Clinal genetic variation and phenotypic plasticity in leaf phenology, growth and stem form in common ash (*Fraxinus excelsior* L.)

C. Rosique-Esplugas[1],*, J.E. Cottrell[2], S. Cavers[1], R. Whittet[2] and R.A. Ennos[3]

[1]UK Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK
[2]Forest Research, Northern Research Station, Roslin, Midlothian EH25 9SY, UK
[3]Institute of Evolutionary Biology, School of Biological Sciences, Ashworth Laboratories, University of Edinburgh, Edinburgh, EH9 3JT, UK

Corresponding author: E-mail: crisiq@ceh.ac.uk

Genetic variation and phenotypic plasticity play a role in determining the performance of a tree provenance at a planting site. This paper explores their relative importance in determining growth, phenology and tree form in a broad geographic sample of 42 British provenances of common ash (*Fraxinus excelsior* L.) grown at two contrasting trial sites. We found significant genetic differences for tree height, timing of leaf flushing and leaf senescence, and stem forking among the provenances. These followed a clear latitudinal and climatic cline, where the northern provenances were shorter, their leaves flushed later and senesced earlier than the southern provenances. Provenance explained a much larger proportion of the variance for spring phenology (63 per cent) than for autumn phenology (15 per cent). The effect of the planting site was contrasting between spring and autumn: spring phenology showed very little plasticity, while autumn phenology presented higher levels of phenotypic plasticity. This could indicate that for ash spring phenology is under stronger selective pressure. We found a correlation between tree height, leaf phenology and forking, with early flushing provenances tending to be taller and more forked, which could reflect repeated frost damage. The findings underline the complexity of predicting performance in novel environments and demonstrate that small gains in tree growth may be counteracted by detrimental effects on stem form, a key contributor to timber value, due to susceptibility to the contemporary environment.

Introduction

The ability of tree populations to cope with climate change has been the subject of considerable debate in recent years (Aitken and Whitlock, 2013; Maier and Simberloff, 2016; Hällfors *et al.,* 2017). Changes in atmospheric composition have resulted in unprecedented increases in global mean temperatures (IPCC, 2013) such that climate may be changing faster than the rate at which plants can adapt or migrate (Zhu *et al.,* 2012; Gray and Hamann, 2013). There are concerns that tree populations may not have the capacity to withstand these environmental changes and so may not be able to persist in their current location (Vitasse *et al.,* 2010; Aitken and Bemmels, 2016). Two parameters will determine whether tree populations succeed in these novel future environments, namely phenotypic plasticity of individuals and genetic variation within populations. Understanding the extent, distribution and drivers of these two key variables within species will be crucial for managing forest resources through the coming changes, and in particular for the development of evidence-based policies for seed sourcing for establishing new populations (Thomas *et al.,* 2015; Whittet *et al.,* 2016).

Phenotypic plasticity is the ability of an individual genotype to produce different phenotypes in response to cues from its environment. Although the extent of phenotypic plasticity within species is limited, it provides one of the most significant ways in which plants can react to rapid environmental change (Sultan, 2004; Pigliucci *et al.,* 2006; Valladares *et al.,* 2006; Ghalambor *et al.,* 2007). It may be particularly important for trees as it contributes to their ability to cope with the wide range of conditions they may experience during typically long lifetimes (Petit and Hampe, 2006). Multi-site common-garden trials provide a tool with which to explore the plastic responses of species to different environmental conditions. Genetic variation may also contribute to the ability of tree populations to survive under future conditions. If local selection has been strong enough, populations of trees will have adapted to their local environments via natural selection, so that locally sourced individuals will exhibit higher fitness in their home environment than non-local individuals (Savolainen *et al.,* 2007). However, tree species are highly effective dispersers of their genes and the consequent immigration of genetic diversity (gene flow) into populations acts in opposition to local adaptation. As a result, although tree populations may show a local mean optimum phenotype, they are typically highly variable around this mean and this variation provides the raw material for future adaptation (Davis and Shaw, 2001; Petit and

Hampe, 2006). Common garden trials have demonstrated that tree populations are frequently differentiated for adaptive traits (Whittet *et al.,* 2019) and that an understanding of this variation for a range of key adaptive traits is vital to predicting their ability to adapt to future conditions (Alberto *et al.,* 2013).

Globally, there are ambitions to increase woodland area in order to mitigate climate change (Verdone and Seidl, 2017; Bastin *et al.,* 2019). An important consideration in this endeavour is the sourcing of well-adapted planting stock. Poleward translocation of genetic material has been proposed as a measure that may help tree populations to keep pace with the rate of change, a practice understood within a suite of conservation actions broadly known as 'assisted migration' (Whitlock and Millspaugh, 2001; Hällfors *et al.,* 2014). In the northern hemisphere, this strategy for the planting of new woodlands would involve sourcing seeds from warmer areas further south, in the expectation that they will be better adapted to the projected future climate of the planting site. However, many uncertainties surround this strategy, not least the fact that southern-sourced populations may be poorly adapted to current conditions at northern sites. For example, seed sourced from a southern population should be adapted to local seasonal timing and at northern locations may flush leaves early in spring and senesce late in autumn leaving them vulnerable to early or late frosts in contemporary environments (Broadmeadow *et al.,* 2005; Vitasse *et al.,* 2018). Damage incurred in early growth stages may not be overcome even if individuals survive. Spring phenology is advancing under climate change (Fu *et al.,* 2014; Roberts *et al.,* 2015; Thackeray *et al.,* 2016). However, advances in the timing of key spring phenological events such as bud-burst can be greater than the advance in the date of the latest spring frost (Klein *et al.,* 2018; Vitasse *et al.,* 2018), and Zohner *et al.* (2020) found that late-spring frost risk has increased in Europe since 1959. Furthermore, some environmental factors, such as photoperiod, will not vary under climate change and interactions may be important. Both temperature and photoperiod have a role in controlling the timing of bud burst, although the effects vary among species (Vitasse and Basler, 2013; Tansey *et al.,* 2017), and there are both genetic and plastic components to leaf phenology variation within species (Wilson and Baldocci, 2000).

In order to inform the debate on assisted migration, we have gathered growth, phenology and stem form data from two common ash (*Fraxinus excelsior* L.) trials each consisting of a large number of provenances representative of the British range of the species. The trials are located in Northern England and South Wales and were assessed prior to the onset of the current ash dieback epidemic. We explore phenotypic plasticity and among-population genetic variation in the traits with the objective of evaluating the effects of transferring material from southern to northern locations, such as might occur under an assisted migration strategy. In addition, we used the trials to compare performance of southern provenances in current conditions at the northern site relative to more local provenances, as challenging conditions can expose differences between provenances that may remain obscured under favourable conditions (Cundall *et al.,* 1998; Donnelly *et al.,* 2018).

Common ash is a medium-sized European tree species prized for its timber and ecological value, which is widespread and native to Britain. It is tolerant of drought but intolerant of spring frosts (Thomas, 2016). The climate in Britain is predicted to warm by 3–5°C by 2080 (Murphy *et al.,* 2009), which could result in a lengthening of the annual growing period through earlier leaf flushing and later leaf senescence, but with a consequent risk of exposure to late frost. The risk is particularly acute in ash, which has a terminal bud above a pair of lateral buds so that loss of the terminal bud inevitably results in forking, poor form and ultimately a reduction in survival and/or the value of the crop (Kerr, 1995). In addition, mistiming of leaf senescence, an essential process of nutrient remobilization, can have a detrimental effect on growth during the subsequent year. Late leaf senescence may permit storage of more of the products of photosynthesis accumulated over a growing season, but it comes with the risk of greater losses if an early frost causes premature leaf fall (Keski-talo *et al.,* 2005). We hypothesized that traits would covary to reveal a trade-off between maximum exploitation of the growing season (long period in leaf leading to greater annual growth rates but greater incidence of damage) and conservative growth (shorter period in leaf, lower growth rates, but less frequent frost damage).

Methods

Experimental design

Seed was collected from a minimum of 20 mother trees in each of 42 self-sown semi-natural British populations of common ash (*F. excelsior* L.) (populations hereafter referred to as provenances) (Supplementary Table 1 and Figure 1). In order to optimize the chances of sampling native stands, the seed collection sites were selected 'as being ancient semi-natural woodland under continuous cover since 1600 by reference to old maps and land management records' (Sutherland *et al.,* 2010). Care was taken not to bias selection of mother trees towards superior phenotypes, and, where possible, mother trees were located at least 100 m apart. Seed from each provenance was combined to constitute the provenance sample and was grown in nurseries located near the trial sites at Whixley, Yorkshire (53.99°, −1.32°) and Carmarthen, South Wales (51.83°, −4.23°).

In 2007, 1-year-old seedlings were planted in two common garden experiments (hereafter referred to as trial sites). The two trial sites (Table 1 and Figure 1) are located in South Wales (Llandovery) and Yorkshire (North York Moors). The Llandovery trial contains trees from the 42 provenances, the one in the North York Moors has 40 provenances (Supplementary Table 1).

At each trial site, the provenances were grown in a randomized block experiment. Each provenance was present as a single plot in each of three blocks. The plots consisted of 36 (6 × 6) trees in Llandovery and 30 (6 × 5) trees in North York Moors. Trees were planted with a spacing of 2 × 2 m.

Measurements and scorings

The trees were assessed for height at 5 years old, measured to the nearest centimetre with an extendable measuring rod. Stem diameter was assessed using DBH (diameter at a breast height of ∼1.35 m) when trees were 8 years old. Stem forking was assessed at age 8 years, counting the number of forks (i.e. number of times the main stem lost apical dominance). This was assessed
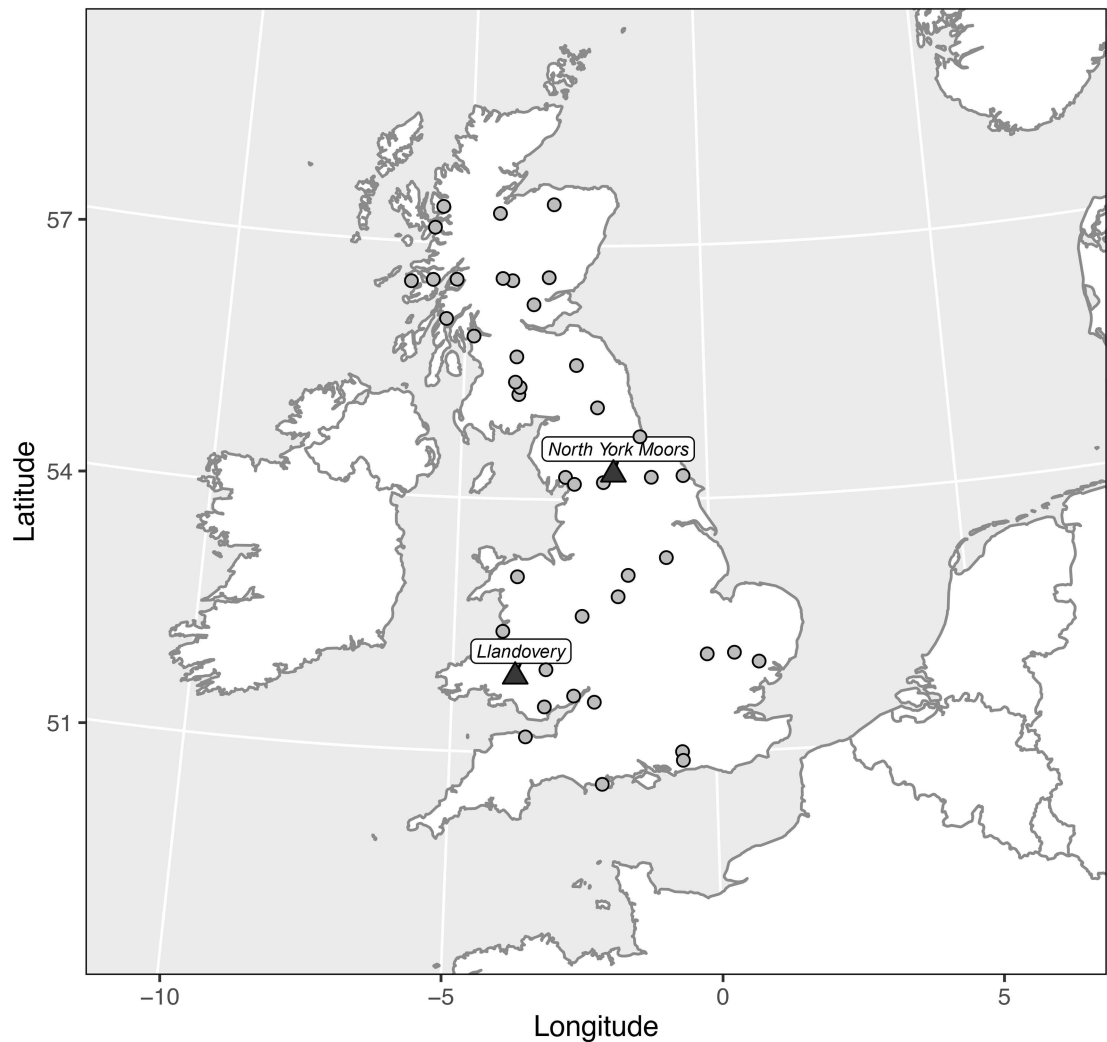
Figure 1 Locations from which ash provenances were sourced (grey circles) and the two trial site locations (black triangles).

Table 1 Coordinates and associated environmental information for the trial sites at Llandovery and North York Moors.

Trial site	Code	Lat	Lon	Alt	CT	AP	GSL	GDD	GFD
Llandovery	Llan	51.9	-3.8	215	8	1372	294	1433	104
North York Moors	NYM	54.3	-1.9	113	9	960	251	1158	130

Lat = latitude, in degrees; Lon = longitude, in degrees; Alt = altitude, in metres; CT = continentality, which corresponds to the Conrad Index (Conrad, 1946) (CT = 1.7 [A/sin (ϕ +10)] – 14, where A is the difference between the mean temperature of the warmest and coldest month in degrees Celsius and ϕ is latitude in degrees; lower values indicate more oceanic climates). The other variables are extrapolated climatic data provided by Met Office, 5 × 5 km polygons, annual averages for 1970–2011 (Perry and Hollis, 2005): AP = annual precipitation (in mm); GSL = growing season length (days where temperature mean is over 5°C for over 5 consecutive days); GDD = growing degree days ($\sum$(daily mean temperature − 5.5) whenever daily mean temperature > 5.5°C); GFD = ground frost days (Count of days when the minimum temperature is below 0°C).

by following the main stem from the ground up, including the subsequent branches originated from each fork up to the crown, excluding the small twigs.

Spring phenology was assessed using a six-stage ordinal morphological scale. The top bud of each tree was visually assessed to determine which of the six stages best described the development stage of the leaf (leaf flushing). In this scoring system, stage 1 corresponds to a dormant fully closed bud, while stage 6 corresponds to a fully expanded bud (Supplementary Table 2, Figure 2). The terminal bud of each tree was assessed and scored on each visit. If the terminal bud was damaged, missing or dead then the next highest bud on the
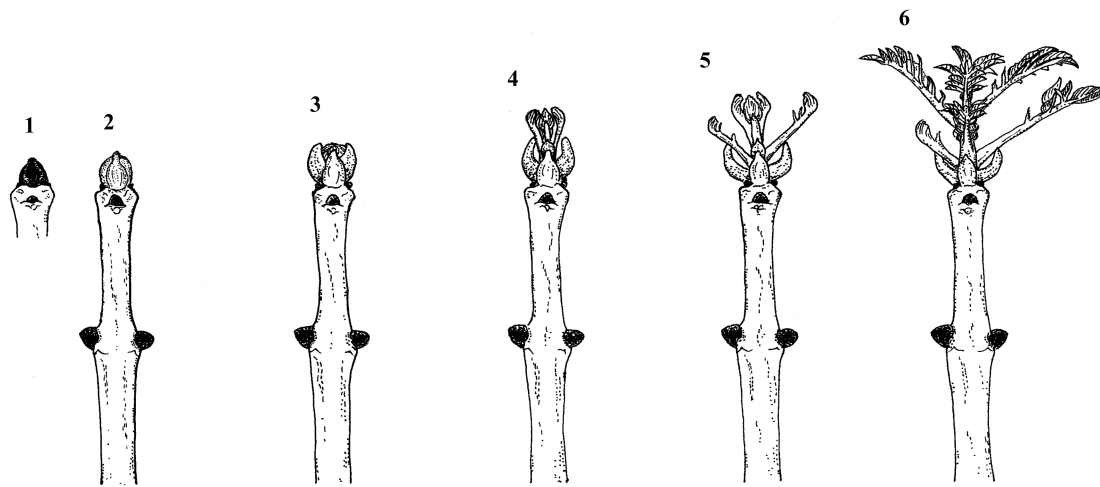
Figure 2 Stages of bud flushing and their corresponding score. Drawing provided by Gabriel Hemery (gabrielhemery.com).

main stem was assessed. If the tree had more than one leading stem (i.e. was forked), then the bud on the stem with the largest diameter was assessed. Where the two stems were found to be equal in diameter, the highest bud was assessed. If forks were equal in height and diameter then the bud giving the highest score was recorded. The trees were assessed at age 7 years old between April and June 2013, on 13 occasions in Llandovery and on 15 occasions in North York Moors.

Assessments of autumn leaf senescence phenology were based on foliage throughout the entire crown rather than a single leaf or a sub-set of leaves. The crown of the tree was visually inspected, and assessment was based on the proportion of the crown that was visible to the assessor standing on the south-facing side of each tree. Leaf senescence was measured as the percentage of the canopy which had shed its leaves (Supplementary Table 2). This ranged from stage 1 (0 per cent leaf loss) to stage 6 (100 per cent leaf loss). Both trials were assessed between September and November 2014, on 20 occasions in Llandovery and 23 in North York Moors.

Measurements were made for individual trees, with missing and dead trees excluded when calculating plot mean values. All trees per plot were measured in the case of height and spring phenology. For the rest of the traits (DBH, forking and autumn phenology), only the trees at the centre of the plot were assessed, 16 (4×4) trees in Llandovery and 12 (3×4) trees in North York Moors. All measurements in the Llandovery trial were taken before the trial showed any signs of infection by ash dieback, causing pathogen *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz and Hosoya. In North York Moors, all the measurements were collected before the trees were infected with the exception of DBH and forking, which were measured in the same year when a small number of trees had started showing some signs of infection. Since 2016, both trial sites have shown high levels of infection.

Data analysis

All data analyses were performed in the R statistical environment (R version 3.2.3, Core Team, 2015). To determine the effects

of provenance, site and their interaction on each trait the plot mean values were analyzed in analysis of variance (ANOVA) using a linear model. Missing and dead trees were excluded in the calculation of plot mean values. Two types of ANOVA were used for each trait. The first type of analysis of variance was done by individual trial site, where provenance was a fixed factor and block was a random factor

$$Y_{ijk} = \mu + \text{Prov}_i + \text{Block}_j + \epsilon_{ijk}.$$

The second type of analysis of variance included all trial sites combined where site, provenance and site by provenance interaction were fixed effects and block nested within site was a random factor

$$Y_{ijkl} = \mu + \text{Prov}_i + \text{Site}_j + (\text{Prov} \, {}^*\text{Site})_{ij} + \text{Block}_{k(j)} + \epsilon_{ijkl}.$$

Logarithmic transformation was applied to the forking data to ensure that they fitted a normal distribution. An Arcsine transformation was applied for survival data. For the analysis of variance across sites, the provenances that were absent from one of the trial sites were excluded, which meant excluding two provenances (Supplementary Table 1). With the ANOVA table of the analysis of variance across sites, the proportion of variance explained by each factor was calculated for each trait.

For each trait at each site, univariate linear regressions were applied to test the relationship between plot mean values and latitude, longitude and climatic variables of the provenance's home site (adjusted for block). Values of climatic covariates were extracted from long-term average climate data provided by the Met Office. The datasets interpolate observations from weather stations onto a 5×5 km grid for the whole of Great Britain for the period 1960–2000. Full details of generation of the long-term average data are provided in Perry and Hollis (2005). The following predictors were taken forward for use in the analyses: Growing degree days (GDD), as the annual accumulated temperature $\sum$(daily mean temperature $- 5.5$) whenever daily mean temperature $> 5.5°$C; the growing season length (GSL) of

Table 2 Summary of analysis of trait variation, by trial site.

Trait	Trial site	ANOVA			REGRESSION	
		Prov	Site	Prov × Site	Latitude	GDD
Height	LLAN	$P < 0.001$			R^2: 0.46, $P < 0.001$ slope: −0.13	R^2: 0.44, $P < 0.001$ slope: 0.11
	NYM	$P < 0.05$	$P < 0.001$	$P < 0.05$	R^2: 0.40, $P < 0.001$ slope: −0.05	R^2: 0.33, $P < 0.001$ slope: 0.03
DBH	LLAN	$P < 0.001$			R^2: 0.36, $P < 0.001$ slope: −0.2184	R^2: 0.33, $P < 0.001$ slope: 0.001
	NYM	ns	$P < 0.001$	ns	R^2: 0.39, $P < 0.001$ slope: −0.16	R^2: 0.17, $P < 0.01$ slope: −0.003
Number of forks	LLAN	ns			ns	ns
	NYM	$P < 0.001$	$P < 0.01$	ns	R^2: 0.23, $P < 0.001$ slope: −0.11	R^2: 0.19, $P < 0.01$ slope: 2.2e−04
Flushing (JD50_Flush)	LLAN	$P < 0.001$			R^2: 0.43, $P < 0.001$ slope: 1.09	R^2: 0.43, $P < 0.001$ slope: −9.4e−03
	NYM	$P < 0.001$	$P < 0.001$	ns	R^2: 0.39, $P < 0.001$ slope: 0.84	R^2: 0.42, $P < 0.001$ slope: −7.4e−03
Senescence (JD50_Senesce)	LLAN	$P < 0.001$			R^2: 0.33, $P < 0.001$ slope: −1.27	R^2: 0.33, $P < 0.001$ slope: 0.01
	NYM	$P < 0.01$	$P < 0.001$	ns	R^2: 0.44, $P < 0.001$ slope: −0.53	R^2: 0.44, $P < 0.05$ slope: 0.004

LLAN = Llandovery, NYM = North York Moors. Significance of the provenance effect (Prov), the site effect (Site) and the provenance by site interaction (Prov × Site), where P is the P-value for statistical significance and 'ns' means not significant. Also the significance (P), R-squared (R^2) and slope of the regressions are given for individual univariate regressions of latitude and GDD, the annual accumulative sum of degrees ((daily mean temperature—5.5) in days when mean temperature > 5.5°C) at provenance site of origin against each assessed trait.

the provenance site was measured as the annual sum of days where temperature mean is over 5°C for over 5 consecutive days; ground frost days (GFD), the annual count of days when the minimum temperature is below 0°C; Mean temperature of February, the coldest month of the year (MTF); and the mean temperature of July, one of the warmest months of the year (MTJ). To test for covariation between traits, Pearson's correlation coefficients were calculated using provenance means from the individual sites.

For analysis of the leaf phenology data, calendar dates were transformed into Julian days from January 1 (JD). The large numbers of observations of spring and autumn phenology allowed us to construct an accurate model of leaf phenology of the trees. To predict the timing of transition between ordinal stages, ordinal logistic regression was applied using 'cumulative link models'. Using these models, we estimated the number of JD until 50 per cent of trees per plot were at the fully flushed stage (Stage 6), hereafter 'JD50_Flush', and the JD until 50 per cent of the trees in the plot reached full defoliation (100 per cent leaf loss), hereafter 'JD50_Senesce'. For each plot, curves were modelled with a common slope, which mirrored the raw data distribution. For each trait, the mean JD50 per provenance was the average of fitted JD50 from three plots per provenance. Cumulative link models were processed using the 'clm' command in the 'ordinal' package in R (Christensen, 2015).

Results

Growth

There was a significant provenance effect for tree height differences at both trial sites, less significant at North York Moors due to a large block effect (Table 2). The range of provenance mean heights was larger at Llandovery than North York Moors; however, in both sites, the tallest provenance was 45 per cent taller than the shortest provenance. Provenance explained 13 per cent of the variation, while site explained 70 per cent (Figure 3). There was a significant site effect: all provenances were shorter at North York Moors than Llandovery. The average height was 50.2 per cent greater at Llandovery than at North York Moors. There was a significant site by provenance effect for height, due to the larger range of heights among provenances in the southern trial. The range of height at Llandovery was from 1.7 to 4.1 m (2.4 m), while at North York Moors, it was 0.6–1.9 m (1.3 m).

For the stem diameter, there was a significant provenance effect in Llandovery but not in North York Moors (Table 2). There was a significant site effect ($P < 0.001$), but no significant site by provenance interaction. DBH was on average 54.7 per cent higher at Llandovery than North York Moors. There was a very big Block effect for stem diameter, which was larger in North York Moors.
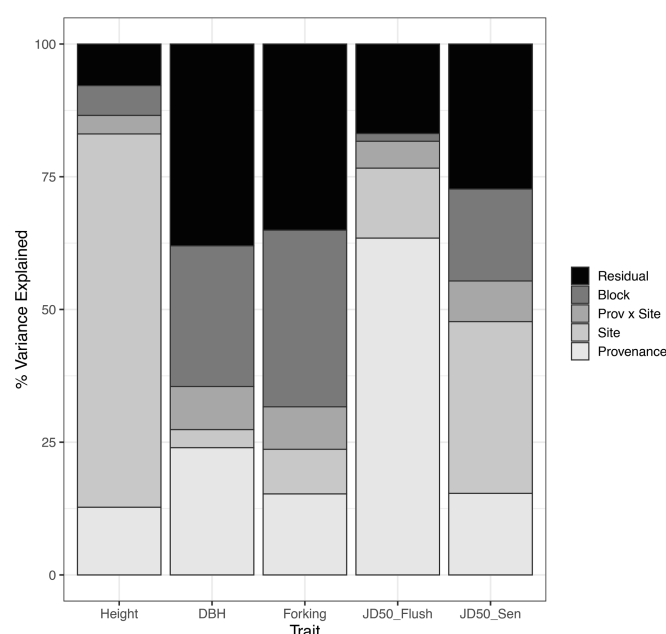
Figure 3 Proportion of variance explained by each factor of the model (provenance, site, site by provenance, block and residual) for Height, DBH, forking, flushing and senescence. These were calculated with the analysis of variance across sites.

Spring phenology

Significant differences were found among provenances for the timing of spring leaf flush (JD50_Flush) at both sites. The difference between JD50_Flush of the earliest and latest provenances was 18 days at Llandovery (May 9th to June 6th) and 11 days at North York Moors (May 20–31st). The site effect was significant (Table 2). However, provenance explained over 64 per cent of the variance, while site explained 13 per cent (Figure 3). All provenances, except two, flushed earlier at North York Moors, with the site mean JD50_Flush being 3 days earlier (24th of May) than it was at Llandovery (27th of May). Only nine provenances flushed on average more than 3 days later in Llandovery than North York Moors, the largest difference being 7 days for the same provenance between sites. No significant interaction was found between provenance and trial site.

Autumn phenology

The differences among provenances for the timing of leaf senescence (JD50_Senesce) were only significant at North York Moors (Table 2). The difference between the earliest and latest provenances was larger at Llandovery (37 days, Oct 5th to Nov 11th) than North York Moors (24 days, Oct 6th–30th). There was a significant site effect, with senescence occurring on average 8 days earlier at North York Moors than Llandovery. All provenances except one (from a northern latitude) lost their leaves earlier at the North York Moors trial than at Llandovery. Over half of the provenances (21) senesced >8 days on average earlier in North York Moors compared with Llandovery, the largest difference between sites being 22 days. There was no significant interaction

between provenance and trial site. Site effect explained 30 per cent of the variance, while provenance explained 15 per cent (Figure 3).

Forking

There was a significant provenance effect in stem forking among provenances at North York Moors but not at Llandovery (Table 2). The difference between the most and least forked provenances was much greater at North York Moors (79 per cent more) than Llandovery (57 per cent more). There was a significant site effect but no significant provenance by site interaction. Incidence of forking was 18.8 per cent higher at Llandovery than North York Moors. All provenances, apart from four (from the south of England), forked less at North York Moors.

Survival

At the time of the measurement of the traits, which was before the symptoms of Ash dieback infection appeared in any of the trees in the trials, survival on average was very high at both trial sites (92 per cent survival at Llandovery and 90 per cent at North York Moors) and no significant differences among provenances were found.

Geographic variation and relation with climatic variables

We found significant patterns of geographic variation. For all traits, there were significant regressions with latitude (Table 2; Figure 4), but not with longitude or with multiple regression for latitude and longitude. For all traits, except for stem forking and survival, the latitude of provenance origin explained ~40 per cent of the variation in both trial sites. Northern provenances were shorter and had smaller DBH than southern provenances in both trials. In both trials, southern provenances flushed earlier and senesced later than northern provenances. For stem forking, we found a significant association with latitude only in North York Moors, where the northern provenances were less forked.

The annual cumulative temperature, measured as GDD, was found to explain more variation than any of the other variables tested (Supplementary Table 3). The GDD of the provenances' origin explained ~40 per cent of the variation for height and the leaf phenology traits, for both sites, in regressions with the opposite sign of the slope coefficient from latitude (Table 2). In Great Britain, temperature is strongly correlated with latitude (Supplementary Figure 1, Supplementary Table 4); the higher the latitude, the colder the climate and the shorter the length of the growing season for trees to grow. The GDD and the latitude of the provenance's site were strongly correlated (GDD ~ Lat, R: −0.77, $P < 0.001$). Latitude proved to be a very good explanatory variable, aligning well with both the strong climatic and photoperiod clines in Great Britain.

Correlations between traits

Height and DBH were significantly correlated with leaf phenology at both trial sites. The tallest provenances flushed earlier (Llandovery: $R = -0.82$, $P < 0.001$; North York Moors: −0.58, $P < 0.001$) and senesced later (Llandovery: $R = 0.52$, $P < 0.001$; North York
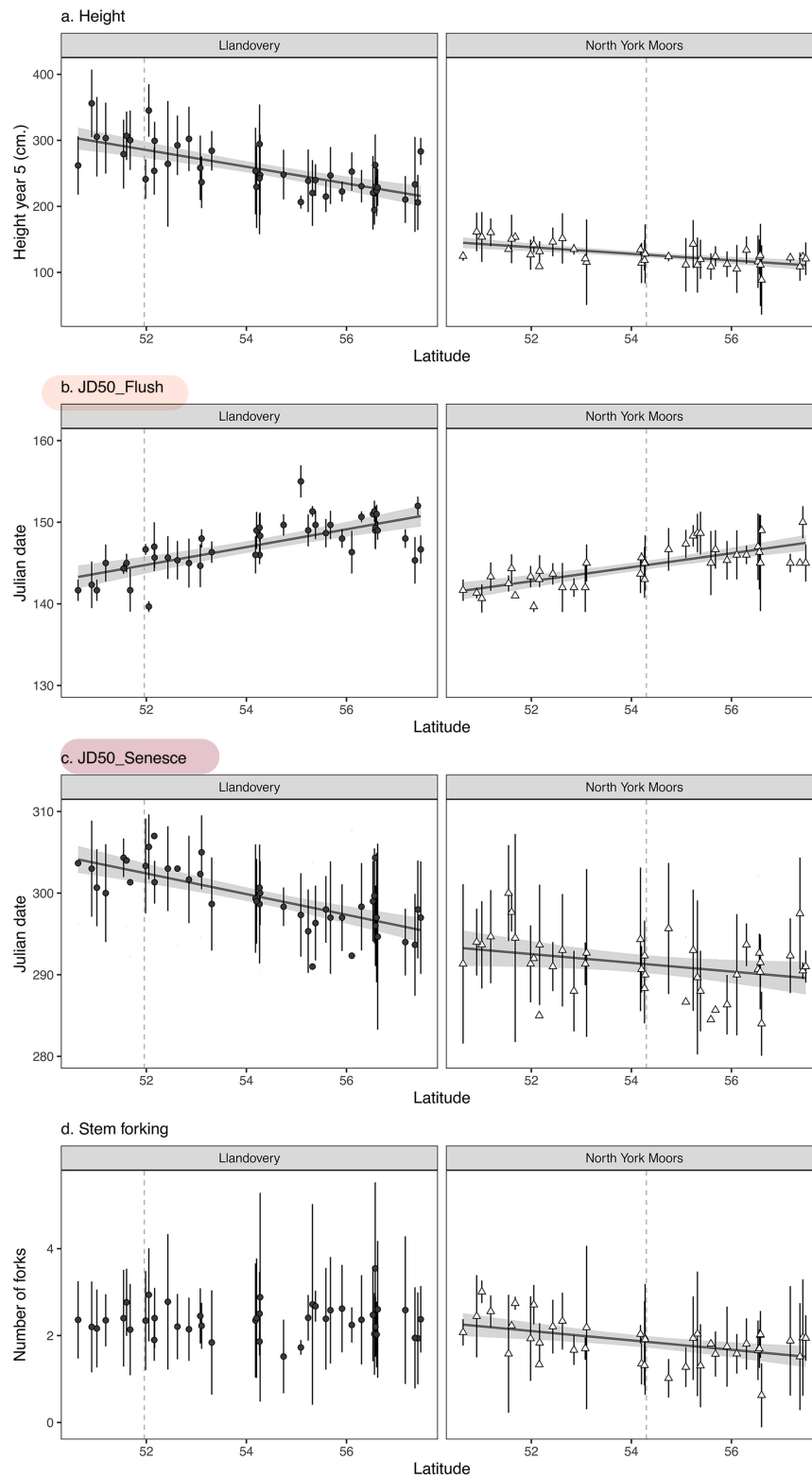
Figure 4 Linear regression with latitude for height (a), leaf flushing (b), leaf senescence (c) and stem forking (d); by trial site (Llandovery and North York Moors). Each dot represents a provenance mean with lines showing confidence intervals. All regressions are statistically significant except for forking in Llandovery (Table 1). Vertical dotted line indicates the latitude of the trial site.

Moors: $R = 0.58$, $P < 0.001$). The provenances with larger stem diameter flushed earlier (Llandovery: $R = -0.73$, $P < 0.001$; North York Moors: $R = -0.51$, $P < 0.001$) and senesced later (Llandovery: $R = 0.54$, $P < 0.001$; North York Moors: $R = 0.72$, $P < 0.001$). Tree height and DBH were significantly positively correlated (Llandovery: $R = 0.89$, $P < 0.001$; North York Moors: $R = 0.88$, $P < 0.001$).

There was a significant negative correlation between leaf flushing and leaf senescence for both trial sites (Llandovery: $R = -0.50$, $P < 0.001$; North York Moors: $R = -0.35$, $P < 0.05$), where provenances that flushed earlier senesced later.

For stem forking, there were only significant correlations at North York Moors. There were more forks in the tallest trees ($R = 0.76$, $P < 0.001$), the trees that flushed earliest ($R = 0.60$, $P < 0.001$), and the trees that senesced latest ($R = 0.42$, $P < 0.01$). However, DBH showed a significant positive correlation with forking in both trial sites (Llandovery: $R = 0.31$, $P < 0.05$; North York Moors: $R = 0.68$, $P < 0.001$).

Discussion

Genetic differences

We have shown significant differences among provenances of common ash in Great Britain for growth traits, stem form and leaf phenology. The pattern of trait variation was clinal, with greater growth, earlier leaf flushing and later senescence, and higher frequency of stem defects (one site only) in southern provenances compared with northern provenances. Differences among provenances and the strength of the clinal trend were stronger at the southern site (Llandovery). Other studies on common ash across its natural range have found significant genetic differences at population or family level in these traits (Savill *et al.*, 1999; Cundall *et al.*, 2003; Pliura and Baliuckas, 2007; Mwase *et al.*, 2008; Pliura *et al.*, 2011). However, the clear latitudinal cline found in our study was not previously detected in provenance tests of ash within Britain, perhaps due to insufficient numbers of provenances or sampling from a more limited geographic range (Cundall *et al.*, 2003). In our study, plants from southern latitudes were taller and had greater DBH than those from more northerly latitudes at both trial sites, although the differences between provenances were more evident at the southern trial site. These differences may be due to the longer growing season achieved by southern provenances through earlier flushing and later leaf senescence.

The significant differences among provenances for leaf flushing and leaf senescence showed a geographical pattern. For both sites and both traits latitude explained between 33 and 44 per cent of the variation, where the southern provenances flushed earlier and senesced later than the northern ones when grown under the same environmental conditions. This demonstrates genetic variation in these traits and, as variation was correlated with latitude and climatic variables (such as GSL and GDD, suggests adaptation to conditions at site of origin). Reviews by Alberto *et al.* (2013) and Aitken and Bemmels (2016) found that genetic differentiation along clines is generally stronger for autumn phenology than for spring phenology, both

in broadleaved and conifer trees, although the effect varies among species. However, we found that the opposite was the case in our study, where provenance explained a much larger proportion of the variance for spring phenology (63 per cent) than for autumn phenology (15 per cent). Several studies in common garden experiments in deciduous trees showed a genetic component in leaf phenology. Vitasse *et al.* (2009c) showed that among population differences in spring flushing time of ash and oak were related to the climate in origin, where the trees from warmer climates flushed earlier. Similarly, Ducousso *et al.* (1996) showed timing of bud burst in oak populations followed geographical pattern related to the site of origin (both latitude and altitude) and spring frost tolerance, where the northern provenances flushed later than the southern ones, in accordance with our results. However, other tree species follow the opposite pattern for bud flush (Vitasse *et al.*, 2009a; Whittet *et al.*, 2021) or show no pattern for spring phenology but instead exhibit a pattern for autumn phenology (e.g. *Populus deltoides*, Friedman *et al.*, 2011). Our results show that the effect of provenance in ash leaf flushing is stronger than for leaf senescence.

Ash is very prone to frost damage and even though leaf emergence in ash is late in relation to other species, damage by winter cold, and autumn and spring frost can occur for two reasons. Firstly, when the tree is dormant, air temperatures below its cold hardiness tolerance will result in 'winter injury'. The cold hardiness tolerance threshold reduces as the winter progresses towards spring when it rises from $-27°C$ in midwinter to $-3°C$ at the bud swelling stage in spring (Etherington, 1982). The second basis for damage is unseasonal frosts before the tree has become dormant in autumn or after it has flushed in spring. For example, Wardle (1961) reported that young ash leaves could be killed if they are subjected to long periods in which air temperatures are only as low as $-3°C$. Evidence of a genetic effect on forking has been provided by provenance and progeny trials and Kerr (1995) concluded that there was both a genetic and an environment effect on forking. Kleinschmit *et al.* (1996) and Sminita (1995) both stressed the importance of correct choice of provenance when planting ash in mainland Europe. Both demonstrated that provenances from latitudes from further south than the planting site were less cold hardy or flushed too early and resulted in forking. Similarly, Baliuckas *et al.* (1999) discovered a positive and significant relationship between early bud flushing and frost damage in a 4-year-old ash trial in southern Sweden based on Swedish provenances. Our results at North York Moors agree with this observation, where provenances from more southerly latitudes showed a higher incidence of forking than those from more northerly latitudes. As with the results of Kleinschmit *et al.* (1996) and Sminita (1995), our findings demonstrate that the southern provenances at North York Moors flush earlier and lose their leaves later than northern provenances and this longer growing season may leave them vulnerable to exposure to the damaging environmental events mentioned earlier. Clearly, therefore, although transfer of southern provenances to more northerly planting sites as a strategy for rapid adaptation to climate change may result in higher relative growth rates, it may have negative side-effects for traits of economic importance.

Phenotypic plasticity

Growth, form, phenology and survival varied substantially among sites. Site effect contributed most to overall variation (Figure 3) in height and leaf senescence. All provenances attained considerably greater height (on average 50 per cent) and diameter at the southern site, Llandovery, where the climate was generally warmer and wetter. Results from an earlier multi-site provenance trial series in Britain attributed 60 per cent of total variation in 5-year height to the effect of trial site (Cundall *et al.,* 2003).

Site also had an effect on leaf phenology, but this effect was much greater in leaf senescence (site contributed to 33 per cent of the variance) than flushing (site contributed to 13 per cent of the variance). Nearly, all provenances flushed slightly later in Llandovery than in North York Moors (on average 2.6 days later, up to 7 days). On the other hand, leaf senescence took place 8 days earlier on average (up to 22 days) at North York Moors than Llandovery. The slight earlier flushing in the southern site was contrary to our expectations and many examples in other species (such as Vitasse *et al.,* 2010; Salmela *et al.,* 2013; Rosique-Esplugas, 2018), we had expected trees to flush earlier at the warmer Llandovery site than in North York Moors.

Our results show that autumn senescence was more plastic than spring flushing for ash in the different years in which each trait was recorded. This contrasts with the results of *in situ* studies (along an altitudinal gradient, not latitudinal gradient; therefore, photoperiod was constant) that found that ash presented the highest sensitivity to temperature in flushing compared with other species (Vitasse *et al.* (2009a), while temperature did not have a significant effect on ash trees leaf senescence (Vitasse *et al.,* 2009b). A possible explanation for our results is that photoperiod at the trial sites influenced plasticity in autumn phenology. Photoperiod is a driver for autumn phenology in several deciduous tree species (including white ash, *Fraxinus americana* L.) (Thomas and Vince-Prue, 1997; Gill *et al.,* 2015; Liang, 2019) but was shown to have had no effect on spring phenology in common ash (Basler and Körner, 2012). Other autumn phenology events (cold hardiness and bud set) have been shown to have a lower phenotypic plasticity than spring events in many tree species (Howe *et al.,* 2003; Savolainen *et al.,* 2007). Vitasse *et al.* (2013) found that bud set in ash occurred later at higher altitudes. Leaf senescence is a key phenological process which protects the trees from frost by remobilization of nutrients such as nitrogen and photosynthates out of the leaves prior to leaf shedding. The timing can influence growth in the subsequent year and late senescence involves a risk–benefit trade-off. It can provide a longer season during which photosynthates can be produced by the leaves, but it can result in loss of accumulated photosynthates if autumn frosts arrive before these have been moved out of the leaves (Keskitalo *et al.,* 2005). The higher plasticity we have shown for leaf senescence compared with leaf flushing may suggest that, for ash in Britain, the damage from a spring frost exerts stronger selective pressure than autumn frost.

We show a site effect for stem form, where trees had higher stem forking in the southern site (Llandovery) than North York Moors, despite the fact that since 2007 (the date when the trees were planted), the incidence of frosts has been higher in the North York Moors area than in Llandovery, and the date of the last spring frost has been later. Winter dormancy in forest trees starts with a rest phase during which buds remain inactive even if they are exposed to growth promoting conditions. To break dormancy, a chilling period is needed; this is followed by transition from rest to quiescence after which buds can respond to environmental cues (Hannerz *et al.,* 2003; Robson *et al.,* 2013). A series of studies on 15 UK tree species (Murray *et al.,* 1989) showed that higher winter temperatures resulted in a delay in bud break in many species because trees need a certain number of chilling hours below +5°C in order to be able to break bud when conditions permit in the spring. Ash has the longest rest requirement and the shortest quiescence requirement of eight native European tree species (Kramer, 1994). The higher winter temperatures (and hence slower accumulation of chilling hours) experienced at Llandovery could explain the observed delay in bud flush. However, despite having a slightly later date of bud flushing, trees at Llandovery showed a 19 per cent higher incidence of forking compared with North York Moors. From the 40 provenances common to both sites, only four provenances (which were from the most southern latitudes) were more forked in North York Moors than Llandovery. The higher forking in Llandovery suggests that the delayed onset of bud flush in the milder southern site was still insufficient to avoid the late frosts that are a known risk in northern oceanic climates. Indeed, Kerr (1995) recommends that sites which experience late frosts should not be planted with ash. It has been suggested that once trees meet a threshold height their terminal buds may be above the level of damaging frost (Kerr and Boswell, 2001). However, despite the Llandovery trees being taller than those at North York Moors, they exhibited a greater degree of forking. The reason is therefore more likely to be due to the occurrence of frost when the buds are at a vulnerable stage in Llandovery. Another explanation would be (not measured) micro-climatic conditions in both our trial sites, as Llandovery is in an NW facing slope and North York Moors experiment in flat valley next to a river.

Implications for forest management and assisted migration

Growth traits, such as height and diameter, are regularly used as indirect measures of fitness in provenance and progeny trials as they are both relatively easy to measure and are of clear silvicultural importance (Whittet *et al.,* 2019). Their use as a proxy for fitness is justified for two reasons. Firstly, that bigger individuals have survived and grown well and so have competed successfully for resources. Secondly, because large stature provides a reproductive advantage, both in terms of possible number of inflorescences and the capacity to catch pollen and disperse pollen and seed (Petit and Hampe, 2006; Ying and Yanchuk, 2006). For these reasons, growth data are often used as a basis on which to recommend particular provenances, define seed transfer limits or make inferences about patterns of local adaptation (Ying and Yanchuk, 2006). Our results show a strongly clinal latitudinal genetic pattern of variation in growth, phenology and forking, with trees from lower latitudes showing greater growth but a larger number of stem defects. We hypothesize that this represents a trade-off between growth and frost avoidance which is associated with timing of leaf flushing and senescence.

Therefore, growth considered in isolation may not be an appropriate single measure of fitness or adaptability, highlighting the need to assess a range of traits at appropriate ages and explore interactions and covariances among them to guide seed transfer limits (Viherä-Aarnio *et al.,* 2013). In our case, trait covariance reveals a clear risk in assisted migration. We show that spring phenology changes very little across the two sites, while autumn phenology is more affected by the planting site. If, as suggested by Vitasse *et al.* (2009c), temperature has little influence on leaf senescence in ash, it may be that photoperiod plays a more prominent role. This is potentially important as much of the justification for moving plants northwards to prepare for climate change is based on temperature being the major driver of trait variation. In conclusion, we recommend that care is taken in assessing transfer, by using species-specific analyses that incorporate multiple traits and drivers, and by favouring the use of conservatively adapted provenances, especially in frost-prone sites.

The medium-term future for ash across Europe is uncertain due to the devastating impact of ash dieback disease. Resistance breeding efforts so far have found moderate to high heritability values for variation in dieback tolerance in young ash trials (McKinney *et al.,* 2011, 2012; Pliura *et al.,* 2011; Stener, 2013; Lobo *et al.,* 2015; Muñoz *et al.,* 2016) and have proposed that early leaf senescence may be a source of exapted resilience to dieback due to shortening the window in which infection can take hold and invade stem tissues (McKinney *et al.,* 2012; Stener, 2013; Landolt *et al.,* 2016). We found consistently earlier leaf senescence in trees from northern populations that had been transferred south. In parallel with this, lower ash dieback susceptibility scores of material from Central Scotland have been observed in mass screening trials growing in East Anglia (Stocks *et al.,* 2017). If early leaf senescence does play a role in avoidance or tolerance of ash dieback, there could be an argument for targeting selection of putatively tolerant trees from the north of Britain for inclusion within a resistance-breeding population. Finally, the clear geographical pattern of genetic variation observed in ash suggests that responses to natural selection in the species are efficient. Genetic variation, coupled with the species' capability for plastic responses, offers some hope for the long-term persistence of ash in the landscape.

Data availability statement

The data underlying this article are available in the article and in its online supplementary data.

Supplementary data

Supplementary data are available at *Forestry* online.

Acknowledgements

Conflict of interest statement

Funding

References

Aitken, S.N. and Bemmels, J.B. 2016 Time to get moving: Assisted gene flow of forest trees. *Evol. Appl.* **9**, 271–290.

Aitken, S.N. and Whitlock, M.C. 2013 Assisted geneflow to facilitate local adaptation to climate change. *Annu. Rev. Ecol. Evol. Syst.* **44**, 367–388.

Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A. *et al.* 2013 Potential for evolutionary responses to climate change – Evidence from tree populations. *Glob. Chang. Biol.* **19**, 1645–1661.

Baliuckas, V., Ekberg, I., Eriksson, G. and Norell, L. 1999 Genetic variation among and within populations of four Swedish hardwood species assessed in a nursery trial. *Silvae Genet.* **48**, 17–24.

Basler, D. and Körner, C. 2012 Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric. For. Meteorol.* **165**, 73–81.

Bastin, J.F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D. *et al.* 2019 The global tree restoration potential. *Science* **365**, 76–79.

Broadmeadow, M.J.S., Ray, D. and Samuel, C.J.A. 2005 Climate change and the future for broadleaved tree species in Britain. *Forestry* **78**, 145–161.

Christensen, R.H B. 2015 Ordinal - Regression Models for Ordinal Data. *R package version 2015.6–28*. http://www.cran.r-project.org/package=ordinal/.

Cundall, E.P., Cahalan, C.M. and Connolly, T. 2003 Early results of ash (*Fraxinus excelsior* L.) provenance trials at sites in England and Wales. *Forestry* **76**, 385–400.

Cundall, E.P., Cahalan, C.M. and Plowman, M.R. 1998 Early results of sycamore (*Acer pseudoplatanu*s) provenance trials at farm-forestry sites in England and Wales. *Forestry* **71**, 237–245.

Davis, M.B. and Shaw, R.G. 2001 Range shifts and adaptive responses to quaternary climate change. *Science* **292**, 673–679.

Donnelly, K., Cavers, S., Cottrell, J.E. and Ennos, R.A. 2018 Cryptic genetic variation and adaptation to waterlogging in Caledonian scots pine, *Pinus sylvestris* L. *Ecol. Evol.* **8**, 8665–8675.

Ducousso, A., Guyon, J.P. and Krémer, A. 1996 Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl). *Ann. For. Sci.* **53**, 775–782.

Etherington, J.R. 1982 *Environment and Plant Ecology*. Wiley.

Friedman, J.M., Roelle, J.E. and Cade, B.S. 2011 Genetic and environmental influences on leaf phenology and cold hardiness of native and introduced riparian trees. *Int. J. Biometeorol.* **55**, 775–787.

Fu, Y.S.H., Campioli, M., Vitasse, Y., De Boeck, H.J., Van den Berge, J., AbdElgawad, H. *et al.* 2014 Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proc. Natl. Acad. Sci.* **111**, 7355–7360.

Ghalambor, C.K., McKay, J.K., Carroll, S.P. and Reznick, D.N. 2007 Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21**, 394–407.

Gill, A.L., Gallinat, A.S., Sanders-DeMott, R., Rigden, A.J., Short Gianotti, D.J., Mantooth, J.A. *et al.* 2015 Changes in autumn senescence in northern hemisphere deciduous trees: A meta-analysis of autumn phenology studies. *Ann. Bot.* **116**, 875–888.

Gray, L.K. and Hamann, A. 2013 Tracking suitable habitat for tree populations under climate change in western North America. *Clim. Change* **117**, 289–303.

Hällfors, M.H., Vaara, E.M., Hyvärinen, M., Oksanen, M., Schulman, L.E., Siipi, H. *et al.* 2014 Coming to terms with the concept of moving species threatened by climate change–a systematic review of the terminology and definitions. *PLoS One* **9**, e102979.

Hällfors, M.H., Aikio, S. and Schulman, L.E. 2017 Quantifying the need and potential of assisted migration. *Biol. Conserv.* **205**, 34–41.

Hannerz, M., Ekberg, I. and Norell, L. 2003 Variation in chilling requirements for completing bud rest between provenances of Norway spruce. *Silvae Genet.* **52**, 161–168.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. and Chen, T.H. 2003 From genotype to phenotype: Unraveling the complexities of cold adaptation in forest trees. *Can. J. Bot.* **81**, 1247–1266.

IPCC 2013 Summary for policymakers. In *Climate Change 2013 The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. T.F., Stocker, D., Qin, G.-K., Plattner, M., Tignor, S.K., Allen, J., Boschung *et al.* (eds.). Cambridge University Press.

Kerr, G. 1995 The silviculture of ash in southern England. *Forestry* **68**, 63–70.

Kerr, G. and Boswell, R.C. 2001 The influence of spring frosts, ash bud moth (*Prays fraxinella*) and site factors on forking of young ash (*Fraxinus excelsior*) in southern Britain. *Forestry* **74**, 30–41.

Keskitalo, J., Bergquist, G., Gardestrom, P. and Jansson, S. 2005 A cellular timetable of autumn senescence. *Plant Physiol.* **139**, 1635–1648.

Klein, G., Rebetez, M., Rixen, C. and Vitasse, Y. 2018 Unchanged risk of frost exposure for sub-alpine and alpine plants after snowmelt in Switzerland despite climate warming. *Int. J. Biometeorol.* **62**, 1755–1762.

Kleinschmit, J., Svolba, J., Enescu, V., Franke, A., Rau, H.M. and Reutz, W. 1996 First results of provenance trials in *Fraxinus excelsior* established in 1982. *Forstarchiv.* **67**, 114–122.

Kramer, K. 1994 A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in the Netherlands and Germany. *Plant Cell Environ.* **17**, 367–377.

Landolt, J., Gross, A., Holdenrieder, O. and Pautasso, M. 2016 Ash dieback due to *Hymenoscyphus fraxineus*: What can be learnt from evolutionary ecology? *Plant Pathol* **65**, 1056–1070.

Lobo, A., McKinney, L.V., Hansen, J.K., Kjær, E.D. and Nielsen, L.R. 2015 Genetic variation in dieback resistance in *Fraxinus excelsior* confirmed by progeny inoculation assay. *For. Pathol.* **45**, 379–387.

Liang, L. 2019 A spatially explicit modeling analysis of adaptive variation in temperate tree phenology. *Agric. For. Meteorol.* **266**, 73–86.

Maier, D.S. and Simberloff, D. 2016 Assisted migration in normative and scientific context. *J. Agric. Environ. Ethics.* **29**, 857–882.

McKinney, L.V., Nielsen, L.R., Hansen, J.K. and Kjær, E.D. 2011 Presence of natural genetic resistance in *Fraxinus excelsior* (Oleraceae) to *Chalara fraxinea* (Ascomycota): An emerging infectious disease. *Heredity* **106**, 788–797.

McKinney, L.V., Thomsen, I.M., Kjær, E.D. and Nielsen, L.R. 2012 Genetic resistance to *Hymenoscyphus pseudoalbidus* limits fungal growth and symptom occurrence in *Fraxinus excelsior*. *For. Pathol.* **42**, 69–74.

Muñoz, F., Marçais, B., Dufour, J. and Dowkiw, A. 2016 Rising out of the ashes: Additive genetic variation for crown and collar resistance to *Hymenoscyphus fraxineus* in *Fraxinus excelsior*. *Phytopathology* **106**, 1535–1543.

Murphy, J.M., Sexton, D.M.H., Jenkins, G.J., Boorman, P.M., Booth, B.B.B., Brown, C.C. *et al.* 2009 *UK Climate Projections Science Report: Climate change projections*. Met Office Hadley Centre, pp. 21–35.

Murray, M.B., Cannell, M.G.R. and Smith, R.I. 1989 Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* **26**, 693–700.

Mwase, W.F., Savill, P.S. and Hemery, G. 2008 Genetic parameter estimates for growth and form traits in common ash (*Fraxinus excelsior* L.) in a breeding seedling orchard at little Wittenham in England. *New Forests.* **36**, 225–238.

Pliura, A. and Baliuckas, V. 2007 Genetic variation in adaptive traits of progenies of Lithuanian and western European populations of *Fraxinus excelsior* L. *Baltic Forestry* **13**, 28–38.

Pliura, A., Lygis, V., Suchockas, V. and Bartkevicius, E. 2011 Performance of twenty four European *Fraxinus excelsior* populations in three Lithuanian progeny trials with a special emphasis on resistance to *Chalara fraxinea*. *Baltic Forestry* **17**, 17–34.

Perry, M. and Hollis, D. 2005 The generation of monthly gridded datasets for a range of climatic variables over the UK. *Int. J. Climatol.* **25**, 1041–1054.

Petit, R.J. and Hampe, A. 2006 Some evolutionary consequences of being a tree. *Annu. Rev. Ecol. Evol. Syst.* **37**, 187–214.

Pigliucci, M., Murren, C.J. and Schlichting, C.D. 2006 Phenotypic plasticity and evolution by genetic assimilation. *J. Exp. Biol.* **209**, 2362–2367.

R Development Core Team 2015 *R A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Roberts, A.M.I., Tansey, C., Smithers, R. and Phillimore, A.B. 2015 Predicting a change in the order of spring phenology in temperate forests. *Glob. Chang. Biol.* **21**, 2603–2611.

Robson, T.M., Rasztovits, E., Aphalo, P.J., Alia, R. and Aranda, I. 2013 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. *Agric. For. Meteorol.* **180**, 76–85.

Rosique-Esplugas, C. 2018 *Can native woodlands cope with climate change? Measuring genetic variation & phenotypic plasticity in British populations of ash, rowan and silver birch*. PhD thesis. University of Edinburgh, p. 248.

Salmela, M.J., Cavers, S., Cottrell, J.E., Iason, G.R. and Ennos, R.A. 2013 Spring phenology shows genetic variation among and within populations in seedlings of scots pine (*Pinus sylvestris* L.) in the Scottish highlands. *Plant. Ecol. Divers.* **6**, 523–536.

Savill, P.S., Spencer, R., Roberts, J.E. and Hubert, J.D. 1999 Sixth year results from four ash (*Fraxinus excelsior*) breeding seedling orchards. *Silvae Genet.* **48**, 92–100.

Savolainen, O., Pyhäjärvi, T. and Knürr, T. 2007 Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Evol. Syst.* **38**, 595–619.

Sminita, I. 1995 Fifteen years of European ash (*Fraxinus excelsior* L.) provenance trials in Romania. In: Caring for the Forest. Research in a changing world. IUFRO meeting, Tampere, Poster abstracts, p. 72.

Stener, L.-G. 2013 Clonal differences in susceptibility to the dieback of *Fraxinus excelsior* in southern Sweden. *Scand. J. For. Res.* **28**, 205–216.

Stocks, J.J., Buggs, R.J. and Lee, S.J. 2017 A first assessment of *Fraxinus excelsior* (common ash) susceptibility to *Hymenoscyphus fraxineus* (ash dieback) throughout the British isles. *Sci. Rep.* **7**, 1–7.

Sultan, S.E. 2004 Promising directions in plant phenotypic plasticity. *Perspect. Plant Ecol. Evol. Syst.* **6**, 227–233.

Sutherland, B.G., Belaj, A., Nier, S., Cottrell, J.E., Vaughan, S.P., Hubert, J. *et al.* 2010 Molecular biodiversity and population structure in common ash (*Fraxinus excelsior* L.) in Britain: Implications for conservation. *Mol. Ecol.* **19**, 2196–2211.

Tansey, C.J., Hadfield, J.D. and Phillimore, A.B. 2017 Estimating the ability of plants to plastically track temperature-mediated shifts in spring phenological optimum. *Glob. Chang. Biol.* **23**, 3321–3334.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S. *et al.* 2016 Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245.

Thomas, B. and Vince-Prue, D. 1997 *Photoperiodism in Plants*. Elsevier.

Thomas, E., Jahonen, R., Loo, J. and Bozzano, M. 2015 Avoiding failure in forest restoration: The importance of genetically diverse and site-matched germplasm. *Unasylva* **66**, 29–36.

Thomas, P.A. 2016 Biological Flora of the British isles: *Fraxinus excelsior*. *J. Ecol.* **104**, 1158–1209.

Valladares, F., Sanchez-Gomez, D. and Zavala, M.A. 2006 Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. *J. Ecol.* **94**, 1103–1116.

Verdone, M. and Seidl, A. 2017 Time, space, place, and the Bonn challenge global forest restoration target. *Restor. Ecol.* **25**, 903–911.

Viherä-Aarnio, A., Kostiainen, K., Piispanen, R., Saranpää, P. and Vapaavuori, E. 2013 Effects of seed transfers on yield and stem defects of silver birch (*Betula pendula* Roth). *For. Ecol. Manage.* **289**, 133–142.

Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.Y., Louvet, J.M., Kremer, A. *et al.* 2009a Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agric. For. Meteorol.* **149**, 735–744.

Vitasse, Y., Porte, A.J., Kremer, A., Michalet, R. and Delzon, S. 2009b Responses of canopy duration to temperature changes in four temperate tree species: Relative contributions of spring and autumn phenology. *Oecologia* **161**, 187–198.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R. and Kremer, A. 2009c Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can. J. For. Res.* **39**, 1259–1269.

Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R. and Delzon, S. 2010 Quantifying phenological plasticity to temperature in two temperate tree species. *Funct. Ecol.* **24**, 1211–1218.

Vitasse, Y. and Basler, D. 2013 What role for photoperiod in the bud burst phenology of European beech. *Eur. J. For. Res.* **132**, 1–8.

Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Scheepens, J.F. *et al.* 2013 Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia* **171**, 663–678.

Vitasse, Y., Schneider, L., Rixen, C., Christen, D. and Rebetez, M. 2018 Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. *Agr. For. Meteorol.* **248**, 60–69.

Wardle, P. 1961 Biological flora of the British isles. *Fraxinus excelsior* L. *J. Ecol.* **49**, 739–751.

Whitlock, C. and Millspaugh, S.H. 2001 A paleoecologic perspective on past plant invasions in Yellowstone. *West. N. Am. Naturalist* **61**, 316–327.

Whittet, R., Cottrell, J., Cavers, S., Pecurul, M. and Ennos, R. 2016 Supplying trees in an era of environmental uncertainty: Identifying challenges faced by the forest nursery sector in great Britain. *Land Use Policy* **58**, 414–426.

Whittet, R., Cavers, S., Ennos, R. and Cottrell, J. 2019 Genetic considerations for provenance choice of native trees under climate change in England. In *Forestry Commission Research Report*. Forestry Commission, p. 44.

Whittet, R., Lopez, G. and Rosique-Esplugas, C. 2021 Mid-rotation variation in growth, form and phenology of sycamore (*Acer pseudoplatanus* L.) provenances in field trials in England. *Forestry* **00**, 1–10.

Wilson, K.B. and Baldocci, D.D. 2000 Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America. *Agric. For. Meteorol.* **100**, 1–18.

Ying, C.C. and Yanchuk, A.D. 2006 The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. *For. Ecol. Manage.* **227**, 1–13.

Zhu, K.A.I., Woodall, C.W. and Clark, J.S. 2012 Failure to migrate: Lack of tree range expansion in response to climate change. *Glob. Chang. Biol.* **18**, 1042–1052.

Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.C., Vitasse, Y., Benito, B.M. *et al.* 2020 Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proc. Natl. Acad. Sci.* **117**, 12192–12200.