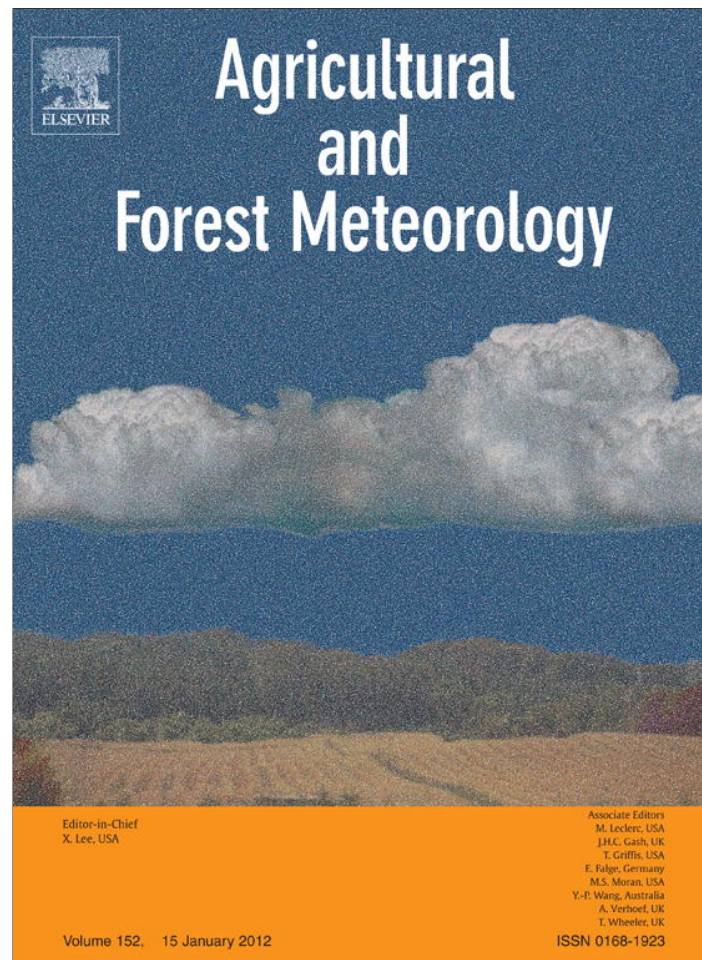


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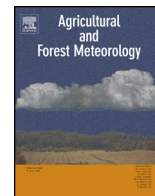
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Flushing phenology and fitness of European beech (*Fagus sylvatica* L.) provenances from a trial in La Rioja, Spain, segregate according to their climate of origin



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ABSTRACT

European beech (*Fagus sylvatica*) reaches the south-western limit of its distribution in northern Spain, beyond which the Mediterranean climate is thought to restrict further expansion of the species range. Consequently, current and future climate change in the region is expected to push back the range margin and threaten the survival of local beech populations. In a provenance trial of pan-European beech populations growing under harsh conditions in La Rioja, we tested whether associations between the timing of spring phenology assessed over three years affected the performance of beeches at the site, and whether they exhibited a trade off between growth rate and survival. In particular, we considered whether the relationship between performance under conditions of summer drought and spring frost at the trial site was dependent on the climate at the site of provenance origin. We report that early-flushing provenances from continental climates in the south-east and parts of central Europe were among the tallest after ten years of growth in the trial: for instance from Val di Sella, northern Italy (mean bud burst day 114 and height 173 cm); Gotze Delchev, Bulgaria (day 115, height 135 cm); and Aarberg, Switzerland (day 118, height 151 cm). While late-flushing provenances from maritime climates in northern and western Europe were among the shortest in the trial: for instance from Soignes, Belgium (day 124, height 73 cm); Gullmarsberg, Sweden (day 122, height 69 cm); and Bathurst Estate, southern England (day 122, height 85 cm). There was no evidence that early flushing increased the mortality of trees at the trial site. The large-scale geographical patterns in flushing strategy reflected a trade off between pre-emptive growth before the summer drought and susceptibility to late frosts. Our findings emphasise the need to conserve populations from the range edge in the south of Europe, the Balkans and western Alps, whose combination of early flushing and drought resistance may become desirable traits for the improved future performance of beech in response to climate change.

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1. Introduction

European beech (*Fagus sylvatica*) is an important temperate forest species with a wide distribution across Europe (Giescke et al., 2007; Muñoz Sobrino et al., 2009). Northern and central Spain represent the south-western range limit of natural European beech woodland, beyond which the Mediterranean climate is thought to prohibit its further spread (Ramil-Rego et al., 2000; Fang and Lechowicz, 2006). Consequently, current and future climate change in the region is expected to push back the range margin

and threaten the survival of local beech populations (Jump et al., 2006; Kunstler et al., 2007).

The timing and regulation of flushing in European beech (*F. sylvatica* L.) has been keenly studied for many years (Klebs, 1914) as a potentially important control on fitness (Kramer et al., 2000). Flushing phenology is known to be genetically controlled and is a trait that varies greatly along geographical clines (Kramer, 1995; Falusi and Calamassi, 1996; Doi et al., 2009). Although the timing of flushing is clearly correlated to several crude environmental variables, such as elevation and spring temperature, the complex patterns of processes controlling leaf flush are hard to disentangle and continue to stimulate scientific research (Badeck et al., 2004; Körner and Basler, 2010; Vitasse and Basler, 2013).

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The potential interplay among those physiological responses that are generally known to influence plant phenology, and their relationship with various environmental cues, has proven an intriguing but elusive question to investigate in beech (Kramer, 1994; Hänninen and Kramer, 2007). Early studies under controlled conditions suggested that the photoperiodic switch from short to long days can bring flushing forward in seedlings (Wareing, 1953), a result confirmed by subsequent work suggesting that photoperiodic control allows greater seasonal stability in flushing as a safeguard against late frosts (Heide, 1993). Under controlled conditions, two months of winter chilling ($<10^{\circ}\text{C}$), functioning in tandem with day length, will release of beech buds from dormancy (Falusi and Calamassi, 1990). Warm spring temperatures have an auxiliary role in hastening flushing once dormancy is broken. The environmental cues needed for breaking dormancy (chilling and photoperiod), and physiological priming (temperature response) of the bud, suggest that at least two physiological mechanisms determine the timing of bud burst. Various models have attempted to marry the parallel mechanisms that control development, either in series, concomitantly, or with some interaction (Schieber, 2006; Hänninen and Kramer, 2007; Vitasse and Basler, 2013). However, as more parameters are added to increase the realism of process-based models, degrees of freedom are lost, meaning that the improvements of fit resulting from greater complexity are often insignificant in increasing the models' explicative value (Richardson and O'Keefe, 2009). These models of the environmental controls on phenology require large-scale experimental testing for validation. Common-garden field trials provide the ideal platform for these tests.

European beech trees from the same parent population grown at different geographical locations (Robson et al., 2011) or, alternatively, a variety of populations of different provenance grown at a common location (Robson et al., 2012), can provide an insightful comparison of the genotypic component versus phenotypic plasticity of flushing. Such trials give more pertinent mechanistic information, going beyond observational studies and controlled environmental manipulations, since they allow for an intraspecific comparison of beech populations of known provenance.

When a mixture of provenances is grown together in a common-garden trial, the timing of flushing among provenances has tended to be more heterogeneous than results obtained from earlier experiments under controlled conditions or tests using excised branches (Heide, 1993). Trees under natural conditions do not always follow a similar pattern to detached twigs, suggesting that intricate organismal-scale signalling integrates multiple environmental cues to initiate flushing. For instance, phenological assessment of a set of 158 beech provenances grown in a common-garden trial in Grosshansdorf, northern Germany, established that pronounced genetically governed patterns of flushing and leaf senescence exist related to the geographical origin of European beech populations (von Wühlisch et al., 1995). In that study, temperature sum of degree days above 5°C from 1st January was used as a biologically meaningful proxy for time until flushing. This revealed a gradient in the trial from early-flushing provenances in south-east and central Europe to late flushing in regions with more maritime climates and from western Europe and around the Baltic and North Seas. Several candidate factors may contribute to this pattern, such as gradients in spring temperatures and day length with latitude or in chilling requirement from milder more maritime climates. The ranking was also modified by altitude as a secondary factor, since as long as the chilling requirements are fulfilled, provenances from high elevations tend to flush and senesce early when grown together with low elevation provenances as they require less temperature forcing (von Wühlisch et al., 1995), this is despite the fact that *in situ* flushing is delayed by elevation as a safeguard against late frosts (Davi et al., 2011). However under sub-Mediterranean

conditions and other environments where water deficit during the summer is liable to impede growth, an early-flushing strategy can be advantageous since it enables plants to pre-empt summer drought and concentrate their carbon fixation early in the growing season (Gordo and Sanz, 2010; Gundererson et al., 2012; Monnier et al., 2012).

Here we test the genetically determined differences in flushing phenology among provenances growing at a stressful site on the range margin of beech, and examine the relationship of the timing of phenology with height growth and tree survival in populations from a very wide selection of populations spanning the range of European beech. We also examine consistency in the timing of spring phenology among these provenances over several years and how differences in the weather, particularly whether a sustained hard late frost in late-April–May of 2010, negate any advantage of flushing early.

This is the first study of phenology in a beech provenance trial at its southern–western range margin, where the sub-Mediterranean climate imposes a prolonged dry period during July–September at a site also subject to cold snowy winters with late frosts and poor soils. We tested the hypotheses that (1) provenances from the south-east of the range suffer high mortality to early-flushing buds, and that this would be particularly evident following the late frosts of 2010; and that (2) growth and fitness of provenances from the north and west of the range would be most-severely affected by summer drought at the trial site (that was particularly harsh in 2009). We also looked to identify general trends and correlations in the phenology and growth of trees originating along Europe-wide geographical gradients of climate and elevation, and to examine the consistency of these trends over several field seasons. With this information we can consider the possible implications of climate change and the northwards movement of beech populations.

2. Materials and methods

2.1. Study site

We report on the timing and duration of bud burst in 32 provenances spanning the range of beech across Europe, grown together in one common-garden trial planted in 1998 at a site near to Ezcaray in the south of La Rioja, northern Spain. The trial is one of a series planted by the German Federal Research Institute for Forestry in Grosshansdorf for an evaluation of beech genetic resources for sustainable forestry. Seeds from at least 50 mother trees from the parent population were used for each provenance. One-hundred-and-fifty, one-year old seedlings of each provenance receiving the same mycorrhizal inoculum, were transplanted to the site from a common nursery in Grosshansdorf, Germany.

The trial site is located amid beech and pine forests in a mountainous region of La Rioja at 1340 masl ($42^{\circ}18'30''\text{N}$, $02^{\circ}55'46''\text{W}$). The soil is loose stony (50%) and light-sandy brown-soil of poor fertility and a pH 5.5. The soil texture is sand (44%), silt (45%), clay (11%), and total N content is $3\text{--}4\text{ g g}^{-1}$ in the top 10-cm depth. The 50-year average, mean annual temperature is 9.9°C , the warmest summer month 18.2°C and coldest month 2.9°C . Very little of the annual precipitation (861 mm) falls during the growing season (only 137 mm, May–September), indicating that summer drought is frequent. The trial is managed by CIFOR-INIA SILVADAT and has been weeded twice in 2002 and 2008. Growth and survival of the beech provenances was monitored previously in 2000 and 2002 (by the La Rioja Nature Resources Administration), in 2008, 2010 and 2011 for the present study. The trial is fenced to exclude browsing animals and the trees exhibit little or no evidence of insect damage. Planting is arranged in a complete-block design with three blocks containing all 32 provenances in groups of 50 individuals (1600 trees in total).

2.2. Sampling

Flushing of all 32 provenances was monitored over three years, on 1st May 2008, 11th–13th May 2010, and 24th–26th April 2011. Seven of these provenances were monitored more intensively on three occasions during bud burst in 2008 to establish whether the progression from bud swelling to full flush proceeded similarly among the provenances in the trial. Spring phenology was assessed using a seven point scale developed by Teissier Du Cros et al. (1988). All trees were monitored by the same person for consistency.

1. Dormant bud
2. Buds swollen and elongated
3. First green becomes visible between bud scales. Bud adopts a silver-grey sheen
4. First folded hairy leaves become visible but remain partially held by the bud
5. Entire leaves cascade from the bud, but are still largely folded and flaccid
6. Leaves are unfolded but still corrugated, fan-shaped and hairy
7. Leaves are fully unfolded, smooth and flat

Leaf senescence was monitored for all trees on one occasion on the 1st–2nd October 2008. The progression of senescence was determined from a point at two-thirds height up each sapling by estimating the proportion of green leaves against the proportion of senescent (discoloured) plus fallen leaves at that height. The validity of this colour change assessment was confirmed against non-invasive leaf chlorophyll content data (SPAD-502 chlorophyll metre, Minolta Camera Co., Osaka, Japan). A census of tree height and survival was made prior to the 2008 growing season.

2.3. Weather data

Continuous daily weather data from 2006 onwards was obtained from the nearby permanent automatic monitoring station (CR10X datalogger, Campbell Scientific, Logan, Utah, USA) at La Fonfria, Monte de Suso at 1304 masl, (42°20'32" N, 02°54'44" W) belonging to the Agricultural Agency of the Provincial Government of La Rioja. Maximum, minimum and mean temperature, and precipitation and radiation were recorded every 15 min. These data were used to calculate the degree hours above each of 0 °C, 5 °C and 8 °C, from 1st January (AcDH) and 1st April (EqAcDH) for each of the years when flushing was monitored (2008, 2010, 2011). The entire data set was used to obtain a mean value for last eight years of growth.

2.4. Data analysis

Differences in bud burst, height and survival among all 32 provenances were determined using ANOVA, with *P*-values adjusted using Bonferroni's correction to reduce the possibility of type-one errors and restricted maximum likelihood estimation. Correlations among the climate at provenance origin and the measured response variables in the trial, describing spring phenology, senescence, mortality, tree height and diameter, were examined by principal components analysis using the open-source software R version 2.8.1 (The R foundation for statistical computing, Vienna, Austria), the relationships between bud burst and these factors and other abiotic variables were tested using linear regression.

Fifty-year average weather data from the sites of origin of each of the beech provenances in the trial were calculated from data extracted from the WorldClim database (Hijmans et al., 2005 in Rasztoivits, 2011) to complement data on their geographical location.

In addition to this, the Weibull function ($y = a - be^{-(cx^d)}$) was fitted to individual-tree data from the seven provenances (indicated in Table 1) monitored on three dates in 2008 plus both a later date when leaf expansion and unfolding had been completed in all trees (flushing stage 7), and a start-date prior to bud swelling in all trees (flushing stage 1). Non-linear fitting was performed in R using self-starting function SSweibull with estimates for the four constants: [a] the horizontal asymptote (Asym) for large values of *x*; [b] the difference from Asym to the *y* intercept *x* = 0 (Drop); [c] the natural logarithm of the rate constant (Lrc); [d] the power (pwr) to which *x* is raised (Crawley, 2007). This provided an estimate of bud burst date from which a population mean was obtained for each provenance (detailed procedure given in Robson et al., 2011, 2012). Bud burst date was considered to be the date at which flushing stage 2.5 was attained. The duration of flushing from bud-swelling (stage 2) to full unfolding (stage 7) was also calculated from the fitted function for each tree. A fitted Weibull function of standard shape, achieved using the mean flushing duration of the seven provenances but displaced along the *x*-axis according to flushing stage on day 122 of 2008 was used to obtain the estimated bud burst dates in all 32 provenances in the trial. This approximation excludes inter-provenance variability in duration of flushing which could slightly alter the bud burst date, but among the seven provenances tested this was a relatively small difference unlikely to significantly affect the ranking of provenances. The mean ± 1 SE within-provenance variability in flushing of these seven provenances in 2008 was 95.5 ± 2.3 accumulated degree hours (AcDH) above 5 °C after the vernal equinox which is the equivalent of 0.6 days (range 0.3–1.0 days) at the mean temperature for this period. The seven provenance mean ± 1 SE duration of flushing was 3264.6 ± 95.5 AcDH above 5 °C after the vernal equinox in 2008, the equivalent of 11.6 days (actual range 9.7–13.6 days).

3. Results

3.1. Bud burst and height growth of beech provenances in the common-garden trial

The provenances in the trial maintained distinct flushing patterns from each other and these remained largely consistent during the three years of monitoring (Table 1). The estimated mean provenance flushing date over the whole trial ranged over 10 days between day 115 and day 125 of the year, and the distribution was skewed right (late), meaning that there was a tail of early-flushing provenances.

Across the 32 provenances in the trial there were two overriding geographical trends in the timing of bud burst (Fig. 1A). Provenances from the south-east, east and central Europe flushed earliest and those from the north and west of Europe flushed latest (Fig. 1). The secondary trend was for some provenances in the trial originating from low elevations to flush later than those from high elevations (Fig. 1A). However, it was not straightforward to distinguish these two factors (Fig. 1A), since most of the southern and eastern European provenances in our trial came from high elevation sites.

The phenological development of the local Spanish provenances occurred close to the median flushing time for the trial. Whereas, a few mapped provenances particularly deviate from the norm, such as Idrija in Slovenia (54-SO): which was among the last to flush, and whose properties are counter to the general geographical trend, as is particularly apparent because of its close proximity to the earliest-flushing provenance from Val de Sella in Italy (37-IT) and other surrounding early-flushing provenances (Fig. 1A and Table 1). The behaviour of this exceptional provenance was consistent in other parallel trials throughout Europe (Robson et al.,

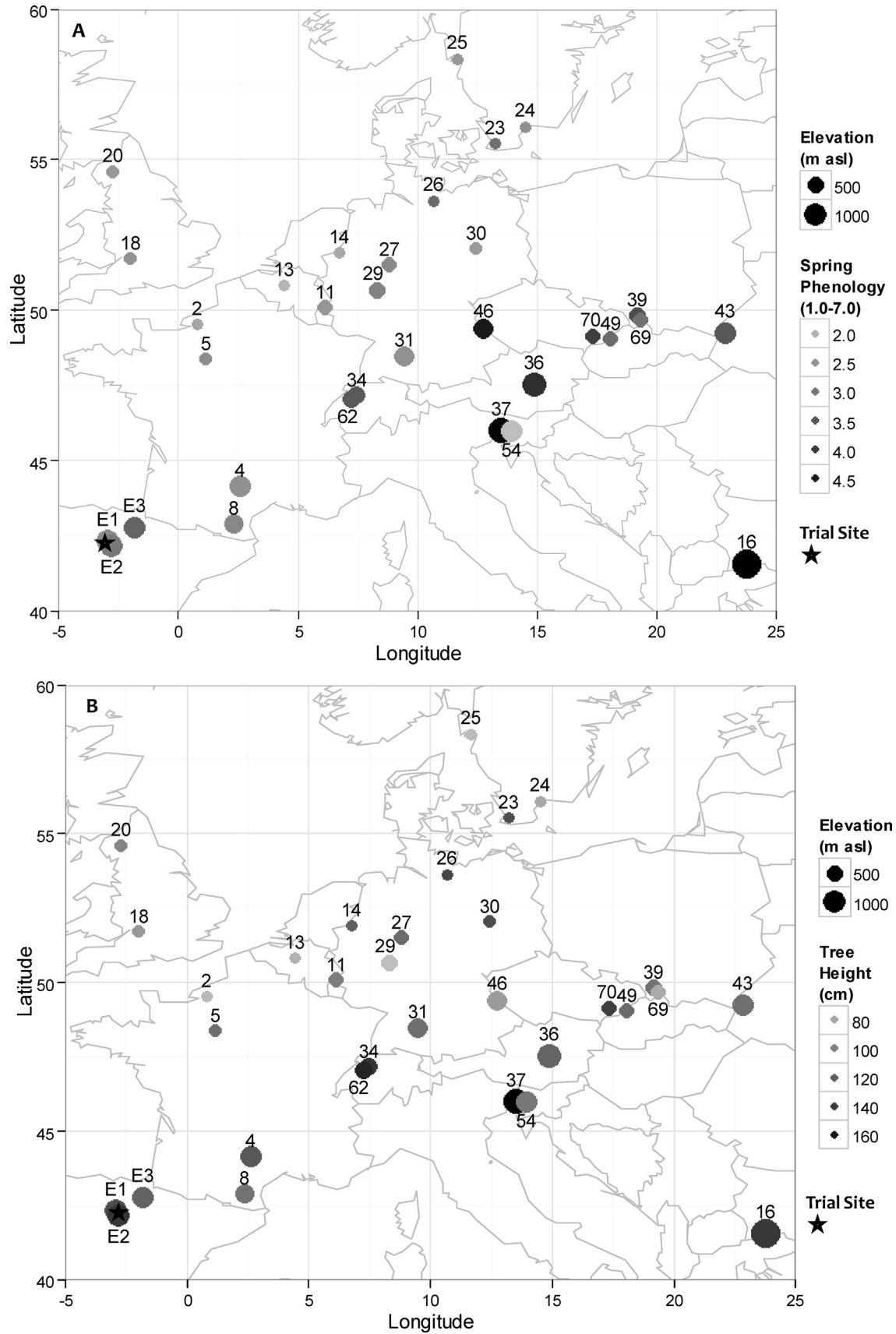


Fig. 1. Mapped representation of (A) the 3-year average flushing stage 1–7 (SprPhen) at the beginning of May (2008, 2010, 2011), and (B) tree height (cm) in 2008, for all provenances from the common-garden trial close to Ezcaray, La Rioja, Spain at their origin. Bubble size is elevation in metres above sea level (masl). The detailed numerical data on the variability in spring phenology each year are given in Table 1.

Table 1
Flushing stage of each provenance from the Ezcaray trial as measured in 2008, 2010, and 2011. Provenance name, country of origin, and numeric code are given. Mean flushing stage ± 1 SE for the entire population (originally 150 trees). Rank order is from earliest–latest to flush. Flushing stage scale from 1 to 7, with bud burst at 2.5 and complete leaf unfolding at 7. Provenances marked with * were sampled on multiple occasions during flushing to assess the response of bud development to spring temperatures and for cross-validation of bud burst date calculations.

Provenance			01/05/2008		13/05/2010		26/04/2011	
Name	C	Code	Mean \pm SE	Rank	Mean \pm SE	Rank	Mean \pm SE	Rank
Bordure	FR	2	2.43 \pm 0.08	29	2.48 \pm 0.13	29	1.73 \pm 0.08	30
SudMassif	FR	4	2.68 \pm 0.12	22	3.07 \pm 0.11	20	1.99 \pm 0.06	21
Bretagne	FR	5	2.83 \pm 0.07	20	3.01 \pm 0.10	22	2.02 \pm 0.06	19
Pyrenees*	FR	8	3.04 \pm 0.08	16	3.04 \pm 0.14	21	2.02 \pm 0.04	20
Heinerscheid	LU	11	2.61 \pm 0.07	24	2.92 \pm 0.12	24	1.87 \pm 0.06	28
Soignes	BE	13	1.99 \pm 0.07	31	2.21 \pm 0.12	31	1.65 \pm 0.07	31
Aarmink	NL	14	2.25 \pm 0.09	30	2.41 \pm 0.11	30	1.85 \pm 0.08	29
GotzeDelchev*	BG	16	5.06 \pm 0.12	2	6.22 \pm 0.11	1	3.67 \pm 0.14	1
Bathurst	GB	18	2.58 \pm 0.07	26	3.16 \pm 0.12	18	1.88 \pm 0.05	27
Lowther	GB	20	2.50 \pm 0.08	28	2.86 \pm 0.11	27	1.95 \pm 0.08	22
Torup	SE	23	3.29 \pm 0.09	13	3.77 \pm 0.13	13	2.25 \pm 0.07	13
Trolle	SE	24	2.90 \pm 0.09	19	2.87 \pm 0.12	26	1.95 \pm 0.08	23
Gullmarsberg	SE	25	2.56 \pm 0.13	27	2.93 \pm 0.16	23	1.92 \pm 0.07	24
Farchau*	DE	26	3.30 \pm 0.09	12	3.92 \pm 0.10	12	2.36 \pm 0.05	11
GrafvWestfalen	DE	27	2.90 \pm 0.09	18	3.22 \pm 0.15	17	1.89 \pm 0.07	26
Dillenburg	DE	29	2.95 \pm 0.09	17	3.31 \pm 0.16	16	2.08 \pm 0.07	18
Belzig	DE	30	2.61 \pm 0.08	25	2.63 \pm 0.10	28	1.92 \pm 0.06	25
Urach	DE	31	2.66 \pm 0.08	23	2.90 \pm 0.12	25	2.13 \pm 0.08	17
Oberwil	CH	34	3.63 \pm 0.10	9	4.34 \pm 0.12	7	2.51 \pm 0.06	9
Eisenerz	AT	36	4.39 \pm 0.12	4	5.16 \pm 0.14	4	3.05 \pm 0.11	4
ValdiSella	IT	37	5.20 \pm 0.10	1	5.86 \pm 0.13	2	3.57 \pm 0.11	2
Jaworze*	PL	39	3.81 \pm 0.13	7	4.70 \pm 0.13	6	2.55 \pm 0.08	7
Jawornik	PL	43	3.89 \pm 0.12	6	4.09 \pm 0.19	10	2.61 \pm 0.11	6
Domazlice	CZ	46	4.78 \pm 0.13	3	5.75 \pm 0.16	3	3.13 \pm 0.12	3
Brumov*	CZ	49	3.36 \pm 0.09	11	4.04 \pm 0.12	11	2.15 \pm 0.05	16
Idrija	SI	54	1.95 \pm 0.07	32	2.18 \pm 0.09	32	1.31 \pm 0.06	32
Aarberg	CH	62	3.67 \pm 0.10	8	4.22 \pm 0.13	9	2.55 \pm 0.10	8
Sucha	PL	69	3.12 \pm 0.13	14	3.54 \pm 0.17	14	2.64 \pm 0.16	5
Buchlovice	CZ	70	4.23 \pm 0.11	5	5.04 \pm 0.15	5	2.49 \pm 0.08	10
Zorraquins	ES	E1	2.72 \pm 0.09	21	3.11 \pm 0.11	19	2.16 \pm 0.06	15
LaDemanda*	ES	E2	3.08 \pm 0.07	15	3.44 \pm 0.11	15	2.34 \pm 0.05	12
Urbasa	ES	E3	3.39 \pm 0.10	10	4.24 \pm 0.15	8	2.24 \pm 0.06	14

2012), presumably reflecting a peculiarity of its local climate or biogeographical history (Sittler, 1981; Brus, 2010).

Later flushing, presumably to avoid late frosts, did not facilitate greater height growth in Idrija from Slovenia (54-SO), particularly when compared with its neighbouring population Val de Sella in Italy (37-IT), the tallest provenance in the trial (Fig. 1B). While most provenances of northern and maritime origin grew poorly, those from northern Germany did better than might be expected from the general geographical trends (Fig. 1B).

There was a very large range of variation among provenances in both mean height growth (65.0–172.6 cm) and survival (34–98%). The positive correlation between these two metrics was especially close among mid-to-late-flushing provenances, which tended both to grow smaller and have lower survival than those that flushed early (Tables 1 and A1 and Fig. A2). Overall, the timing of bud burst among provenances was significantly negatively correlated with their height (i.e. early flush with more growth; Fig. 1B), but not with their survival (Fig. 1A).

3.2. Correlations between performance of beech populations in the common-garden trial and their origin

The provenances were well segregated along two statistically significant principal component axes (Fig. 2). Principal component 1 (PC1, explaining 32% of the variability) was mainly associated with latitude, elevation and growing season (May–September) temperature at origin, while principal component 2 (PC2, explaining 29% of the variability) was mainly associated with growing season precipitation (May–September), longitude and winter temperature at origin (Fig. A1). Lower order principal component

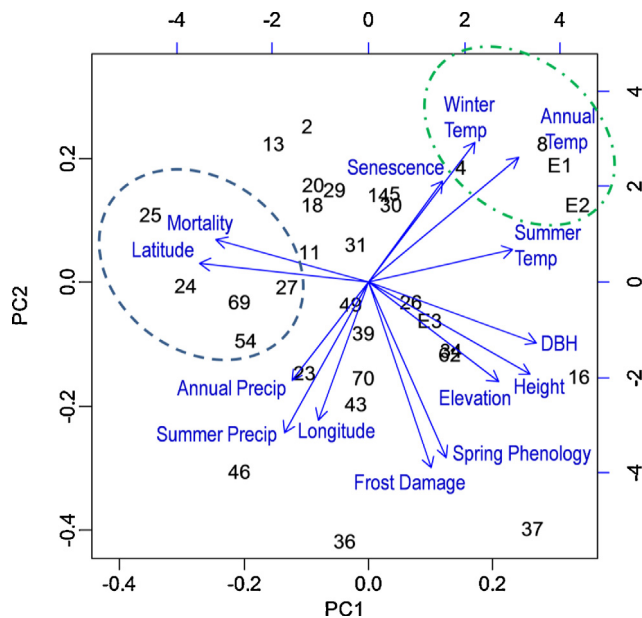


Fig. 2. Principal components analysis of the relationship between provenance origin and performance of trees in the common-garden trial close to Ezcaray, La Rioja, Spain. Ordination plot of the principal components calculated from the covariance matrix. Each provenance (ProvCode: see Table 1 for provenance codes) is plotted on the upper and right axes (–4 to +4), and loading factors are superimposed using arrows plotted on the lower and left axes. Five provenances from the Mediterranean, indicated by a dot-dash circle, group together with high positive values on PC1 and on PC2. A group of poorly performing provenances from cool northern Europe are highlighted, in a dashed circle, with negative values on PC1 and moderate positive values on PC2.

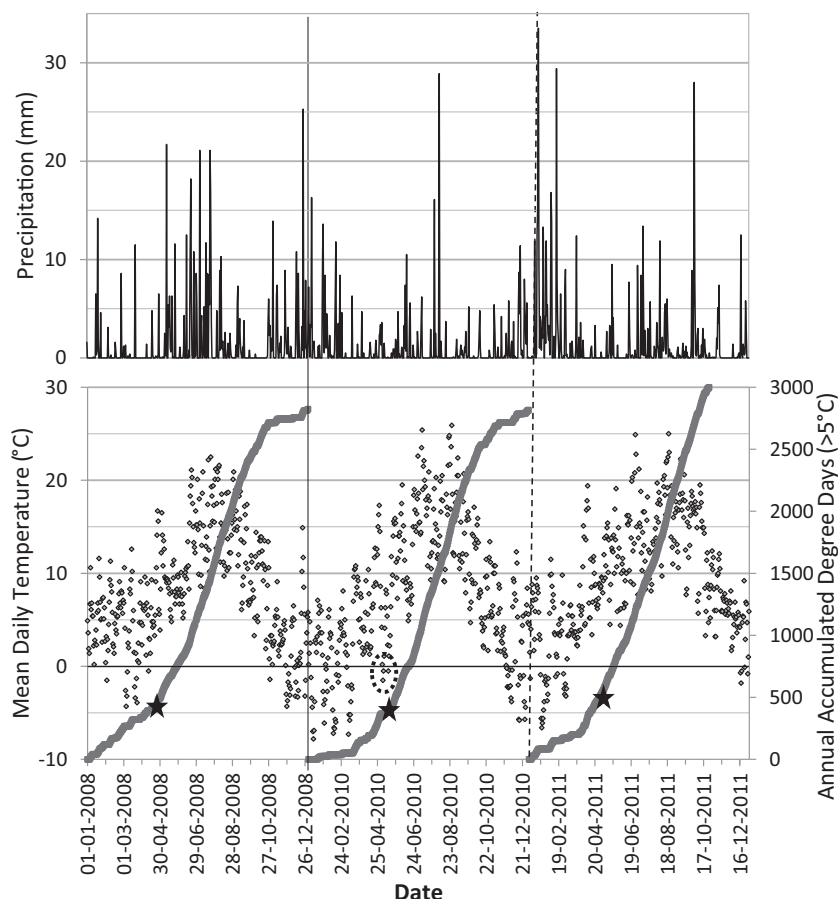


Fig. 3. Daily weather data from the Fonfria weather station for the 3 years (2008, 2010, 2011) of phenology census at the trial site. Daily mean temperature (blue diamonds) and daily precipitation data (grey triangles) are plotted on the left-hand axis, and annual accumulated degree days $>5^{\circ}\text{C}$ from January 1st are plotted on the right-hand axis. A star marks the timing of the main phenology census each year, and the 2010 late spring frosts are circled.

axes each explained less than 5% of the variance. Provenances that performed well in the trial tended towards the positive PC1 and negative PC2. Provenances from the Mediterranean grouped together (Fig. 2: in the upper-right part of the plot), and poorly performing provenances from cool northern Europe formed a group (Fig. 2: on the left of the plot).

Various strong and predictable relationships were confirmed by the PCA, such as those of spring phenology with frost damage, and height with diameter. The timing of senescence was highly correlated with temperature at origin, but, surprisingly, senescence was not correlated with the bud burst date of provenances (Fig. 2). That said, three provenances (Fig. 2), Gotze Delchev (16-BG), Domazlice (46-CZ), and Eisenerz (36-A), were distinctly early flushing and late senescing (Fig. 4). The overall performance of these three provenances was rather dissimilar from each other and from the rest of the provenances in the trial (Fig. 2), 16-BG is performing well in the trial, 46-CZ poorly in the trial, and 36-A attained average height and mortality (Table A1). The other distinct provenance on the PCA was Val di Sella (37-IT) which segregates from the rest thanks to its early flush and high growth rate for its geographical origin.

Mortality, like senescence, was not closely related to spring phenology, suggesting that frost damage was not sufficiently severe or frequent to kill early-flushing trees (Fig. 2). However, mortality and the effects of latitude did segregate similarly, as mortality was highest among provenances from high latitudes (Fig. 2). Simple linear regression revealed burst date to be significantly correlated with longitude ($R = -0.44$; $F_{1,30} = 10.1$; $P = 0.003$) and with altitude ($R = -0.60$; $F_{1,30} = 12.0$; $P = 0.002$) but not with other individual variables related to provenance origin (Table A4).

3.3. Inter-annual variability in the phenology and performance of beech populations

There were large differences in the winter and early-spring weather during the three years when phenology was monitored (Fig. 3). In particular, the cold winter and spring of 2010 delayed the mean bud burst date of the beech trial as a whole. Nevertheless, the ranking of provenances flushing over the three years of sampling remained remarkably consistent (Table 1 and Fig. 3).

The climate at the trial site is harsh for European beech and during the period of measurements the trees were subject to both low rainfall and high summer temperatures. Evaporative demand is generally considered excessive for beech if the vapour pressure deficit (VPD) surpasses 2 kPa (Granier et al., 2003). The maximum daily VPD during the summer was greater than 2 kPa on 3 days in 2008, 13 days in 2009, 11 days in 2010, and 7 days in 2011. There were also extended periods of 37–39 days with little or no rainfall during the summers of 2010 and 2011, when there were respectively only 127 mm and 148 mm of rain from May to September (Table A5).

Growth and mortality during the first four years after planting were highly correlated ($R^2 = 0.64$), but growth of the saplings once established (2001–2008) was much less closely correlated with survival ($R^2 = 0.17$). Mean height growth of the provenances once established (2001–2008) was only weakly correlated ($R^2 = 0.22$) with height during establishment (1998–2001: Fig. A2).

Some initial seedling mortality may be due to problems in becoming established following the stress of transplanting, so it is also interesting to see that most trends in mortality persisted over

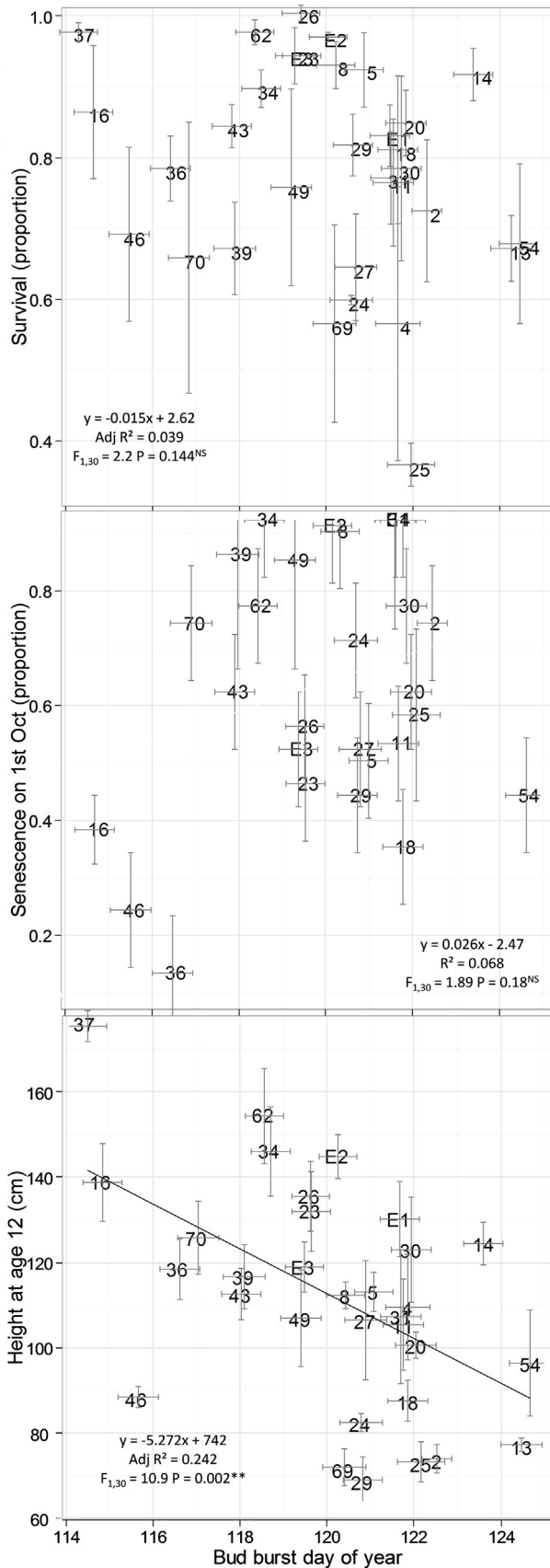


Fig. 4. Correlation of bud burst day for each provenance with (a) survival, (b) the timing of leaf senescence and (c) height at age 12, in 2008. Senescence is given as the proportion of trees with senescent (discoloured) leaves in each population. Three early-flushing outliers on the bottom left in panel (b) are Gotzedechev (16-BG), Domazlice (46-CZ), and Eisenerz (36-A).

time (Table A4). Notably, mortality continued to increase steadily (~5% per year) between each census, even after 10 years, for provenances 29-Dillenburg, 13-Soignes, 4-Sud Massif and 69-Sucha, all of which were already among the least successfully performing in the trial.

The effects of the 2010 late frosts during the first week of May (Fig. 3; circled) were evident in provenances, E3-Urbsa, 70-Buchlovice, 62-Aaberg, whose development was sufficiently advanced to be damaged and set-back by the late frosts during 2010. In fact, all these provenances even exhibited some mortality (10–15%) in the following year as well as a later ranking in flushing date (Table A5). However, high mortality in 2011 was not restricted to early-flushing provenances, since 23-Torup, 14-Aarnink, and 5-Bretagne, from northern maritime climates also suffered high mortality in 2011.

4. Discussion

4.1. Timing of beech spring flush at the trial site

Evidence from previous research into the phenology of beech provenances would suggest that at our trial site, flushing should start relatively late because it lies in the west of the distribution (von Wühlisch et al., 1995; Falusi and Calamassi, 1996; Chmura and Rożkowski, 2002). Likewise, since the site is at high elevation and subject to late spring frosts, a late flush would be expected to be favourable for survival. However, if populations are able to avoid or withstand spring frosts, early phenological development during the spring should enable them to exploit soil water availability before the onset of summer drought which restricts optimal physiological functioning of beech at the site (Robson et al., 2012).

Using a temperature sum model of bud burst allows assessment of the influence of temperature on bud development of trees grown in parallel at different sites. Previously, von Wühlisch et al. (1995) reported that 158 beech provenances in a trial in northern Germany flushed between an accumulated degree hour sum above 0 °C (AcDH) from 1st January of 7600–14,650. This compares with 13,000–15,200 AcDH from 1st January calculated for the beeches flushing in our trial (Robson et al., 2011). This represents much less variation in Ezcaray than in Grosshansdorf, Germany and a far higher temperature sum requirement in our trial than in the German trial on average. These differences between sites and models highlight the need to incorporate differences in chilling and latitude into such physiological models to give them better cross-site comparability and improve our understanding of the mechanisms involved.

4.2. The consequences of early and late flushing among European beech provenances

There was a 10-day difference in bud burst between the earliest and latest-flushing provenances considering the entire trial (using a standardised flushing rate approximation through stages 2–6). This time span is comparable to that reported for a provenance trial in central Europe that contains many of the same beech provenances as ours (Gömöry and Paule, 2011). The significant positive correlation between early flushing and increased height growth would suggest that early flushing confers an advantage, while late flushing represents a large sacrifice in potential annual carbon assimilation. Only for particular provenances, such as Gotzedechev (16-BG), Domazlice (46-CZ), and Eisenerz (36-A), was early flushing partially offset by early-senescence as estimated through both leaf chlorophyll loss and discolouration; nevertheless the benefit of extra growth allowed by early-season development appears to outweigh the risks of frost damage in this trial. This differs from

trials in central Europe where frost damage was strongly correlated with mortality and delayed senescence to extend the growing season most significantly correlated with height growth (Gömöry and Paule, 2011). It could be argued that late flushing reduces the optimum period for growth in sites where drought negatively affects carbon balance in beech (Aranda et al., 2005; Meier and Leuschner, 2008; Fotelli et al., 2009) while at those sites where summer is less harsh late season assimilation counter balances any opportunity cost of late flushing (Vitasse et al., 2009; Gömöry and Paule, 2011). There was little evidence to support our hypothesis that damaging late frosts at our site, particularly prevalent in 2010, penalised early-flushing provenances affecting mortality, growth or form. The advantage achieved through carbon gained in spring balanced against earlier autumn senescence is not always apparent (Vitasse et al., 2009), but the outcome in this trial suggests that early photosynthetic competency allows early-flushing provenances to capitalise on abundant water in spring prior to the summer drought (Robson et al., 2012), and that damage by late spring frosts was insufficiently frequent to compromise this strategy by reducing their height growth (Augsburger, 2008; Wieh, 2009).

Increased mortality and reduced growth of provenances from the north and west of the range supported our second hypothesis, that these provenances would be most-severely affected by summer drought at the trial site. To confirm that the high mortality of these provenances was due to drought stress their hydraulic sufficiency would need to be examined. Nevertheless evidence of reduced photosynthesis, water use efficiency and hydraulic conductance in northern provenances compared to those from southern Europe from a study at this trial site (Robson et al., 2012), further suggests that summer drought is responsible for many of the differences exhibited among these provenances. In beech, stomatal control is sensitive to low soil moisture (Aranda et al., 2000, 2005) and to high evaporative demand (Lendzion and Leuschner, 2008; Fotelli et al., 2009), which leads to reduced carbon assimilation during summer at this and similar sites at the southern range edge for beech (Kramer et al., 2000; Jump et al., 2006; Robson et al., 2012). The apparent success of this strategy contrasts with the frequent finding of reduced growth in early-flushing populations of beech due to frost damage (Hänninen, 1991; Kreyling et al., 2012). The relationship between the timing of bud burst and survival was not statistically significant ($P=0.144$), suggesting that neither mortality caused by frost damage nor drought-pre-emption through early-season growth had an overriding effect on survival of different provenances at the site.

4.3. Europe-wide trends in beech phenology and their implications for fitness

If frost damage generally penalises early-flushing individuals by potentially causing a reduction in fitness (Hänninen, 1991), this would explain why the local provenances Zorraquins (E1-ES) and La Demanda (E2-ES), historically subject to particularly frequent late frosts, flush relatively late. However, it is difficult to predict how future climate changes may differentially affect early- and late-flushing populations. Warmer early-spring temperatures might be expected to help early flushers that can capitalise on favourable spring conditions and compete for soil moisture before the onset of summer drought (Kramer et al., 2000). However, early-flushing populations are likely to further advance their phenology so may also be even more susceptible to spring frosts, and, given predictions for large fluctuations in temperature in the future, the long-term cost of frost damage to tree form may out-weight the benefits of early growth in some susceptible provenances. When early-flushing Bulgarian- and later-flushing German provenances were compared in a German trial, the stage of bud burst when frosted was important for the extent of damage, meaning that

the impact of late frosts was not always worst for the earliest-flushing provenances whose fully-flushed leaves were sometimes able to resist frost damage (Kreyling et al., 2012). The potential future trend of earlier flushing with warming is also complicated by the greater need for chilling in continental and high elevation provenances compared with maritime provenances. If winter temperatures increase and southerly provenances move northward to milder or coastal sites a delay in breaking dormancy over mild winters may offset the promotion of early flushing by warm temperatures during spring (Vitasse and Basler, 2013).

Our results reinforce the expectation that environmental stresses combine with genetic predetermination to influence phenology, and in doing so provide a hierarchy of controls on development. Consequently, the safeguards against frost damage provided by late flushing should buffer the promotion of early flushing by future climate warming. Presumably, although early flushing may be advantageous in the medium term even in frost exposed sites, just occasional severe damage by frosts may impede development towards a mature seed-producing tree, and cause a reduction in fitness that could hinder the propagation of this trait – something that should be possible to study as this trial ages and its beeches are exposed to more of these infrequent extreme weather events (Tebaldi et al., 2006).

Early flushing, early senescence and good performance were not always correlated in provenances from different regions (Table 1 and Fig. 4), indicating that even though adaptation to disparate climates has led to a convergence in the timing of spring phenology among some far-flung provenances (e.g. ES and BG), other differences in functional strategy can be more important in determining their overall success. Although large-scale geographical variability was significantly correlated with the timing of flushing among provenances, a significant portion of the variability in response among populations was not explained by geographical distribution. It is likely that site specific factors at provenance origin, related to local climate, biogeographical history or the historical transfer of reproductive material may provide populations with valuable traits, as already shown by local-scale studies (e.g. Kramer, 1995; Falusi and Calamassi, 1996; Jazbec et al., 2007; Kreyling et al., 2012).

5. Conclusions about future beech performance

Provenances growing for 12 years in a trial under harsh site conditions for beech in northern Spain maintain distinct, genetically determined, flushing patterns. The timing of bud burst and senescence appeared not to be very important in determining mortality in the trial. The effects of abiotic stresses, such as summer drought (Robson et al., 2012) and impoverished soils (Nielsen and Jørgensen, 2003) at the trial site, may explain why the expected association between early flushing and early senescence was not evident. Presumably provenances from south-eastern (and some from central) Europe can combine early flushing with physiological adaptation to water stress, allowing them to maintain physiological activity through a long growing season (Sánchez-Gómez et al., 2013). In the Ezcaray trial presented here, this enables them to perform as well or better than some southern, western, and Mediterranean provenances which are drought tolerant but fairly late flushing, and north-eastern European mountain provenances from Poland and the Czech Republic which flush relatively early but appear less-well adapted to water stress (Robson et al., 2012). This result, demonstrating complex interactions between local environmental cues and phenology, emphasises the need to conserve as many populations as possible, particularly including those from the range edge in the south of Europe, the Balkans, Austria and Switzerland, which may hold desirable traits for the improved future performance of beech elsewhere in Europe under future climate changes. Under

future climates the correlation between the different environmental cues and the variables affecting growth, phenology and fitness are likely to change (Morin et al., 2007; Jump et al., 2010). Only by comparing the growth and phenology of disparate populations at different sites can we hope to achieve a better understanding of the mechanisms underlying performance differences, allowing us to select context-appropriate forest reproductive material in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2013.05.008>.

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