

## Article (refereed) - postprint

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

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

34

## 35 Introduction

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

49 Phenotypic plasticity is the ability of an individual genotype to produce different phenotypes in  
50 response to cues from its environment. Although the extent of phenotypic plasticity within species is  
51 limited, it provides one of the most significant ways in which plants can react to rapid environmental  
52 change (Sultan, 2004; Pigliucci *et al.*, 2006; Valladares *et al.*, 2006; Ghalambor *et al.*, 2007). It may be  
53 particularly important for trees as it contributes to their ability to cope with the wide range of  
54 conditions they may experience during typically long lifetimes (Petit and Hampe, 2006). Multi-site  
55 common-garden trials provide a tool with which to explore the plastic responses of species to  
56 different environmental conditions. Genetic variation may also contribute to the ability of tree  
57 populations to survive under future conditions. If local selection has been strong enough,  
58 populations of trees will have adapted to their local environments via natural selection, so that  
59 locally sourced individuals will exhibit higher fitness in their home environment than non-local  
60 individuals (Savolainen *et al.*, 2007). However, tree species are highly effective dispersers of their  
61 genes and the consequent immigration of genetic diversity (gene flow) into populations acts in  
62 opposition to local adaptation. As a result, although tree populations may show a local mean  
63 optimum phenotype, they are typically highly variable around this mean and this variation provides  
64 the raw material for future adaptation (Davis and Shaw, 2001; Petit and Hampe, 2006). Common  
65 garden trials have demonstrated that tree populations are frequently differentiated for adaptive  
66 traits (Whittet *et al.*, 2019) and that an understanding of this variation for a range of key adaptive  
67 traits is vital to predicting their ability to adapt to future conditions (Alberto *et al.*, 2013).

68 Globally, there are ambitions to increase woodland area in order to mitigate climate change  
69 (Verdone and Seidl, 2017; Bastin *et al.*, 2019). An important consideration in this endeavour is the  
70 sourcing of well-adapted planting stock. Poleward translocation of genetic material has been  
71 proposed as a measure that may help tree populations to keep pace with the rate of change, a  
72 practice understood within a suite of conservation actions broadly known as 'assisted migration'  
73 (Whitlock and Millspaugh, 2001; Hällfors *et al.*, 2014). In the northern hemisphere, this strategy for  
74 the planting of new woodlands would involve sourcing seeds from warmer areas further south, in  
75 the expectation that they will be better adapted to the projected future climate of the planting site.  
76 However, many uncertainties surround this strategy, not least the fact that southern-sourced  
77 populations may be poorly adapted to current conditions at northern sites. For example, seed

78 sourced from a southern population should be adapted to local seasonal timing and at northern  
79 locations may flush leaves early in spring and senesce late in autumn leaving them vulnerable to  
80 early or late frosts in contemporary environments (Broadmeadow *et al.*, 2005; Vitasse *et al.*, 2018).  
81 Damage incurred in early growth stages may not be overcome even if individuals survive. Spring  
82 phenology is advancing under climate change (Roberts *et al.*, 2015; Fu *et al.*, 2014; Thackeray *et al.*,  
83 2016). However, advances in the timing of key spring phenological events such as bud-burst can be  
84 greater than the advance in the date of the latest spring frost (Vitasse *et al.*, 2018; Klein *et al.*, 2018),  
85 and Zohner *et al.* (2020) found that late-spring frost risk has increased in Europe since 1959.  
86 Furthermore, some environmental factors, such as photoperiod, will not vary under climate change  
87 and interactions may be important. Both temperature and photoperiod have a role in controlling the  
88 timing of bud burst, although the effects vary among species (Vitasse and Basler, 2013; Tansey *et al.*,  
89 2017), and there are both genetic and plastic components to leaf phenology variation within species  
90 (Wilson and Baldocchi, 2000).

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

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

116

117 **Methods**

118

## 119 *Experimental design*

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

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

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

136 **Figure 1 here please (Map)**

137 **Table 1 here please**

## 138 *Measurements and scorings*

139 The trees were assessed for height at 5 years old, measured to the nearest centimetre with an  
140 extendable measuring rod. Stem diameter was assessed using DBH (diameter at a breast height of  
141 around 1.35 m) when trees were 8 years old. Stem forking was assessed at age 8 years, counting the  
142 number of forks (i.e. number of times the main stem lost apical dominance). This was assessed by  
143 following the main stem from the ground up, including the subsequent branches originated from  
144 each fork up to the crown, excluding the small twigs.

145 Spring phenology was assessed using a six-stage ordinal morphological scale. The top bud of each  
146 tree was visually assessed to determine which of the six stages best described the development  
147 stage of the leaf (leaf flushing). In this scoring system stage 1 corresponds to a dormant fully closed  
148 bud while stage 6 corresponds to a fully expanded bud (Table 2 Suppl., Figure 2). The terminal bud of  
149 each tree was assessed and scored on each visit. If the terminal bud was damaged, missing or dead  
150 then the next highest bud on the main stem was assessed. If the tree had more than one leading  
151 stem (i.e., was forked), then the bud on the stem with the largest diameter was assessed. Where the  
152 two stems were found to be equal in diameter, the highest bud was assessed. If forks were equal in  
153 height and diameter then the bud giving the highest score was recorded. The trees were assessed at  
154 age 7 years old between April and June 2013, on 13 occasions in Llandovery and on 15 occasions in  
155 North York Moors.

156 Assessments of autumn leaf senescence phenology were based on foliage throughout the entire  
157 crown rather than a single leaf or a sub-set of leaves. The crown of the tree was visually inspected,  
158 and assessment was based on the proportion of the crown that was visible to the assessor standing  
159 on the south-facing side of each tree. Leaf senescence was measured as the percentage of the  
160 canopy which had shed its leaves (Table 2 Suppl.). This ranged from stage 1 (0% leaf loss) to stage 6  
161 (100% leaf loss). Both trials were assessed between September and November 2014, on 20  
162 occasions in Llandovery and 23 in North York Moors.

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

173 **Figure 2 here please (Leaf flushing drawing)**

#### 174 *Data analysis*

175 All data analyses were performed in the R statistical environment (R version 3.2.3, Core Team, 2015).  
176 To determine the effects of provenance, site and their interaction on each trait the plot mean values  
177 were analysed in analysis of variance (ANOVA) using a linear model. Missing and dead trees were  
178 excluded in the calculation of plot mean values. Two types of ANOVA were used for each trait. The  
179 first type of analysis of variance was done by individual trial site, where provenance was a fixed  
180 factor and block was a random factor:

$$181 \quad Y_{ijk} = \mu + Prov_i + Block_j + \epsilon_{ijk}$$

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

$$184 \quad Y_{ijkl} = \mu + Prov_i + Site_j + (Prov*Site)_{ij} + Block_{k(j)} + \epsilon_{ijkl}$$

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

190 For each trait at each site, univariate linear regressions were applied to test the relationship  
191 between plot mean values and latitude, longitude and climatic variables of the provenance's home  
192 site (adjusted for block). Values of climatic covariates were extracted from long-term average  
193 climate data provided by the Met Office. The datasets interpolate observations from weather  
194 stations onto a 5 x 5 km grid for the whole of Great Britain for the period 1960-2000. Full details of

195 generation of the long-term average data are provided in Perry and Hollis (2005). The following  
196 predictors were taken forward for use in the analyses: Growing degree days (GDD), as the annual  
197 accumulated temperature  $\sum(\text{daily mean temperature} - 5.5)$  whenever daily mean temperature  $> 5.5$   
198  $^{\circ}\text{C}$ ; the growing season length (GSL) of the provenance site was measured as the annual sum of days  
199 where temperature mean is over  $5^{\circ}\text{C}$  for over five consecutive days; Ground frost days (GFD), the  
200 annual count of days when the minimum temperature is below  $0^{\circ}\text{C}$ ; Mean temperature of February,  
201 the coldest month of the year (MTF); and the mean temperature of July, one of the warmest months  
202 of the year (MTJ). To test for covariation between traits, Pearson's correlation coefficients were  
203 calculated using provenance means from the individual sites.

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

214

## 215 **Results**

### 216 *Growth*

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

226 For the stem diameter, there was a significant provenance effect in Llandovery but not in North York  
227 Moors (Table 2). There was a significant site effect ( $p < 0.001$ ), but no significant site by provenance  
228 interaction. DBH was on average 54.7% higher at Llandovery than North York Moors. There was a  
229 very big Block effect for stem diameter, which was larger in North York Moors.

### 230 *Spring phenology*

231 Significant differences were found among provenances for the timing of spring leaf flush  
232 (JD50\_Flush) at both sites. The difference between JD50\_Flush of the earliest and latest provenances  
233 was 18 days at Llandovery (May 9<sup>th</sup> to June 6<sup>th</sup>) and 11 days at North York Moors (May 20<sup>th</sup> to May

234 31<sup>st</sup>). The site effect was significant (Table 2). However, provenance explained over 64% of the  
235 variance, while site explained 13% (Figure 3). All provenances, except two, flushed earlier at North  
236 York Moors, with the site mean JD50\_Flush being three days earlier (24<sup>th</sup> of May) than it was at  
237 Llandovery (27<sup>th</sup> of May). Only nine provenances flushed on average more than 3 days later in  
238 Llandovery than North York Moors, the largest difference being 7 days for the same provenance  
239 between sites. No significant interaction was found between provenance and trial site.

#### 240 *Autumn phenology*

241 The differences among provenances for the timing of leaf senescence (JD50\_Senesce) were only  
242 significant at North York Moors (Table 2). The difference between the earliest and latest  
243 provenances was larger at Llandovery (37 days, Oct 5<sup>th</sup> to Nov 11<sup>th</sup>) than North York Moors (24 days,  
244 Oct 6<sup>th</sup> to Oct 30<sup>th</sup>). There was a significant site effect, with senescence occurring on average 8 days  
245 earlier at North York Moors than Llandovery. All provenances except one (from a northern latitude)  
246 lost their leaves earlier at the North York Moors trial than at Llandovery. Over half of the  
247 provenances (twenty-one) senesced >8 days on average earlier in North York Moors compared to  
248 Llandovery, the largest difference between sites being 22 days. There was no significant interaction  
249 between provenance and trial site. Site effect explained 30% of the variance while provenance  
250 explained 15% (Figure 3).

#### 251 **Figure 3 here please (proportion of variance explained)**

#### 252 *Forking*

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

#### 259 *Survival*

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

#### 264 *Geographic variation and relation with climatic variables*

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

273 The annual cumulative temperature, measured as GDD (growing degree days), was found to explain  
274 more variation than any of the other variables tested (Table 3 Suppl.). The GDD of the provenances'  
275 origin explained around 40% of the variation for height and the leaf phenology traits, for both sites,  
276 in regressions with the opposite sign of the slope coefficient from latitude (Table 2). In Great Britain,  
277 temperature is strongly correlated with latitude (Figure 1 Suppl., Table 4 Suppl.), the higher the  
278 latitude the colder the climate and the shorter the length of the growing season for trees to grow.  
279 The GDD and the latitude of the provenance's site were strongly correlated ( $GDD \sim Lat$ ,  $R: -0.77$ ,  $p <$   
280  $0.001$ ). Latitude proved to be a very good explanatory variable, aligning well with both the strong  
281 climatic and photoperiod clines in Great Britain.

282 **Table 2 here please**

283 **Figure 4 here please (data graphs)**

284 *Correlations between traits*

285 Height and DBH were significantly correlated with leaf phenology at both trial sites. The tallest  
286 provenances flushed earlier (Llandovery:  $R = -0.82$ ,  $p < 0.001$ ; North York Moors:  $-0.58$ ,  $p < 0.001$ ),  
287 and senesced later (Llandovery:  $R = 0.52$ ,  $p < 0.001$ ; North York Moors:  $R = 0.58$ ,  $p < 0.001$ ). The  
288 provenances with larger stem diameter flushed earlier (Llandovery:  $R = -0.73$ ,  $p < 0.001$ ; North York  
289 Moors:  $R = -0.51$ ,  $p < 0.001$ ) and senesced later (Llandovery:  $R = 0.54$ ,  $p < 0.001$ ; North York Moors:  $R$   
290  $= 0.72$ ,  $p < 0.001$ ). Tree height and DBH were significantly positively correlated (Llandovery:  $R = 0.89$ ,  
291  $p < 0.001$ ; North York Moors:  $R = 0.88$ ,  $p < 0.001$ ).

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

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

300

301 **Discussion**

302 *Genetic differences*

303 We have shown significant differences among provenances of common ash in Great Britain for  
304 growth traits, stem form, and leaf phenology. The pattern of trait variation was clinal, with greater  
305 growth, earlier leaf flushing and later senescence, and higher frequency of stem defects (one site  
306 only) in southern provenances compared to northern provenances. Differences among provenances,  
307 and the strength of the clinal trend were stronger at the southern site (Llandovery). Other studies on  
308 common ash across its natural range have found significant genetic differences at population or  
309 family level in these traits (Cundall *et al.*, 2003; Mwase *et al.*, 2008; Pliura and Baliuckas, 2007, Pliura  
310 *et al.*, 2011, Savill *et al.*, 1999). However, the clear latitudinal cline found in our study was not

311 previously detected in provenance tests of ash within Britain, perhaps due to insufficient numbers of  
312 provenances or sampling from a more limited geographic range (Cundall *et al.*, 2003). In our study,  
313 plants from southern latitudes were taller and had greater DBH than those from more northerly  
314 latitudes at both trial sites, although the differences between provenances were more evident at the  
315 southern trial site. These differences may be due to the longer growing season achieved by southern  
316 provenances through earlier flushing and later leaf senescence.

317 The significant differences among provenances for leaf flushing and leaf senescence showed a  
318 geographical pattern. For both sites and both traits latitude explained between 33 and 44% of the  
319 variation, where the southern provenances flushed earlier and senesced later than the northern  
320 ones when grown under the same environmental conditions. This demonstrates genetic variation in  
321 these traits and, as variation was correlated with latitude and climatic variables (such as growing  
322 season length and growing degree days), suggests adaptation to conditions at site of origin. Reviews  
323 by Alberto *et al.* (2013) and Aitken and Bemmels (2016) found that genetic differentiation along  
324 clines is generally stronger for autumn phenology than for spring phenology, both in broadleaved  
325 and conifer trees, although the effect varies among species. However, we found the opposite was  
326 the case in our study, where provenance explained a much larger proportion of the variance for  
327 spring phenology (63%) than for autumn phenology (15%). Several studies in common garden  
328 experiments in deciduous trees showed a genetic component in leaf phenology. Vitasse *et al.*  
329 (2009c) showed that among population differences in spring flushing time of ash and oak were  
330 related to the climate in origin, where the trees from warmer climates flushed earlier. Similarly,  
331 Ducouso *et al.* (1996) showed timing of bud burst in oak populations followed geographical pattern  
332 related to the site of origin (both latitude and altitude) and spring frost tolerance, where the  
333 northern provenances flushed later than the southern ones, in accordance with our results.  
334 However, other tree species follow the opposite pattern for bud flush (Vitasse *et al.*, 2009a; Whittet  
335 *et al.*, 2021) or show no pattern for spring phenology but instead exhibit a pattern for autumn  
336 phenology (e.g. *Populus deltoides*, Friedman *et al.*, 2011). Our results show that the effect of  
337 provenance in ash leaf flushing is stronger than for leaf senescence.

338 Ash is very prone to frost damage and even though leaf emergence in ash is late in relation to other  
339 species, damage by winter cold, and autumn and spring frost can occur for two reasons. Firstly,  
340 when the tree is dormant, air temperatures below its cold hardiness tolerance will result in 'winter  
341 injury'. The cold hardiness tolerance threshold reduces as the winter progresses towards spring  
342 when it rises from -27 °C in midwinter to -3 °C at the bud swelling stage in spring (Etherington,  
343 1982). The second basis for damage is unseasonal frosts before the tree has become dormant in  
344 autumn or after it has flushed in spring. For example, Wardle (1961) reported that young ash leaves  
345 could be killed if they are subjected to long periods in which air temperatures are only as low as -3  
346 °C. Evidence of a genetic effect on forking has been provided by provenance and progeny trials and  
347 Kerr (1995) concluded that there was both a genetic and an environment effect on forking.  
348 Kleinschmit *et al.* (1996) and Sminita (1995) both stressed the importance of correct choice of  
349 provenance when planting ash in mainland Europe. Both demonstrated that provenances from  
350 latitudes from further south than the planting site were less cold hardy or flushed too early and  
351 resulted in forking. Similarly, Baliuckas *et al.* (1999) discovered a positive and significant relationship  
352 between early bud flushing and frost damage in a four-year-old ash trial in southern Sweden based  
353 on Swedish provenances. Our results at North York Moors agree with this observation, where  
354 provenances from more southerly latitudes showed a higher incidence of forking than those from

355 more northerly latitudes. As with the results of Kleinschmit *et al.* (1996) and Sminita (1995) our  
356 findings demonstrate that the southern provenances at North York Moors flush earlier and lose their  
357 leaves later than northern provenances and this longer growing season may leave them vulnerable  
358 to exposure to the damaging environmental events mentioned earlier. Clearly, therefore, although  
359 transfer of southern provenances to more northerly planting sites as a strategy for rapid adaptation  
360 to climate change may result in higher relative growth rates, it may have negative side-effects for  
361 traits of economic importance.

### 362 *Phenotypic plasticity*

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

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

376 Our results show that autumn senescence was more plastic than spring flushing for ash in the  
377 different years in which each trait was recorded. This contrasts with the results of *in situ* studies  
378 (along an altitudinal gradient, not latitudinal gradient, therefore photoperiod was constant) that  
379 found that ash presented the highest sensitivity to temperature in flushing compared to other  
380 species (Vitasse *et al.* (2009a), while temperature did not have a significant effect on ash trees leaf  
381 senescence (Vitasse *et al.*, 2009b). A possible explanation for our results is that photoperiod at the  
382 trial sites influenced plasticity in autumn phenology. Photoperiod is a driver for autumn phenology in  
383 several deciduous tree species (including white ash, *Fraxinus americana* L.) (Thomas and Vince-Prue,  
384 1997; Gill *et al.*, 2015; Liang, 2019) but was shown to have had no effect on spring phenology in  
385 common ash (Basler and Körner, 2012). Other autumn phenology events (cold hardiness and bud  
386 set) have been shown to have a lower phenotypic plasticity than spring events in many tree species  
387 (Howe *et al.*, 2003; Savolainen *et al.*, 2007). Vitasse *et al.* (2013) found that bud set in ash occurred  
388 later at higher altitudes. Leaf senescence is a key phenological process which protects the trees from  
389 frost by remobilisation of nutrients such as nitrogen and photosynthates out of the leaves prior to  
390 leaf shedding. The timing can influence growth in the subsequent year and late senescence involves  
391 a risk-benefit trade-off. It can provide a longer season during which photosynthates can be produced  
392 by the leaves, but it can result in loss of accumulated photosynthates if autumn frosts arrive before  
393 these have been moved out of the leaves (Keskitalo *et al.*, 2005). The higher plasticity we have  
394 shown for leaf senescence compared to leaf flushing may suggest that, for ash in Britain, the damage  
395 from a spring frost exerts stronger selective pressure than autumn frost.

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

#### 422 *Implications for forest management and assisted migration*

423 Growth traits, such as height and diameter are regularly used as indirect measures of fitness in  
424 provenance and progeny trials as they are both relatively easy to measure and are of clear  
425 silvicultural importance (Whittet *et al.*, 2019). Their use as a proxy for fitness is justified for two  
426 reasons. Firstly, that bigger individuals have survived and grown well and so have competed  
427 successfully for resources. Secondly, because large stature provides a reproductive advantage, both  
428 in terms of possible number of inflorescences and the capacity to catch pollen and disperse pollen  
429 and seed (Petit and Hampe, 2006; Ying and Yanchuk, 2006). For these reasons, growth data are often  
430 used as a basis on which to recommend particular provenances, define seed transfer limits or make  
431 inferences about patterns of local adaptation (Ying and Yanchuk, 2006). Our results show a strongly  
432 clinal latitudinal genetic pattern of variation in growth, phenology and forking, with trees from lower  
433 latitudes showing greater growth but a larger number of stem defects. We hypothesise that this  
434 represents a trade-off between growth and frost avoidance which is associated with timing of leaf  
435 flushing and senescence. Therefore, growth considered in isolation may not be an appropriate single  
436 measure of fitness or adaptability, highlighting the need to assess a range of traits at appropriate  
437 ages and explore interactions and covariances among them to guide seed transfer limits (Viherä-  
438 Aarnio *et al.*, 2013). In our case, trait covariance reveals a clear risk in assisted migration. We show

439 that spring phenology changes very little across the two sites, while autumn phenology is more  
440 affected by the planting site. If, as suggested by Vitasse *et al.* (2009c), temperature has little  
441 influence on leaf senescence in ash, it may be that photoperiod plays a more prominent role. This is  
442 potentially important as much of the justification for moving plants northwards to prepare for  
443 climate change is based on temperature being the major driver of trait variation. In conclusion, we  
444 recommend that care is taken in assessing transfer, by using species-specific analyses that  
445 incorporate multiple traits and drivers, and by favouring the use of conservatively adapted  
446 provenances, especially in frost-prone sites.

447 The medium-term future for ash across Europe is uncertain due to the devastating impact of ash  
448 dieback disease. Resistance breeding efforts so far have found moderate to high heritability values  
449 for variation in dieback tolerance in young ash trials (Lobo *et al.*, 2015; McKinney *et al.*, 2011; 2012;  
450 Muñoz *et al.*, 2016; Pliura *et al.*, 2011; Stener, 2013), and have proposed that early leaf senescence  
451 may be a source of adapted resilience to dieback due to shortening the window in which infection  
452 can take hold and invade stem tissues (McKinney *et al.*, 2012; Stener, 2013; Landolt *et al.*, 2016). We  
453 found consistently earlier leaf senescence in trees from northern populations that had been  
454 transferred south. In parallel with this, lower ash dieback susceptibility scores of material from  
455 Central Scotland have been observed in mass screening trials growing in East Anglia (Stocks *et al.*,  
456 2017). If early leaf senescence does play a role in avoidance or tolerance of ash dieback, there could  
457 be an argument for targeting selection of putatively tolerant trees from the north of Britain for  
458 inclusion within a resistance-breeding population. Finally, the clear geographical pattern of genetic  
459 variation observed in ash suggests that responses to natural selection in the species are efficient.  
460 Genetic variation, coupled with the species' capability for plastic responses, offers some hope for  
461 the long-term persistence of ash in the landscape.

462

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### 471 **Supplementary material**

472 The following supplementary material is available at Forestry online: a table with the location of the  
473 provenances and their climatic conditions; a table with detailed description of the scores used to  
474 assess leaf phenology; a table with regressions between each trait and climatic variables of the  
475 provenances' origin; a table of these climatic variables and their correlation with latitude; and a  
476 scatterplot (latitude in y axis, temperature in x axis) of the natural distribution of ash in Great Britain  
477 with the study provenances and sites locations.

478 **Data Availability Statement**

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

480 **Conflict of interest statement**

481 None declared.

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680 **Table and Figure captions**

681 **Figure 1.** Locations from which ash provenances were sourced (grey circles) and the two  
682 trial site locations (black triangles).

683 **Figure 2.** Stages of bud flushing and their corresponding score. Drawing provided by Gabriel  
684 Hemery (gabrielhemery.com)

685 **Figure 3.** Proportion of variance explained by each factor of the model (provenance, site,  
686 site by provenance, block and residual) for Height, DBH, forking, flushing and senescence.  
687 These were calculated with the analysis of variance across sites.

688 **Figure 4.** Linear regression with latitude for height (a), leaf flushing (b), leaf senescence (c),  
689 and stem forking (d); by trial site (Llandovery and North York Moors). Each dot represents a  
690 provenance mean with lines showing confidence intervals. All regressions are statistically  
691 significant except for forking in Llandovery (Table 1). Vertical dotted line indicates the  
692 latitude of the trial site.

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

695 **Table 2.** Summary of analysis of trait variation, by trial site (LLAN=Llandovery, NYM=North  
696 York Moors). The table provides: significance of the provenance effect (Prov), the site effect  
697 (Site) and the provenance by site interaction (Prov x Site), where p is the p-value for  
698 statistical significance and “ns” means not significant. Also the significance (p), R-squared  
699 (R<sup>2</sup>) and slope of the regressions are given for individual univariate regressions of latitude  
700 and growing degree days (GDD, the annual accumulative sum of degrees (daily mean  
701 temperature – 5.5) in days when mean temperature > 5.5 °C) at provenance site of origin  
702 against each assessed trait.

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724 **Table 1.** Coordinates and associated environmental information for the trial sites at  
 725 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

726 Lat = latitude, in degrees; Lon = longitude, in degrees; Alt = altitude, in metres; and CT = continentality, which  
 727 corresponds to the Conrad Index (Conrad, 1946) ( $CT = 1.7 [A/\sin(\phi + 10)] - 14$ , where A is the difference  
 728 between the mean temperature of the warmest and coldest month in degrees Celsius and  $\phi$  is latitude in  
 729 degrees; lower values indicate more oceanic climates). The other variables are extrapolated climatic data  
 730 provided by Met Office, 5x5 km polygons, annual averages for 1970-2011 (Perry and Hollis, 2005): AP = annual  
 731 precipitation (in mm); GSL= growing season length (days where temperature mean is over 5 °C for over 5  
 732 consecutive days); GDD = growing degree days ( $\sum(\text{daily mean temperature} - 5.5)$  whenever daily mean  
 733 temperature > 5.5 °C); GFD = ground frost days (Count of days when the minimum temperature is below 0 °C).

734 **Table 2.** Summary of analysis of trait variation, by trial site (LLAN=Llandovery, NYM=North  
 735 York Moors). The table provides: significance of the provenance effect (Prov), the site effect  
 736 (Site) and the provenance by site interaction (Prov x Site), where p is the p-value for  
 737 statistical significance and “ns” means not significant. Also the significance (p), R-squared  
 738 ( $R^2$ ) and slope of the regressions are given for individual univariate regressions of latitude  
 739 and growing degree days (GDD, the annual accumulative sum of degrees (daily mean  
 740 temperature – 5.5) in days when mean temperature > 5.5 °C) at provenance site of origin  
 741 against each assessed trait.

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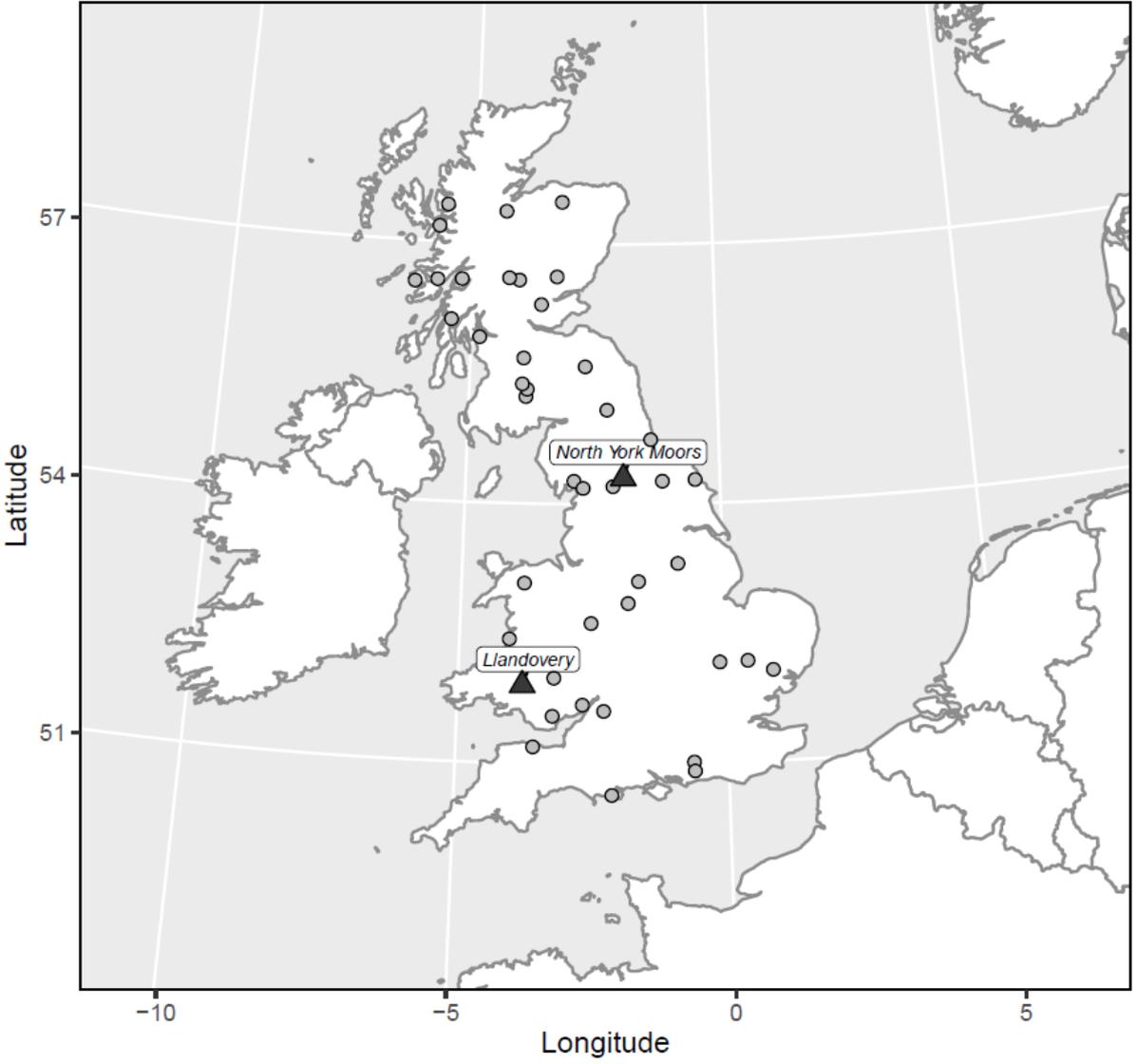
Trait	Trial site	ANOVA			REGRESSION	
		Prov	Site	Prov x Site	Latitude	GDD
Height	LLAN	p<0.001	p<0.001	p<0.05	R <sup>2</sup> : 0.46, p<0.001 slope: -0.13	R <sup>2</sup> : 0.44, p<0.001 slope: 0.11
	NYM	p<0.05			R <sup>2</sup> : 0.40, p<0.001 slope: -0.05	R <sup>2</sup> : 0.33, p<0.001 slope: 0.03
DBH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

					slope: -0.53	slope: 0.004
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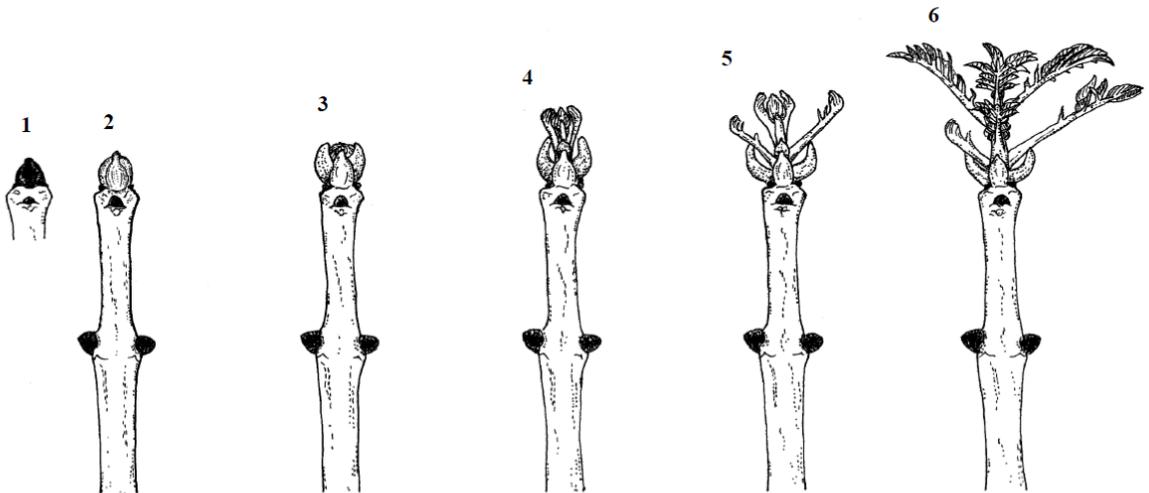
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747 **Figure 1.** Locations from which ash provenances were sourced (grey circles) and the two  
748 trial site locations (black triangles).

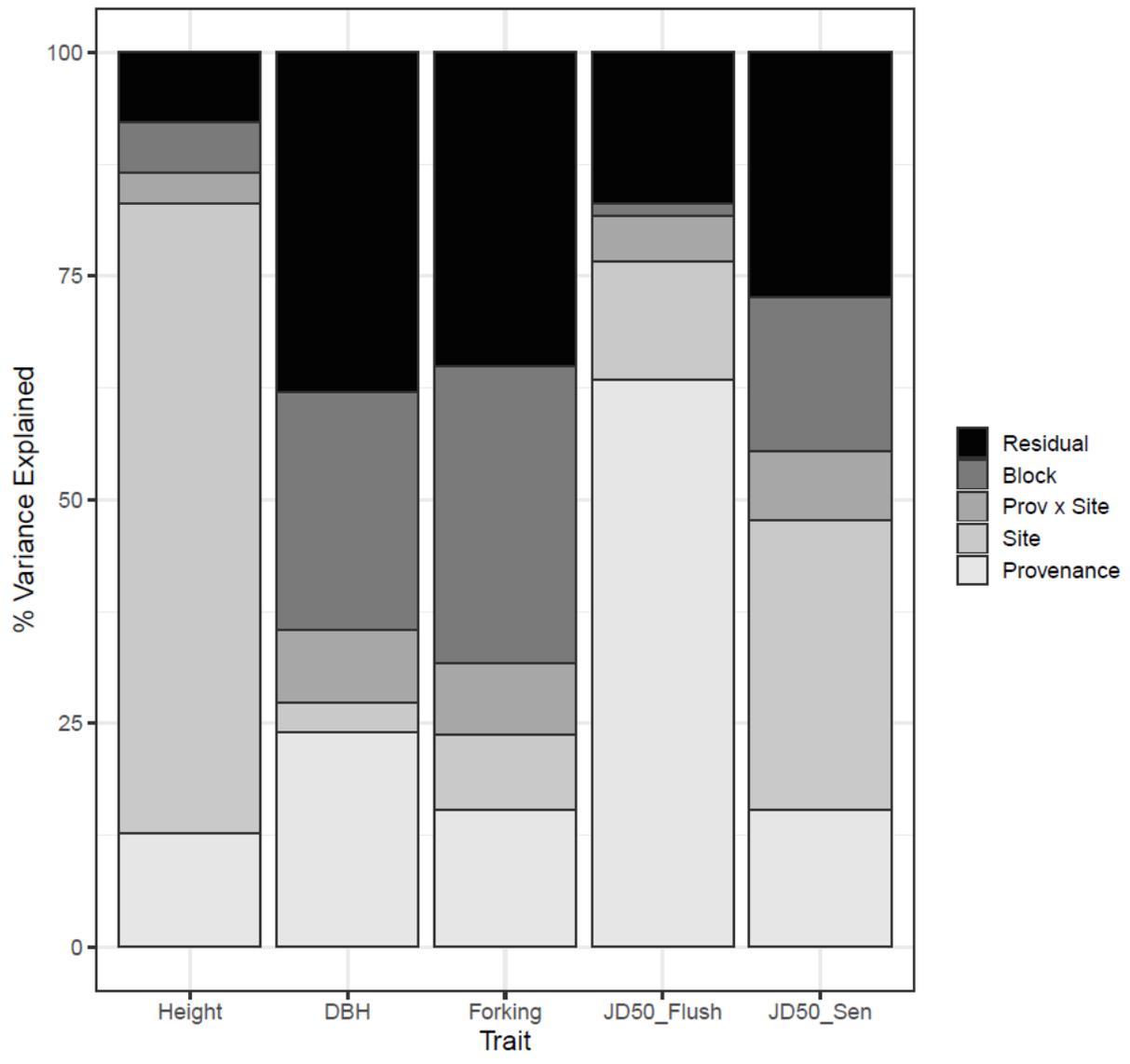
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751 **Figure 2.** Stages of bud flushing and their corresponding score. Drawing provided by Gabriel  
752 Hemery ([gabrielhemery.com](http://gabrielhemery.com))

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755 **Figure 3.** Proportion of variance explained by each factor of the model (provenance, site,  
 756 site by provenance, block and residual) for Height, DBH, forking, flushing and senescence.  
 757 These were calculated with the analysis of variance across sites.

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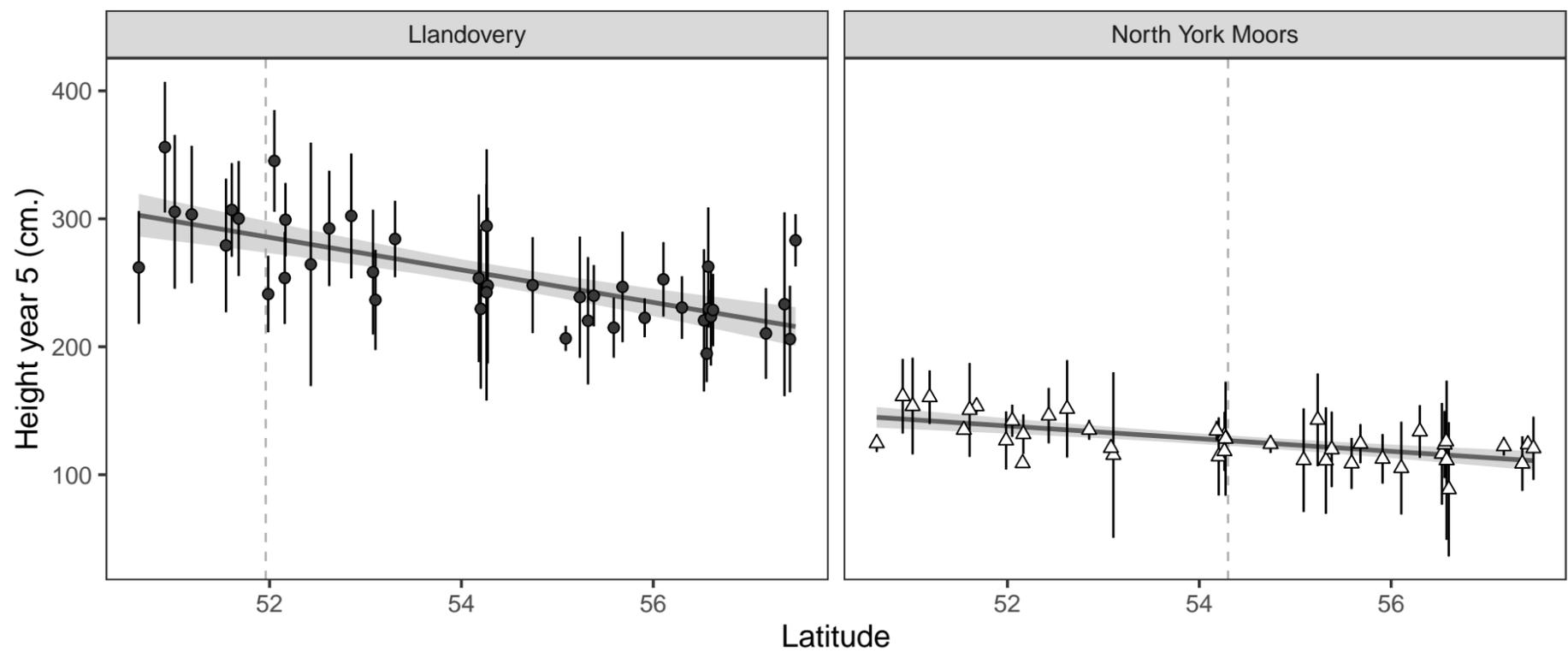
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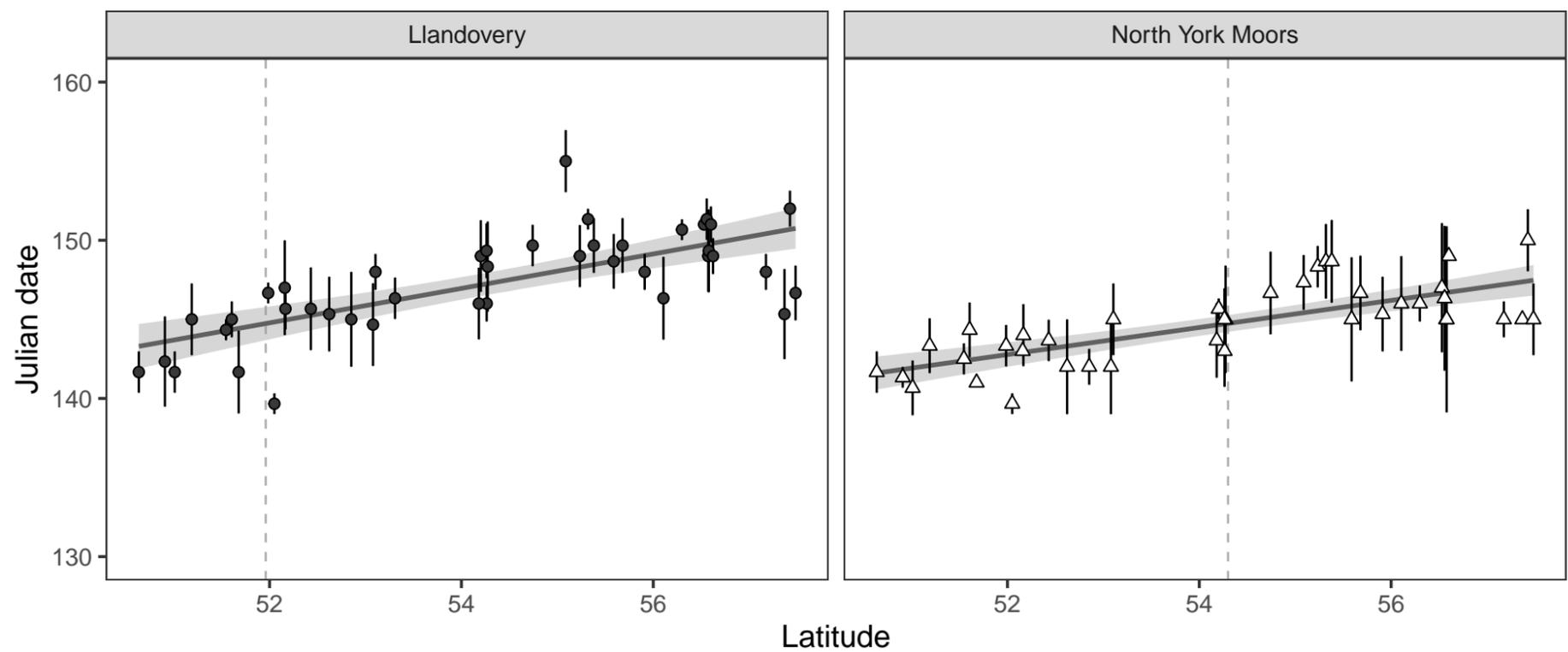
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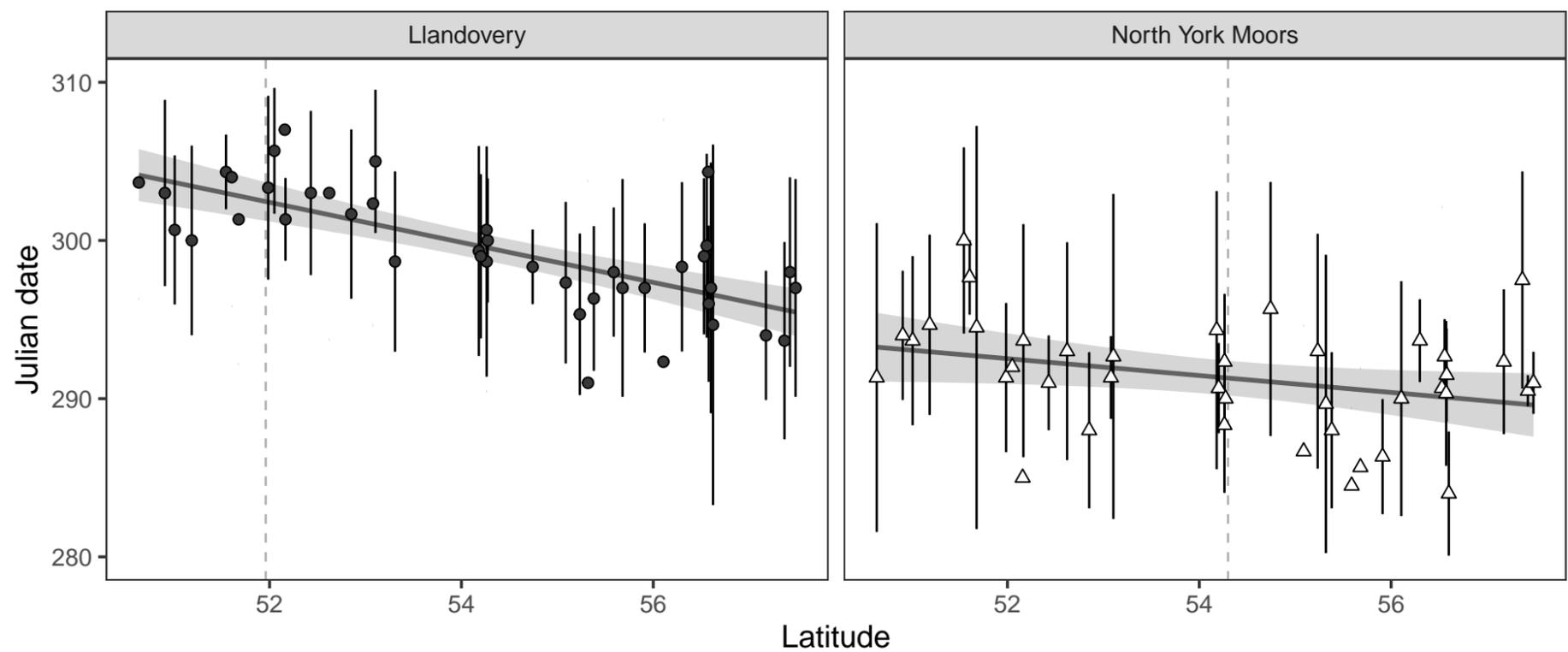
### a. Height



### b. JD50\_Flush



### c. JD50\_Senesce



### d. Stem forking

