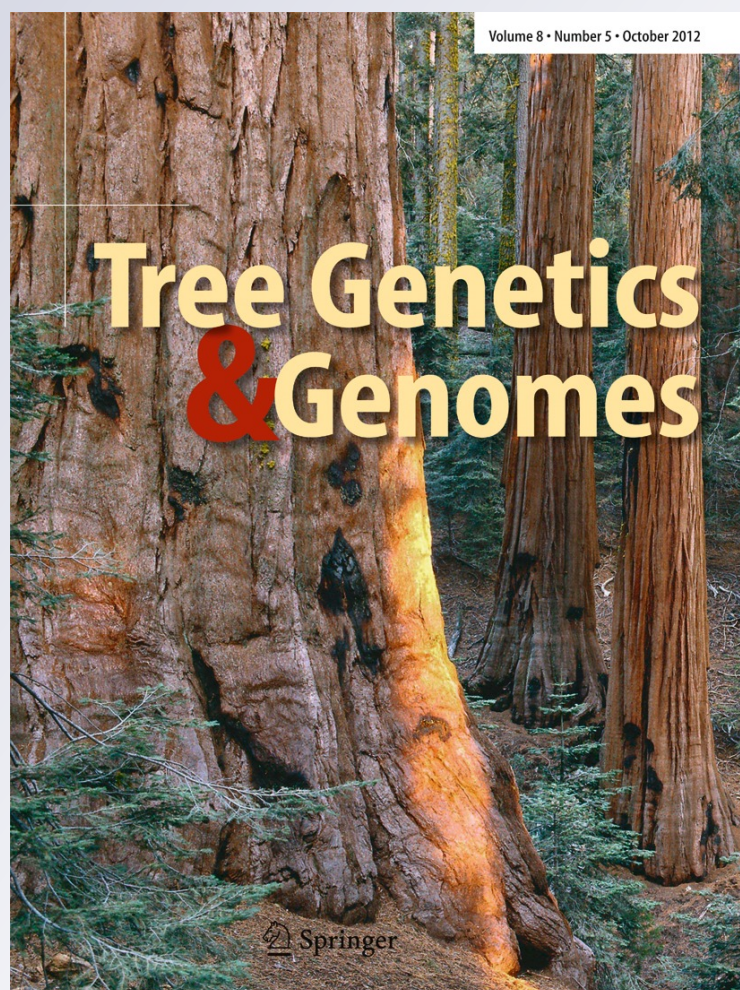
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Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin

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Abstract We assessed the response of 11-year-old saplings from six beech provenances growing in a common-garden trial at the southwestern range limit. Provenances from distinct climatic regions across the European beech distribution were selected. The local Spanish provenance appeared well suited to the site conditions, maintaining high rates of assimilation even in midsummer, but so did the provenance of southern continental origin, from Gotze-Delchev, Bulgaria. Those provenances from cooler sites in central Europe, a continental mountain climate in the Czech Republic and a continental range-edge site in eastern Poland, along with a German provenance of mild maritime origin, had good physiological functionality in early summer but reduced carbon

assimilation (A_{area}) and apparent soil–leaf hydraulic conductivity (K_L) in midsummer. The northern maritime provenance from Sweden demonstrated severely-reduced photosynthetic capacity. These groupings of provenances according to their photosynthetic performance, stable carbon isotope composition ($\delta^{13}\text{C}$; a proxy for water-use efficiency) and leaf water potential under marginal conditions, during late summer in the trial, suggest that they have divergent strategies for water use. The research highlights large intraspecific differences among beech provenances of distinct origin and strategies which are expected to modify their response to drought, requiring future genetic studies to explicitly determine the basis of this eco-physiological differentiation.

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Keywords Common-garden trial · Water-use efficiency · Carbon isotopic composition · Intraspecific variation · Plasticity · Adaptation to climate change

Introduction

The distribution of European beech (*Fagus sylvatica* L.) is widespread across Europe, ranging from central Spain in the South–West, to Sweden in the North and Poland and Ukraine in the East (Paule et al. 1994). The species biogeographical history has created a complex genetic structure. Beech was largely eliminated from Europe during the last glaciation, apart from isolated refugia maintained around the Mediterranean and in the Balkans (Magri et al. 2006; Magri 2008; Gömöry et al. 2010), prior to subsequent post-glacial recolonisation from the South East (Giesecke et al. 2007). The diversity of beech has been widely studied using allozymes and more recently micro-satellite markers (Jump and Peñuelas 2007; Vornam et al. 2004; Chybicki et al. 2009; Gömöry et al. 2010). Most of these studies report high genetic differentiation among

populations and inbreeding within populations, but illustrate the capacity of beech to relatively rapidly evolve local adaptation (Jump et al. 2007). Although some controlled experiments have reported effects of drought on growth (Nielsen and Jorgensen 2003), $\delta^{13}\text{C}$ (Peuke et al. 2006), transpiration (Leonardi et al. 2006) and photochemistry (García-Plazaola and Becerril 2000a, b) among beech seedlings differing in origin, the implications of genetic variability for physiological traits responding to environmental constraints, and consequently for fitness, require further elucidation (Kramer et al. 2008).

Those physiological traits that respond to environmental stress factors can reflect the fitness of individuals to withstand marginal conditions. Under high evaporative demand (Lendzion and Leuschner 2008) or even at moderate soil water stress (Aranda et al. 2000, 2005), seedlings and adult trees alike are subject to a functional compromise between maintaining high rates of photosynthesis throughout the growing season, enabling trees to keep a positive carbon balance, and the stomatal control of water loss. This trade off is particularly acute during recruitment into populations growing under high stress, as experienced at the niche edge or range edge where summer drought can limit regeneration (Aranda et al. 2001, 2004; Robson et al. 2009).

The perceived vulnerability of provenances at the trailing edge of tree species distributions makes field research into their stress responses imperative (Jump et al. 2007; Thuiller et al. 2008; Kramer et al. 2010), and while the physiological basis of response to water stress in beech forests has been widely researched, studies of the differentiation among genetically-distinct provenances of beech adapted to contrasting environments has focused on beech provenances covering a narrow span of the geographical and climate range (Leverenz et al. 1999; Tognetti et al. 1995; Peuke et al. 2002; Rose et al. 2009). In particular, only a few studies consider southern-European provenances (Borghetti et al. 1993; García-Plazaola and Becerril 2000a, b; Leonardi et al. 2006). The comparison of a disparate selection of provenances would provide new insight into the capacity of beech for intraspecific adaptation to drought.

To assess the intraspecific variability of beech under a Mediterranean climate experiencing warm dry summers, we chose six of the most widely-dispersed provenances, in terms of their environment of origin, from 32 provenances growing altogether in a trial at the range edge of beech in La Rioja northern Spain (von Wühlisch 2007). We examined whether genetically determined intraspecific differences in trait responses among beech provenances could be distinguished from differences due to phenotypic plasticity within provenances in allowing acclimatisation to the marginal site conditions, by comparing photosynthetic leaf traits in early summer when abiotic stress was low and in midsummer following a prolonged period without significant rainfall events. We hypothesized that (1) the southern range-edge

provenances would perform better than northern, mountain and maritime provenances due to their greater genetic adaptation to warm dry summers. (2) We predicted that at midsummer, those provenances originating in the most water-stressed environments would exhibit: (a) greatest water-use efficiency, (b) highest pre-dawn leaf water potential (Ψ_{pd}) and (c) the smallest seasonal drop in photosynthetic carbon assimilation capacity ($\text{diff } A_{\text{area}}$). We also monitored the relative response of gas exchange and specific leaf area, along with carbon isotopic discrimination, which we consider to reflect the intraspecific response of beech to water stress. From these results, we aimed to identify provenances that may express interesting traits indicative of adaptations to drought and to relate these to the performance of each provenance.

Materials and methods

Study site for the provenance trial

The study was performed during the spring and summer of 2008 in a common-garden provenance trial located amid beech and pine forests in the north of the *Sierra de La Demanda* at 1,340 m asl on *Monte Ayomal* above the village of Pazuengos in La Rioja, northern Spain. It lies on a NW exposed slope (20° gradient). The trial is one of a series of pan-European provenance trials planted in 1998 designed to enable recommendations on suitable beech reproductive material for forestry (EU Concerted Action AIR-CT94-2091 and Cost Action E52; von Wühlisch 2007). After 11 years of growth, the trees at these sites have now attained a size that allows for effective trait-based measurement of performance to be made.

The soil is loose and light-sandy brown soil of pH 5.5. The trial is fenced to exclude browsing animals, and the trees show very little evidence of insect damage. Planting is arranged in a randomised complete-block design with three blocks each containing 32 provenances, in groups of 50 individuals.

Weather data in the sampling year

The weather data presented is an average from the nearby weather stations belonging to the La Rioja Regional Administration, Ventrosa at Mount Urbaña 1,560 m asl (MTD 2008 CP, Geonica, Madrid, Spain) and Ezcaray at Peña san Torcuato 1,000 m asl (MTD 2008 CP). The trial site is situated between the two stations in its location and altitude. Temperature data were adjusted by 0.5 °C for every 100 m elevation to account for an adiabatic gradient in elevation between the field site and the weather stations. The stations record precipitation (pluviometer, Geonica 52202) temperature and relative humidity (50U-44212 Geonica), and solar radiation (pyanometer spectral range 305–2,800 nm CM-6B

ISO9060, Geonica) every 15 min (Fig. S8). The 8-year average (2000–2008) mean \pm 1 SD annual temperature was 9.5 \pm 1.6 °C and precipitation was 554 \pm 45 mm, the May–June average temperature was 13.1 \pm 3.0 °C and precipitation was 121.0 \pm 56 mm, and the July–August average temperature was 17.2 \pm 1.4 °C and precipitation was 57 \pm 38 mm. The site is subject to frequent late-spring frosts (*ca.* 5 year⁻¹) and early-autumn frosts.

During 2008, mean monthly temperature \pm 1 SD at the trial site was 10.6 \pm 3.9 °C for the May–June period and 16.5 \pm 3.4 for July–August and total monthly precipitation was 278 mm for May–June and 48 mm for July–August: This suggests that while temperatures during the 2008 growing season fell within the usual monthly range for the site, the early summer was slightly wetter and midsummer slightly drier than usual, nevertheless the summer temperatures and VPD were within the normal range for European beech forests (Granier et al. 2000; Fang and Lechowicz 2006).

Selection of representative provenances from the common garden trial

Six provenances from the 32 present in the trial were selected for intensive leaf-trait measurements based on their climate and region of origin, and covering a broad geographical cline. These were: the local Spanish provenance “Zorraquins-Ezcaray” (ES); a provenance from a mild maritime site, “Farchau” in northern Germany (DE); a south-eastern continental European provenance, from “Gotze-Delchev” in Bulgaria (BG); and two provenances from cooler sites in central Europe, one representing a continental-moist climate from “Brumov” in the Czech Republic (CZ) and the other the continental cold range-edge from “Jaworze” in eastern Poland (PL); and finally the most northern provenance from “Gullmarsberg” in Sweden

(SE) with a cold maritime climate (Table 1). At the time of selection in the spring of 2008 the height and basal diameter of all of the trees in the trial was measured (Table 2).

Leaf trait measurements

For each provenance, 12 trees from 50 planted in each of 3 blocks (i.e. 36 trees per provenance) were selected for leaf trait measurements prior to bud burst in the spring of 2008. To avoid edge effects, alternate trees from the middle three rows of each block were measured, excluding atypically large, small or dead trees for each provenance in order to reduce confounding factors. Bud burst was monitored in all trees from each provenance on three occasions, on 25 April 2008 (day of the year—day 115), 1 May 2008 (day 121) and 8 May 2008 (day 128). The bud burst date was calculated from these three measurements (details of the analysis of beech phenology are available in Robson et al. 2011). Leaf senescence was likewise monitored for all trees on one occasion on the 1–2 October 2008, by estimating the proportion of discoloured leaves on each tree.

Measurements of gas exchange and leaf water potential were made in the early summer (9–11 July—days 191–193) and compared with leaves measured in midsummer (13–15 August—days 224–226). Sampling was performed on the third or fourth distal sun-leaf from a south-orientated branch at approximately two-thirds height of the tree, and the same leaves used for gas exchange were later sampled for midday leaf water potential (Ψ_{md}).

Sequential measurements of leaf gas exchange under light-saturated conditions were performed using two cross-calibrated LICOR-6400 IRGA systems (LI-6400; Li-Cor Inc., NE, USA) working in parallel. Each machine was used for half of the twelve plants measured in each plot to avoid

Table 1 The location of the original site of the six beech provenances compared in a common garden trial at the trailing edge of the species range

Provenance country	Longitude (°)	Latitude (°)	Altitude (m asl)	Annual ppt (mm)	May–June ppt (mm)	July–Aug ppt (mm)	Annual Temp (°C)	May–June temp (°C)	July–Aug temp (°C)
Gullmarsberg, Sweden (SE)	11.39	58.22	25	735 \pm 118	107 \pm 40	143 \pm 52	6.7 \pm 1.0	12.5 \pm 1.0	16.1 \pm 1.2
Farchau, Germany (DE)	10.40	53.39	55	673 \pm 121	116 \pm 42	143 \pm 48	8.8 \pm 0.8	13.9 \pm 0.9	17.2 \pm 1.3
Jaworze, Poland (PL)	19.10	49.50	450	740 \pm 152	183 \pm 60	191 \pm 78	8.2 \pm 0.9	14.6 \pm 1.1	17.6 \pm 1.1
Brumov-Sidonie, Czech (CZ)	18.03	49.03	390	685 \pm 131	167 \pm 54	171 \pm 74	7.5 \pm 0.8	13.9 \pm 0.9	17.1 \pm 1.2
Zorraquins-Ezcaray, Spain (ES)	-03.02	42.3	990	595 \pm 115	108 \pm 45	55 \pm 55	11.1 \pm 0.7	19.5 \pm 1.1	19.5 \pm 1.4
Gotze-Delchev, Bulgaria (BG)	23.44	41.34	1450	525 \pm 121	116 \pm 41	75 \pm 38	7.4 \pm 0.7	17.8 \pm 1.3	17.9 \pm 1.3

The monthly mean annual temperature (temp) and precipitation (ppt.) at the site of provenance origin are given. May–June and July–August averages are shown for comparison with weather data from 2008 during the sampling period. Means for the last 50 years \pm 1 SD are taken from the COST E52 database (Robson and Rasztoovits, unpublished)

Table 2 Tree height and basal diameter for the six provenances in spring of 2008 compared in a common garden trial at the trailing edge of the species range

Growth parameter	SE	DE	PL	CZ	ES	BG
Height growth (cm)	71.8±8.0 ^D	159.4±7.8 ^A	127.5±8.0 ^B	112.5±5.2 ^C	151.6±6.3 ^A	153.8±7.2 ^A
Basal diameter (mm)	13.5±1.3 ^D	30.8±1.6 ^A	25.1±1.7 ^B	21.0±1.0 ^C	31.8±1.4 ^A	27.2±1.6 ^A
Bud burst day	121.3±3.8 ^C	118.3±2.9 ^B	117.1±3.4 ^B	118.1±2.8 ^B	118.6±3.6 ^B	114.4±2.3 ^A
Senescence (%)	56±15	54±9	84±20	83±19	90±19	36±6

Growth parameters are means (±SE) of all 150 trees (except any dead trees) per provenance. The bud-burst day (number of days after 1 January 2010) was calculated by fitting the Weibull function for each tree. Senescence is given as the percentage of trees with senescent leaves in each provenance on 1 October 2010. Differences in the superscript letter code (A, B, C and D) denote a statistically significant ($P < 0.05$) difference between provenances for a particular trait measured either in early summer or midsummer (details in the supplemental information Table S1)

SE Gullmarsberg, Sweden; DE Farchau, Germany; PL Jaworze, Poland; CZ Brumov-Sidonie, Czech Republic; ES Zorraquins-Ezcaray; BG Gotze-Delchev, Bulgaria

any systematic measurement errors. Measurements were performed at mid-morning on three consecutive days under clear sky conditions. A LI-6400-40 Leaf Chamber equipped with a LED light-source was used to obtain constant saturating photosynthetic photon flux density (PPFD) during measurements ($1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$). The chamber temperature (ca. 20 °C), CO₂ concentration (400 ppm) and flow rate through the chamber ($500 \mu\text{mol s}^{-1}$) were also maintained. A reading of photosynthesis was taken when the three parameters, internal CO₂ (C_i), net photosynthesis (A_{area}) and stomatal conductance (g_{wv}), were considered to be stable, and the mean of five consecutive stable readings per leaf was used as one replicate in the data analysis.

Leaf water potential was measured with a pressure chamber (PMS 600, Albany, Oregon, USA) on the same days as gas exchange measurements, predawn (Ψ_{pd}) and at midday (Ψ_{md}). The soil-leaf hydraulic conductance (K_L) was calculated as transpiration expressed on a leaf area basis (E_{wv}) divided by the predawn-to-midday leaf water potential difference (Ψ_{diff}).

$$K_L = E_{\text{wv}} / (\Psi_{\text{predawn}} - \Psi_{\text{midday}}) \quad (1)$$

Detached leaves were maintained fresh on ice until they could be scanned for leaf area determination (WinFolia, Regent Instrument Inc., Québec, Canada). These leaves were subsequently oven dried at 65 °C, weighed to obtain their specific leaf area (SLA), and analysed for nitrogen content (CN Analyser, EuroEA3000-Single, EUROvector, Milan, Italy) and stable carbon isotopic composition ($\delta^{13}\text{C}$; Carlo Erba 1108 elemental analyser and Micromass Isochrom-GC/MG mass spectrometer). The $\delta^{13}\text{C}$ composition of beech leaves reflects their degree of stomatal opening during assimilation and thus can be taken as a proxy to assess water-use efficiency integrated over the life span of C assimilated and held in the leaf (Farquhar et al. 1989). Differences in $\delta^{13}\text{C}$ between individuals are only meaningful when comparing trees growing under similar environmental conditions, as was the case in this study.

Data analyses

The effects of provenance origin on functional leaf traits and on photosynthetic performance of the six beech provenances in early and midsummer were tested using a mixed-model ANOVA. This was based on a complete-block design with repeated measures. The two IRGA machines and operators were considered as fixed factors in the ANOVA as a statistical control on the use of two different devices to carry out measurements. Block was included as a random effect in the analysis, and there was a significant effect of block on most leaf traits, however there was no statistically significant block-by-provenance interaction effect, indicating that blocking was effective in accounting for gradients across the site but that provenances were not differentially affected by the blocking. To test whether the correlation coefficient (r) differed significantly from zero in the examined relationships between pairs of traits, a t test was performed. All analyses were performed using the open-source software R, library NLME (R, version 2.8.1., R Development Core Team 2008).

Results

Gas exchange

The physiological performance of all the beech provenances declined through the summer (Table 3), as temperatures increased and precipitation diminished from early- to midsummer. Down-regulation of gas exchange was reflected in reduced light-saturated leaf-area photosynthetic rates (A_{area}), which also differed among provenances: these were highest in the Bulgarian (BG) and Spanish (ES) provenances, and lowest in the Swedish provenance (SE) throughout (Table 3). The other three provenances fell between these extremes, and of these three, A_{area} of the Polish (PL) and German (DE) provenances dropped abruptly between the two measurements

Table 3 Early and midsummer point measurements of gas exchange, leaf traits, and leaf $\delta^{13}\text{C}$ for six beech provenances growing in a common garden trial at the trailing edge of the species range

Leaf trait	Season—prov	SE	DE	PL	CZ	ES	BG
A_{area} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Early summer	9.1±0.3 ^C	11.9±0.3 ^{AB}	11.4±0.4 ^B	10.0±0.4 ^C	12.7±0.4 ^A	12.1±0.3 ^{AB}
	Midsummer	7.8±0.5 ^C	9.8±0.4 ^B	10.1±0.5 ^{AB}	10.0±0.4 ^B	11.5±0.4 ^A	11.0±0.4 ^A
A_{mass} ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	Early summer	64.4±3.3 ^D	97.2±3.5 ^B	99.4±4.4 ^{AB}	79.4±3.5 ^C	108.3±3.6 ^A	104.2±3.6 ^{AB}
	Midsummer	64.4±4.8 ^D	89.6±4.1 ^{BC}	96.1±5.7 ^{BC}	88.3±4.6 ^C	113.2±5.0 ^A	100.0±4.8 ^{AB}
g_{wv} ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	Early summer	0.16±0.01 ^E	0.20±0.01 ^{BC}	0.19±0.01 ^{CD}	0.18±0.01 ^D	0.23±0.01 ^A	0.22±0.01 ^{AB}
	Midsummer	0.16±0.01 ^B	0.16±0.01 ^B	0.16±0.01 ^B	0.16±0.01 ^B	0.19±0.01 ^A	0.18±0.01 ^A
C_i ($\mu\text{mol mol}^{-1}$)	Early summer	285.3±4.1 ^{AB}	269.2±3.3 ^D	278.9±3.2 ^{BC}	290.1±3.5 ^A	276.9±3.7 ^C	274.6±4.0 ^{CD}
	Midsummer	304.8±5.1 ^A	285.0±4.0 ^B	277.8±6.4 ^B	281.6±4.8 ^B	283.9±4.7 ^B	283.1±2.9 ^B
IWUE ($A_{\text{satmass}} / g_{\text{wv}}$)	Early summer	61.8±2.5 ^{AB}	65.1±2.1 ^A	64.9±2.0 ^A	58.4±2.1 ^B	60.4±2.4 ^{AB}	61.1±2.6 ^{AB}
	Midsummer	51.6±3.0 ^B	63.2±2.5 ^A	67.6±3.9 ^A	65.2±2.9 ^A	63.3±2.9 ^A	63.9±1.8 ^A
Leaf $\delta^{13}\text{C}$ (‰)	Midsummer	-30.05±0.16 ^C	-29.18±0.15 ^A	-29.64±0.14 ^B	-29.72±0.12 ^B	-29.19±0.14 ^A	-28.98±0.13 ^A
SLA ($\text{m}^2 \text{ kg}^{-1}$)	Early summer	15.17±0.43 ^A	12.60±0.21 ^{BC}	12.07±0.22 ^{CD}	13.10±0.23 ^B	12.02±0.18 ^D	11.90±0.18 ^D
	Midsummer	13.00±0.34 ^A	11.21±0.17 ^C	11.16±0.26 ^{BC}	11.68±0.29 ^B	10.32±0.19 ^D	11.37±0.28 ^{BC}
Leaf Size (cm^2)	Early summer	11.3±0.5 ^C	17.4±0.7 ^A	16.4±0.6 ^{BA}	16.8±0.5 ^A	15.3±0.5 ^B	17.0±0.6 ^A
	Midsummer	12.6±0.6 ^C	18.2±0.7 ^A	17.1±0.7 ^{AB}	17.0±0.5 ^{AB}	16.5±0.6 ^B	17.8±0.6 ^{AB}
N_g ($\% \text{ g}^{-1}$)	Early summer	2.08±0.05 ^C	2.22±0.04 ^B	2.15±0.05 ^{BC}	2.10±0.04 ^C	2.32±0.04 ^A	2.11±0.03 ^C
	Midsummer	1.65±0.06 ^{BC}	1.68±0.03 ^B	1.61±0.05 ^{BC}	1.70±0.04 ^B	1.90±0.05 ^A	1.56±0.06 ^C
N_{area} (mg m^{-2})	Early summer	1.45±0.05 ^D	1.80±0.05 ^B	1.85±0.06 ^B	1.65±0.05 ^C	1.98±0.05 ^A	1.79±0.04 ^B
	Midsummer	1.34±0.06 ^C	1.53±0.04 ^B	1.50±0.06 ^B	1.50±0.05 ^B	1.90±0.06 ^A	1.43±0.07 ^{BC}
C:N ratio	Early summer	25.2±0.6	23.5±0.4	24.4±0.5	24.9±0.5	22.4±0.4	24.5±0.4
	Midsummer	33.8±1.3	31.1±0.7	33.6±1.2	30.5±0.8	27.8±0.8	36.1±1.8
PNUE (A_{mass} / N_g)	Early summer	6.64±0.19 ^{ABC}	6.83±0.25 ^A	6.39±0.16 ^{BC}	6.23±0.20 ^C	6.55±0.19 ^{ABC}	6.78±0.13 ^A
	Midsummer	6.00±0.36 ^C	6.38±0.26 ^{BC}	7.02±0.42 ^B	6.85±0.35 ^B	6.11±0.22 ^C	8.87±0.57 ^A

Each column contains the mean trait value (\pm SE) of 36 trees per provenance. Differences in the superscript letter code (A, B, C and D) denote a statistically significant ($P < 0.05$) difference between provenances for a particular trait at early summer or midsummer (details in the [supplemental information Table S1](#))

SE Gullmarsberg, Sweden; DE Farchau, Germany; PL Jaworze, Poland; CZ Brumov-Sidonie, Czech Republic; ES Zorraquins-Ezcaray; BG Gotzdelchev, Bulgaria

(Table 3). The same ranking of provenances was maintained when photosynthesis was considered on a mass basis (A_{mass}), but the temporal differences recorded for A_{area} were absent, offset by reduced SLA on the later date (Table 3).

The rate of stomatal conductance (g_{wv}) decreased between the two measurements in line with the decline in A_{area} in all but the SE provenance where g_{wv} was consistently low (Table 3). In early summer, when conditions were still relatively benign, differences in the control of water loss among provenances were relatively large and highly correlated with differences in maximum photosynthetic rates ($r = 0.96$; Fig. 1), illustrating conserved instantaneous water-use efficiency (IWUE) prior to the onset of summer drought (Table 3). However by the time of the later measurement in midsummer, the provenances segregated into two clusters: g_{wv} was similar among the PL, CZ, DE and SE provenances, and remained higher in ES and BG (Table 3; Fig. 1). Although DE and PL had the highest IWUE in early summer, they nevertheless exhibited reduced photosynthetic rates and g_{wv} in midsummer (Table 3; Fig. 1), providing no evidence that initial conservative water use could prolong the period of relatively unstressed gas exchange.

As with g_{wv} , the internal CO_2 concentration (C_i) also varied more in the early summer than in midsummer. In early summer, C_i ranked from lowest to highest $\text{DE} < \text{BG} < \text{ES} < \text{PL} < \text{SE} < \text{CZ}$ (Table 3). In midsummer, C_i was only significantly higher in the SE provenance compared with the rest of the provenances; ranked $\text{PL} \leq \text{CZ} \leq \text{BG} \leq \text{ES} \leq \text{DE} < \text{SE}$ (Table 3). IWUE significantly decreased over time in the SE, whereas it increased or was stable in the other provenances between the two sampling dates (Table 3). The combination of high C_i and low IWUE in SE was mainly due to reduced carbon assimilation (A_{area}) from early summer to midsummer, since g_{wv} was constant between both sampling dates (Table 3). In the other provenances, the improvement in IWUE was mainly due to the lowering of g_{wv} over time (Fig. 1). Within-provenance variability in IWUE, shown by the relationship of A_{sat} and g_{wv} in individual trees, was large (Table 3; Fig. S3). Variability within CZ in early summer, ES in midsummer and DE on both measurement dates was particularly high (Table 3), implying that regulation of water loss was not tightly conserved in these cases.

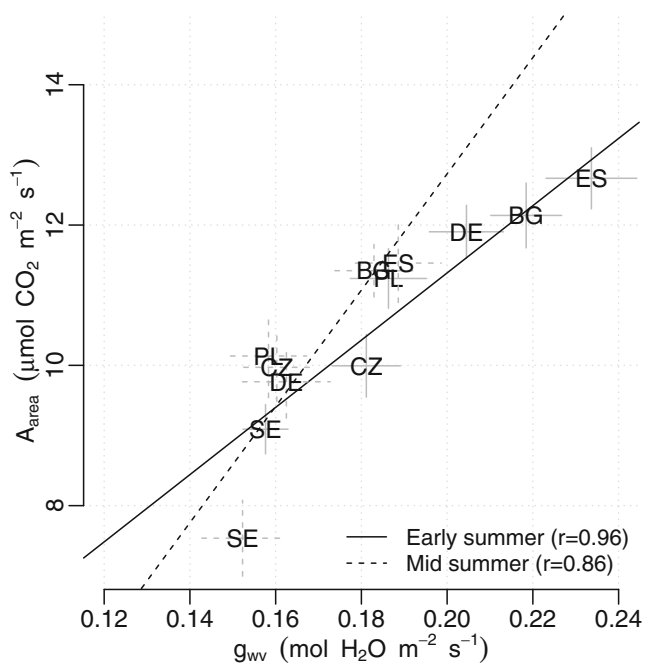


Fig. 1 Instantaneous water-use efficiency (IWUE): the relationship between A_{area} (micromoles of CO_2 per metre square per second) and g_{wv} (moles of H_2O per metre square per second) in early ($P=0.002$) and midsummer ($P=0.029$). Each point is marked by the provenance code, crosses represent the mean value of each provenance ± 1 SE ($N=36$). The relationship of A_{area} with C_i is given in the Fig. S1

Leaf water status and hydraulic conductance

In general, the measured pre-dawn water potentials (Ψ_{pd}) were very high for plants otherwise expected to be suffering water stress and the differences among provenances were relatively small (Table 4). Even in midsummer, all provenances recovered leaf water potential overnight to a Ψ_{pd} around -0.25 MPa (Table 4). We cannot exclude the possibility that the occurrence of overnight dew at the time of sampling in midsummer may have slightly rehydrated the leaves just prior to measurement and could ameliorate the effects of soil dryness (given the near-absence of summer precipitation) during the early morning. However, the mean Ψ_{midday} dropped to below -1.9 MPa in all but the BG provenance which gave the smallest Ψ_{diff} between predawn and midday (Table 4). The DE provenance had the next smallest Ψ_{diff} , while SE and PL produced the largest Ψ_{diff} (Table 4). These water potential measurements suggest that Ψ_{pd} was a poor predictor of the real water stress endured by seedlings in this instance, which according to the precipitation and temperature data was maximal in midsummer (Table 1) and imposed a substantial negative effect on gas exchange (Table 3).

The soil–leaf hydraulic conductance (K_L) illustrated that differences in hydraulic sufficiency among provenances were more pronounced in early summer than midsummer

Table 4 Early and midsummer point measurements of leaf water potential for six beech provenances growing in a common garden trial at the trailing edge of the species range

Leaf trait	Season—prov	SE	DE	PL	CZ	ES	BG
Ψ_{pd} (M Pa)	Early summer	-0.30 ± 0.01^{CD}	-0.27 ± 0.02^{AB}	-0.28 ± 0.02^{BC}	-0.31 ± 0.02^D	-0.28 ± 0.01^{BCD}	-0.25 ± 0.01^A
	Midsummer	-0.17 ± 0.01^A	-0.25 ± 0.02^B	-0.25 ± 0.02^B	-0.23 ± 0.02^B	-0.25 ± 0.01^B	-0.23 ± 0.01^B
Ψ_{mid} (M Pa)	Early summer	-1.80 ± 0.02^D	-1.59 ± 0.02^A	-1.75 ± 0.01^C	-1.70 ± 0.02^{BC}	-1.75 ± 0.01^C	-1.67 ± 0.03^B
	Midsummer	-2.08 ± 0.04^C	-1.99 ± 0.04^B	-2.09 ± 0.03^C	-2.02 ± 0.04^{BC}	-2.03 ± 0.05^{BC}	-1.85 ± 0.04^A
Ψ_{diff} (M Pa)	Early summer	1.49 ± 0.01^A	1.29 ± 0.02^C	1.45 ± 0.02^{AB}	1.34 ± 0.03^C	1.48 ± 0.02^A	1.42 ± 0.03^B
	Midsummer	1.90 ± 0.04^A	1.72 ± 0.03^C	1.82 ± 0.02^B	1.77 ± 0.03^{BC}	1.76 ± 0.04^{BC}	1.60 ± 0.03^D
K_L (mmol m^{-2} MPa^{-1} s^{-1})	Early summer	1.70 ± 0.06^C	2.47 ± 0.11^A	2.11 ± 0.10^B	2.30 ± 0.13^{AB}	2.42 ± 0.09^A	2.41 ± 0.09^A
	Midsummer	0.95 ± 0.04^C	1.10 ± 0.06^B	1.10 ± 0.04^B	1.13 ± 0.04^B	1.22 ± 0.05^A	1.28 ± 0.04^A

Each column contains the mean trait value (\pm SE) of 36 trees per provenance. Differences in the superscript letter code (A, B, C and D) denote a statistically significant ($P < 0.05$) difference between provenances for a particular trait at measured either in early summer or midsummer (details in the supplemental information Table S1)

SE Gullmarsberg, Sweden; DE Farchau, Germany; PL Jaworze, Poland; CZ Brumov–Sidonie, Czech Republic; ES Zorraquins-Ezcaray; BG Gotze-Delchev, Bulgaria

(Table 4). In early summer, K_L was particularly low in SE, and K_L for PL was also lower than for the remaining provenances. By midsummer, K_L had decreased by more than one third in all provenances and was highest in BG and ES (Table 4) reflecting the differences in g_{wv} already mentioned (Table 3). In early summer, g_{wv} and Ψ_{diff} were very weakly associated within provenances, whereas by midsummer the relationship was much stronger (Fig. S4), indicating that soil water stress and evaporative demand only became limiting to gas exchange from midsummer. This relationship varied in strength across the provenances, remaining relatively weak in the BG provenance and non-significant in the DE (Fig S4); the two provenances which exhibited the highest K_L in early summer and smallest Ψ_{diff} on both sampling dates (Table 4).

Comparing instantaneous and seasonally integrated leaf water-use efficiency from $\delta^{13}C$

There were significant differences in mean $\delta^{13}C$ composition among the provenances at midsummer: $\delta^{13}C$ was highest in the ES, DE and BG and lowest in the SE, compared to PL and CZ (Table 3). This segregation of provenances conformed to the general trends in IWUE obtained from gas exchange (Table 3) and water potential (Ψ) point measurements (Table 4), as illustrated by the positive relationships between $\delta^{13}C$ and these variables (Table 5; Fig. S6). The weaker relationship of midsummer $\delta^{13}C$ with A_{area} , g_{wv} and K_L in midsummer than in early summer (Table 5) confirms that the provenances differ in their regulation of gas exchange; with BG and ES maintaining the highest photosynthetic capacity of the provenances in midsummer and DE having more-conservative gas exchange when water stressed, but all three provenances exhibiting relatively high $\delta^{13}C$ (smaller negative values than the other provenances: Table 3). This contrasts with the decline in photosynthetic

Table 5 The relationships of $\delta^{13}C$ (per mille) with gas exchange traits A_{area} (micromoles of CO_2 per metre square per second), g_{wv} (moles of H_2O per metre square per second) and K_L (millimoles per metre square per megapascal per second) in early and midsummer

Relationship with leaf $\delta^{13}C$ (‰)	Season	<i>r</i>	<i>P</i>
A_{area} ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$)	Early summer	0.93	0.018
	Midsummer	0.85	0.008
g_{wv} ($\text{mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$)	Early summer	0.93	0.051
	Midsummer	0.80	0.056
C_i ($\mu\text{mol mol}^{-1}$)	Early summer	-0.74	0.091
	Midsummer	-0.57	0.224
K_L ($\text{mmol m}^{-2} \text{ MPa}^{-1} \text{ s}^{-1}$)	Early summer	0.91	0.011
	Midsummer	0.82	0.044

A *t* test was performed to establish whether the correlation coefficient *r* differed significantly from zero. The correlations among provenances are shown graphically in Fig. S6

capacity suffered by SE, which is also evident as the lowest seasonally integrated water-use efficiency inferred from the low $\delta^{13}C$ (Table 3).

Plant height, leaf morphology and N content

For the early summer measurement only, leaves from the ES provenance had a higher N content than the other provenances (Table 3). The leaf N content decreased in all provenances by midsummer, although this decrease was also smallest for the ES provenance. These decreases in leaf N content reflected lower SLA in all provenances, suggesting that differences in SLA among provenances were largely responsible for the differences in N (Table 3), and also coincided with the increases in C/N ratio.

In early summer, the DE provenance had the highest PNUE and CZ the lowest. Decreases in N coupled with a fairly steady A_{mass} saw PNUE increase in BG, PL and CZ from early to midsummer; whereas maintenance of high leaf N content in ES, decreasing A_{mass} in DE and a combination of these two factors in SE, led to reduced PNUE in these three provenances (Table 3).

The mean trends in tree height from measurements in spring 2008 were well correlated with the trait-based assessments of performance. The DE, BG and ES provenances were significantly taller and had a thicker diameter than the rest, followed by the PL then the CZ provenance with the SE provenance considerably smaller (Table 2). There were notable correlations between height and K_L in early summer ($r=0.97$) and $\delta^{13}C$ in midsummer ($r=0.94$; Fig. S7).

Discussion

Inter-provenance differentiation in functional leaf traits

Following the last glaciation, beech is reported to have been one of the faster species to recolonise Europe (Leonardi and Menozzi 1995; Giesecke et al. 2007; Magri 2008). Studies using molecular markers indicate that high genetic variability exists even among geographically close natural populations (Jump and Peñuelas 2007; Chybicki et al. 2009) and likewise in intensely managed stands (Buiteveld et al. 2007). This high genetic variability together with the phenotypic differences that we present here suggest that irrespective of colonisation rate, beech populations have had time to develop local adaptation. Here, we investigated the response of six very-distinct provenances of beech, spanning its European distribution (Magri et al. 2006) growing together in a common-garden trial at its southwestern range limit in Spain. Our study revealed seasonal differences in physiological and morphological phenotypic traits among these provenances which may influence their capacity to

respond to summer drought. This result reinforces reports of high intraspecific variability in growth-related traits (Borghetti et al. 1993; García-Plazaola and Becerril 2000b), traits reflecting drought-stress response, e.g. $\delta^{13}\text{C}$, cavitation resistance and specific root area (Mátyás et al. 2009a; Rose et al. 2009; Wortemann et al. 2011) of beech growing in more benign climates.

The general pattern that emerged from the study was consistent with our hypothesis that the physiological state of provenances from the south of Europe, ES and BG, permitted photosynthetic function to be maintained closer to their optima through midsummer when compared with central and northern European provenances. The two southern provenances were able to maintain relatively high rates of gas exchange at midsummer without compromising their water-use efficiency and height growth. This result contrasts with other studies which have likewise reported marginal provenances (Rose et al. 2009), or those from more water-stressed environments (Peuke et al. 2002), to be better adapted to cope with prolonged water stress, but only at the expense of growth rates during this period of stress. An explanation for this difference is that our site generally provides more severe conditions (dry summers and a short growing season) than sites normally used for beech trials. Furthermore, previous studies have used young beech seedlings rather than juvenile trees where growth reflects the accumulated effects of harsh conditions integrated over several years (Mátyás et al. 2009a).

Our results are consistent with findings in other tree species of high inter-provenance variability in leaf gas exchange, leaf stable isotope $\delta^{13}\text{C}$ composition, and SLA (Ares et al. 2000; Gratani et al. 2003; Premoli and Brewer 2007), and evidence of pronounced inter-provenance differentiation in traits related to above-ground growth in beech (Meier and Leuschner 2008). In our study, patterns of gas exchange, $\delta^{13}\text{C}$ and leaf water potential were very similar between the local ES and BG provenances, originating from Mediterranean and Continental climates respectively. This similarity is somewhat surprising, because despite originating from relatively warm–dry climates for beech, they exhibit a large difference in phenology. Our data on bud-burst conformed to established Europe-wide patterns of beech phenology from early southeastern to late northern maritime provenances (Robson et al. 2011). The BG provenance was first to flush, on average 4 days before the ES provenance and 7 days ahead of the SW provenance (Table 2). The earlier phenology of the BG provenance was also reflected in its larger decline in leaf N approaching midsummer than the other provenances, hence, the maintenance of a comparable rate of photosynthesis in the two provenances at midsummer gives rise to a higher PNUE in the BG provenance. However by the time of autumn leaf senescence, this difference was no longer apparent; in

fact, the BG provenance retained its leaves longer than the others (Table 2).

There was a loss of photosynthetic capacity in all the provenances going from early to midsummer, but this was most pronounced in the DE provenance, which performed almost on a par with ES and BG in early summer but was more similar to CZ and PL at midsummer. However, despite originating from a relatively mild climate, the DE provenance exhibited enough plasticity to grow well at the site. In contrast, the CZ mountain provenance and the PL provenance from wet climates with cold winters had relatively low rates of gas exchange and stomatal conductance. While this enabled them to maintain high IWUE through the summer, it did not allow them to attain high rates of assimilation and growth, presumably a limitation arising from the more-severe water stress at the trial site than the water stress these provenances normally experience at their origins. It is noteworthy that only the Swedish provenance was unable to increase IWUE to counter the more stressful conditions in midsummer. In addition to poor physiological performance of SW, its accumulated height growth was much less than the other provenances after 11 years growing in the trial and its leaf phenology suggested a shorter growing season (Table 2). This provenance appears to be very poorly adapted to the warm–dry conditions at the site in Spain, since its photosynthetic capacity decreased greatly between early and midsummer despite it maintaining similar rates of stomatal conductance. Above 25 °C, its A_{area} was observed to decrease rapidly (personal observation) suggesting that the leaves of SE were poorly adapted to function at high temperatures. These findings could be interpreted as the action of non-stomatal limitations to leaf carbon uptake triggered in response to the adverse conditions for this provenance, and would warrant further investigation.

Interplay between leaf physiological and morphological variables

Photosynthesis and stomatal conductance of water vapour were highly coupled across provenances and dates (Fig. 1). However, there was some variation in the general relationships among leaf traits between provenances. There were pronounced differences in leaf $\delta^{13}\text{C}$ among provenances, which were of an equivalent magnitude to those reported for other species (Ares et al. 2000; Aspelmeier and Leuschner 2004; Grossnickle and Russell 2010).

The lowest carbon gain for water lost was in the SE provenance, and likewise this result was reinforced by lowest leaf $\delta^{13}\text{C}$ in this provenance; a parameter that can be considered an integrative measure of leaf-level IWUE over the growing season. Furthermore, the leaves of the SE provenance had the highest SLA and lowest degree of sclerophyllia; a trait commonly associated with provenances

from dry habitats (Warren et al. 2005; Ramírez-Valiente et al. 2010). Taken together, these factors indicate that SE has the poorest physiological performance at the site. This is unsurprising given the provenance's northern-maritime climate of origin, which is very different from the conditions at the trial site which approaches a continental-Mediterranean climate. In direct contrast to SE, the BG and ES provenances had the highest $\delta^{13}\text{C}$ and lowest SLA, both traits that should be considered as symptomatic of a more-effective response to dry conditions (Li et al. 2000).

The provenances from PL, CZ and DE exhibited more-conservative resource use than those from ES and BG in both early and midsummer. The differences in $\delta^{13}\text{C}$ compared with changes in other functional leaf traits, reveal a divergence in strategy between the DE provenance and the two southern European provenances, ES and BG, all of which grew similarly well in the trial. The north German provenance exhibited comparable $\delta^{13}\text{C}$ to the two southern European provenances (ES and BG) and attained similarly high early summer light-saturated photosynthesis but reduced gas exchange in midsummer. DE performed relatively well in attainment of greater accumulated height growth than the other provenances, which may be connected with its high leaf area and K_L in the early summer. This result is surprising given that it originates from a very mild wet climate and differs from the findings of Peuke et al. (2002), that a provenance from a similar area of northern Germany compared unfavourably under drought stress with a marginal Polish provenance from a colder climate. This disparity between results may reflect different processes operating on the local or regional scale that promote local adaptations as opposed to the large-scale climatic comparisons that we consider here.

The suggestion that the changes in g_{wv} with provenance may derive from changes in their hydraulic efficiency is supported by differences in the hydraulic proxy (K_L) among provenances, although direct measurements would be needed to verify this result. This assertion is further supported by the fact that provenances with lower hydraulic conductance were also less efficient in water use as inferred from their more negative leaf $\delta^{13}\text{C}$. In fact, there was a particularly strong among-provenance correlation between tree height and both leaf $\delta^{13}\text{C}$ and K_L in the early summer.

Implications for beech provenances under marginal conditions

In other forest tree species, more of the variation in the expression of functional traits is attributable to genetic variability at the intra-provenance level than is explained by inter-provenance variability (Hamrick 2004; Ramírez-Valiente et al. 2010). However, phenotypic plasticity can generally explain even more variability in functional traits

than genetic differences (Herbette et al. 2010), making it difficult in some cases to distinguish phenotypic plasticity from local adaptation (Baquedano et al. 2008; Gimeno et al. 2009). This study reflects differences among beech provenances accumulated over 11 years of growth, but examines differences in their physiological leaf traits measured over just one growing season. To obtain a more complete perspective of their plasticity in response to climate at the trial site at the trailing range-edge, several field seasons of monitoring would be required. For example, while early-flushing provenances (e.g. BG) performed well in 2008, this would not be the case if they had suffered damage from late frosts. Nevertheless, the degree of differentiation in the phenotypic traits among the provenances studied here reinforces the view that intraspecific variability may be important in beech (Peuke et al. 2002; Leonardi et al. 2006; Meier and Leuschner 2008) and that the provenances studied here come from different genetic pools, and experienced different evolutionary histories under contrasting selective pressures (Magri et al. 2006; Magri 2008). Although the hierarchy of variability within and among beech provenances is yet to be well defined, our findings support the premise that extensive fragmentation of beeches' range over areas with different biogeographical histories may have heightened the importance of the contribution made by the adaptation of fragmented populations to local climate (Parelle et al. 2006; Jump et al. 2006; Chybicki et al. 2009; Rose et al. 2009).

This study of the physiological response of provenances from different climatic regions of Europe has demonstrated that provenances from Mediterranean and dry continental conditions to the south of Europe are among the least sensitive to water scarcity and are better equipped to remain productive under warm dry conditions expected to occur more frequently under future climate change scenarios (Jump et al. 2006; Mátyás et al. 2009b). But, although local provenances of forest tree species can adapt to drought stress at the southern limit of the range, their capacity for adaptation is outstripped by the current rate of climate change (Jump et al. 2009; Linares and Tiscar 2010), therefore putting these provenances at particular risk. Since these provenances hold valuable traits for water stress tolerance, their continued study to identify the genetic basis for these responses would be worthwhile.

Conclusions

Our study demonstrated that intrinsic intraspecific variability among beech provenances originating across Europe leads to differences in functional leaf trait responses through the summer at a dry range-edge site. These differences were also apparent as divergence in accumulated height among provenances after 11 years of growth. The susceptibility to

drought of some of the provenances examined at the trailing edge of the range in this trial agrees with previous studies from beech forests in suggesting that beech is among the more susceptible of European temperate tree species to climate change. However, provenances from the southern range of the species may provide useful traits combining good performance with drought resistance under the sort of drier conditions predicted for those parts of Europe that are currently relatively mild.

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