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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°C for over five consecutive days; Ground frost days (GFD), the
200 annual count of days when the minimum temperature is below 0°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 9th to June 6th) and 11 days at North York Moors (May 20th to May

234 31st). 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 (24th of May) than it was at
237 Llandovery (27th 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 5th to Nov 11th) than North York Moors (24 days,
244 Oct 6th to Oct 30th). 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 (R²) 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 ϕ 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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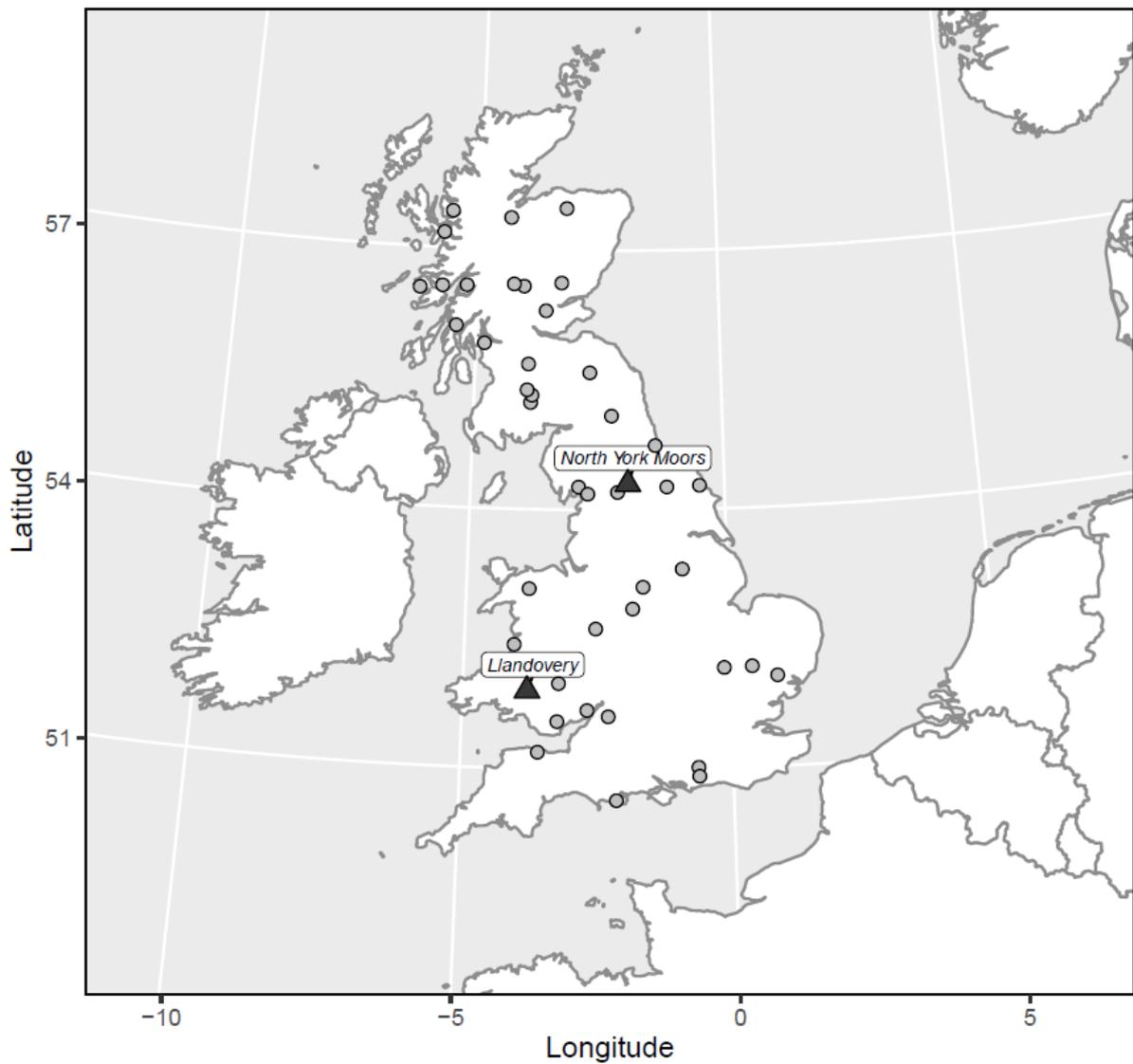
Trait	Trial site	ANOVA			REGRESSION	
		Prov	Site	Prov x Site	Latitude	GDD
Height	LLAN	p<0.001	p<0.001	p<0.05	R ² : 0.46, p<0.001 slope: -0.13	R ² : 0.44, p<0.001 slope: 0.11
	NYM	p<0.05			R ² : 0.40, p<0.001 slope: -0.05	R ² : 0.33, p<0.001 slope: 0.03
DBH	LLAN	p<0.001	p<0.001	ns	R ² : 0.36, p<0.001 slope: -0.2184	R ² : 0.33, p<0.001 slope: 0.001
	NYM	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	p<0.01	ns	ns	ns
	NYM	p<0.001			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	p<0.001	ns	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			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	p<0.001	ns	R ² : 0.33, p<0.001 slope: -1.27	R ² : 0.33, p<0.001 slope: 0.01
	NYM	p<0.01			R ² : 0.44, p<0.001	R ² : 0.44, p<0.05

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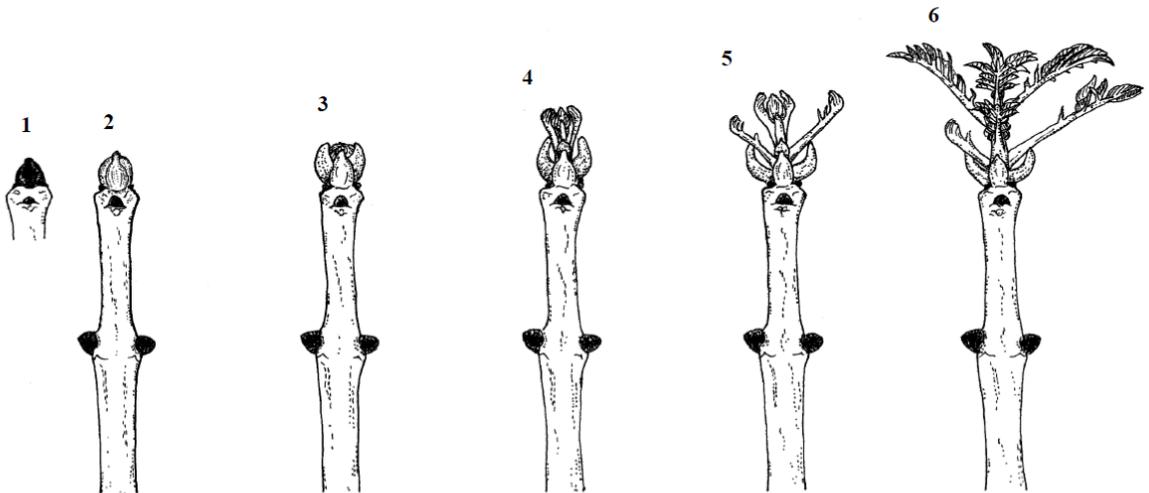
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747 **Figure 1.** Locations from which ash provenances were sourced (grey circles) and the two
748 trial site locations (black triangles).

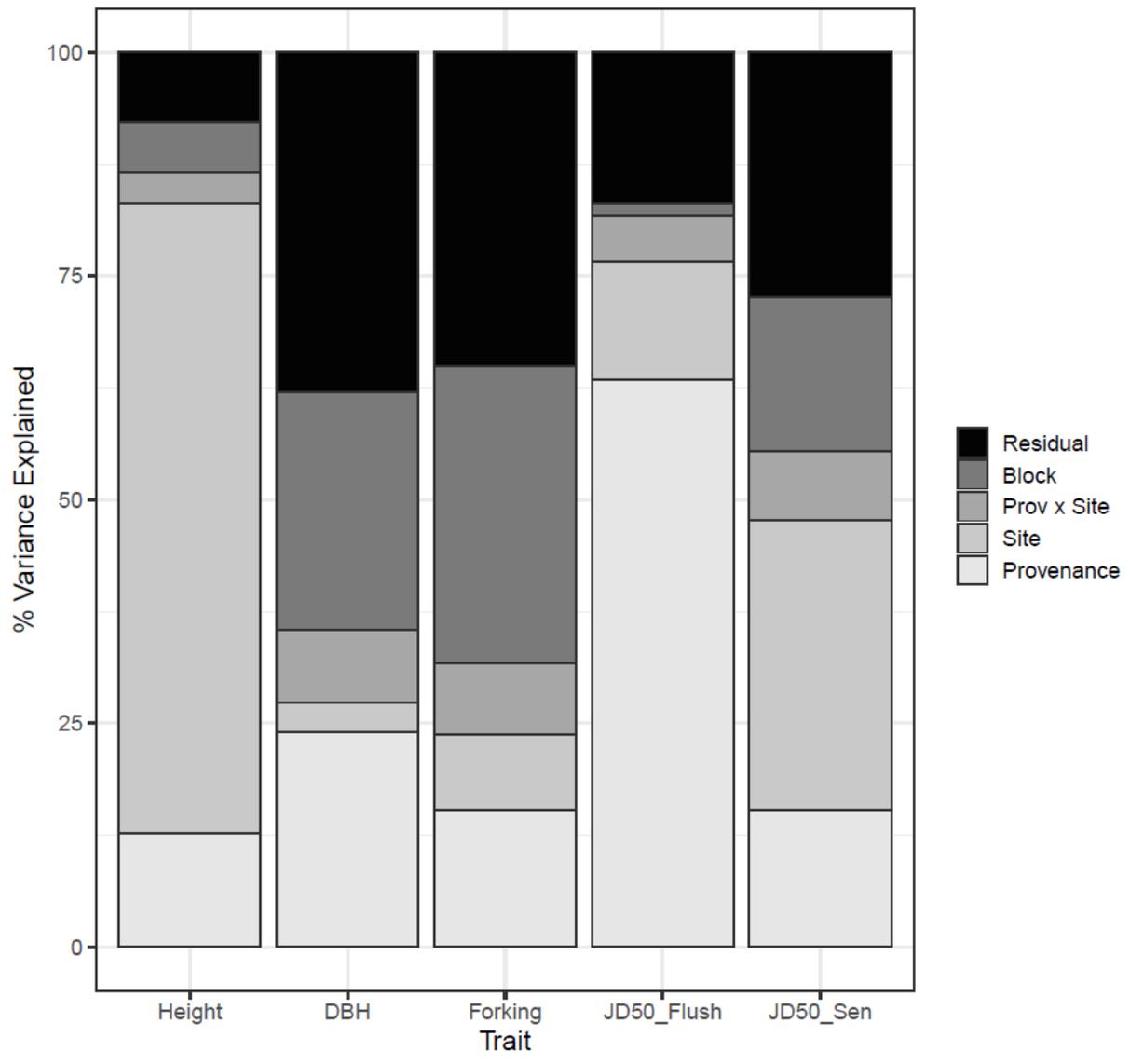
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752 Hemery (gabrielhemery.com)

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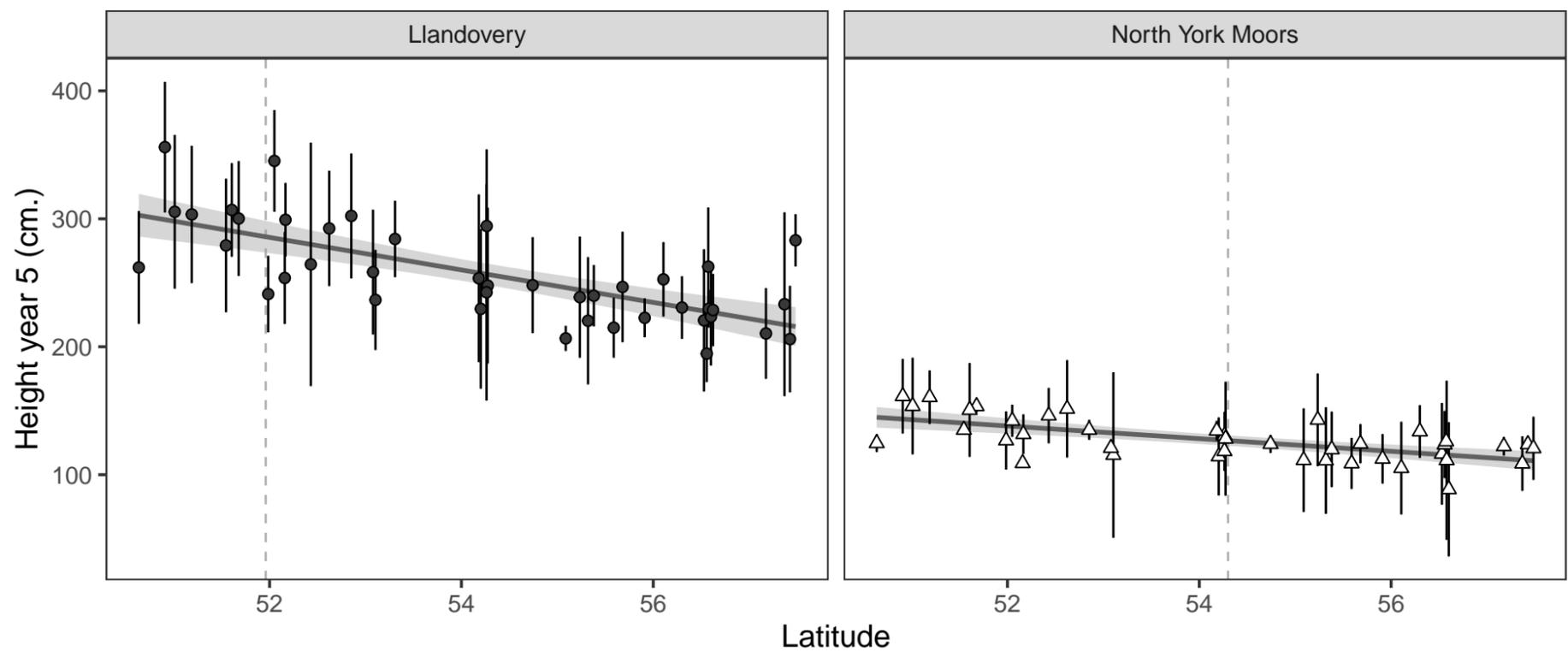
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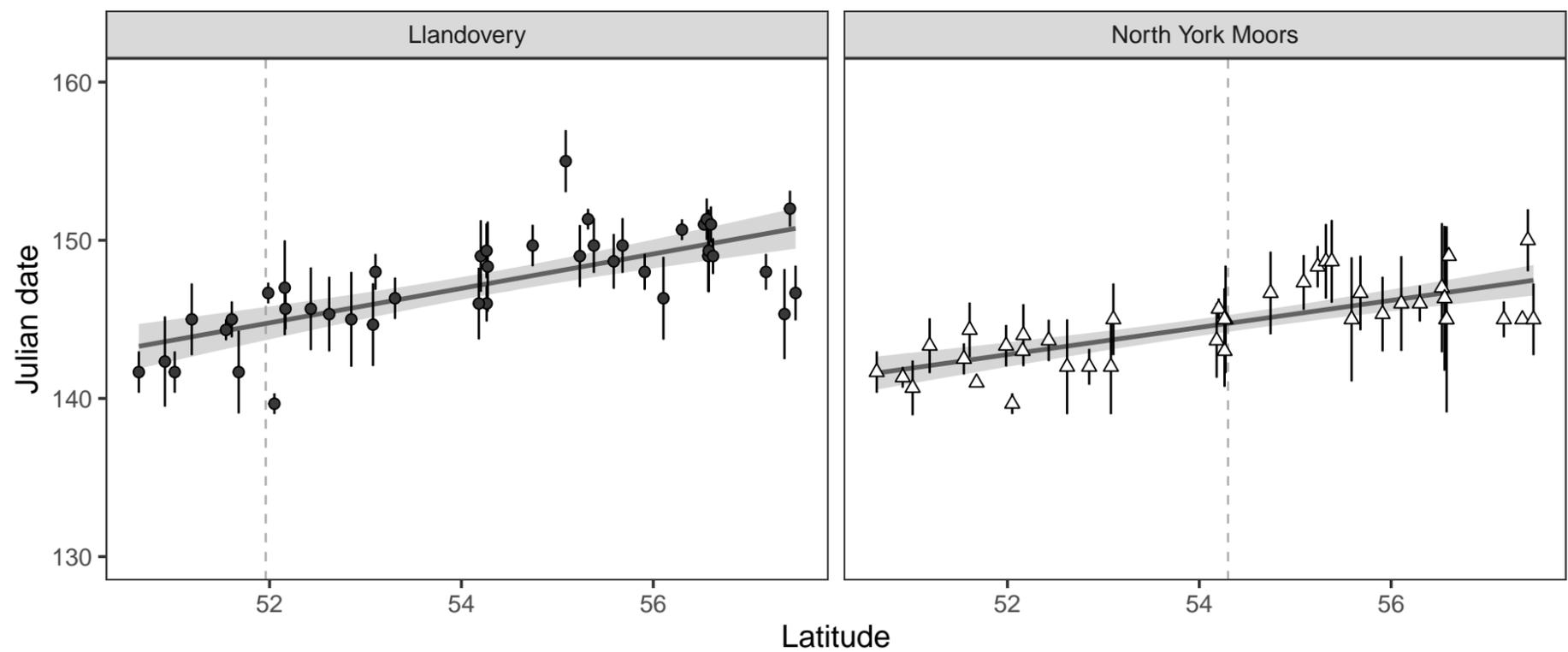
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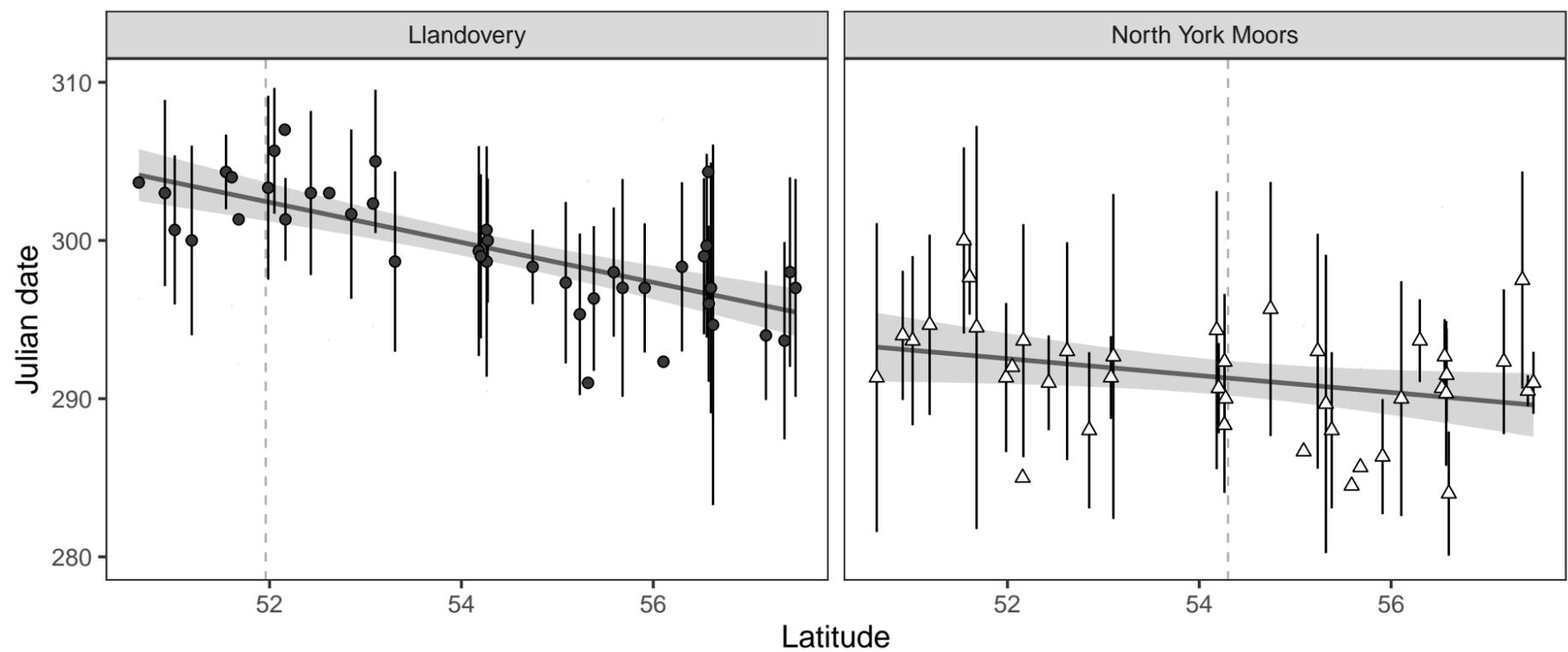
a. Height



b. JD50_Flush



c. JD50_Senesce



d. Stem forking

