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Mid-rotation variation in growth, form and phenology of sycamore (*Acer pseudoplatanus* L.) provenances in field trials in England

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Field trials containing 8–10 sycamore seed sources were established on 'farm woodland' sites in 1992 to identify the most productive and adapted seed sources for use in lowland Great Britain. Early results from these trials found little difference among provenances for growth traits. To guide the next steps of sycamore improvement in the British Isles, three of the five original trials have been revisited and assessed for variation in growth and form at 27 years, which is between one-third and half rotation age. There were large differences in growth among sites but differences among provenances were small or non-significant and showed no interaction across sites. Spring phenology evaluation from one of the trials demonstrated that timing of bud burst was negatively associated with latitude which was the only trait providing any evidence of adaptive differentiation among provenances. However, the effect was small and driven by much later flushing of French and German seed sources than British seed sources. Given the lack of clear provenance differentiation and qualitatively similar rankings across sites, we found no justification for subdividing Britain into breeding zones for sycamore at this stage, nor for excluding material from mainland Europe in planned progeny tests.

Introduction

Sycamore *Acer pseudoplatanus* L. (Sapindaceae) is a fast-growing large-stature hardwood tree native to a large portion of central and southern Europe where it occurs mostly as a minor component of mixed stands. Its scattered status and reputation for invasiveness have meant that it is not regarded as an important forest tree in most European countries, and as such the genetic resources of sycamore are poorly characterized (Krabel and Wolf, 2013) and silvicultural prescriptions are mostly either local in scale, generic or based on anecdotal evidence (Hein et al. 2008).

Recent evaluations of sycamore as a silvicultural resource have regarded it as an undervalued and understudied species, worthy of further investigation (Hein et al. 2008; Krabel and Wolf, 2013). Sycamore is a hardy species capable of surviving under a wide range of site conditions, including conditions of salt-spray and air pollution and, with the exception of serious damage by grey squirrel, currently suffers no serious or epidemic damage from major pests and diseases (Cundall et al., 1998; Joyce et al., 1998). Under plantation conditions, it has the highest yield class (YC 4–12, average YC 6) of major broadleaves in Great Britain (GB) (Matthews et al., 2016) and first-quality logs can attract prices similar, or higher than those of white oaks *Quercus petraea* Matt. Liebl. and *Quercus robur* L. and beech *Fagus sylvatica* L. but can be produced on a shorter rotation of 50–80 years (Cundall et al., 1998). Prices for veneer quality sycamore logs in Germany in 2008

and 2009 ranged from €3200 to €7000/m³ (Krabel and Wolf, 2013).

Traditionally regarded as an enemy of foresters and conservationists alike, sympathetic treatises of the ecological value of sycamore have appeared in the literature repeatedly over the past decades (Taylor, 1985; Stern, 1989; Leslie, 2005; Paillet et al., 2008). Recognition of this ecological value appears to be taking hold in British domestic discourse and policy, particularly since the emergence of the dieback of ash *Fraxinus excelsior* L. caused by *Hymenoscyphus fraxineus* Baral Queloz Hosoya (Holl, 2018). Sycamore is often present as a minor component of mixed ashwoods and is seen as one of the most appropriate ecological analogues for ash due to its ability to efficiently recolonize gaps and its suitability as base-rich substrate for ash-specialist epiphyte communities (Mitchell et al., 2016; Broome et al., 2018).

Although not indigenous to GB, sycamore has been present since at least the 15th century, and in the last 200 years has become naturalized throughout GB, now being the fourth most abundant broadleaved tree species by forest area behind birch, oak and ash (Forestry Commission, 2011). The overwhelming majority of sycamore (>99 percent) is on private land and 75 percent of the resource is in England (Forestry Commission, 2011). The origin of sycamore growing in GB is mostly unknown and unlikely to be easily determined due to multiple introductions, including relatively recent importation of planting stock

from mainland European nurseries (Binggeli and Rushton, 1999). Neophytou et al. (2019) analysed variation at 11 microsatellite (10 nuclear, 1 chloroplast) markers in the German breeding population which is composed of 1043 plus trees selected throughout Germany and central Europe. Results suggest that sycamore colonized Germany via separate migration routes in the south-western and eastern Alps and that German/Central European sycamore represents an admixture zone between the two (Neophytou et al., 2019). Bittkau (2003) studied variation at five chloroplast microsatellite markers among 22 populations of sycamore across Europe and including three from GB which shared a haplotype with a population in north-western Iberia (Slade et al., 2002). The earliest introductions of sycamore into GB are likely to have made the greatest contribution to its naturalization and there is circumstantial evidence that early introductions of seed were predominantly sourced from populations in western Europe, rather than eastern Europe (Binggeli, 1994; Binggeli and Rushton, 1999).

Information about provenance variation in sycamore is far from complete and complicated by the fact that investigation tends to have been conducted outside the native range and led by different motivations. In a trial in Germany planted in 1970, Weiser (1996) reported no differentiation among eight provenances for growth at 31 years but did recognize genetic variation in stem form. In a single-site study involving Czech provenances from 420 to 1100 m above sea level planted at 540 m above sea level in the Bohemian-Moravian Highlands, Volfschütz et al. (2009) found that the highest altitude seed sources showed the greatest growth at age 24 years and that rankings of provenances were relatively stable past the age of 10. In a reciprocal transplant experiment involving seed sources sampled along an altitudinal gradient in the Pyrenees, Vitasse et al. (2009) found no significant differences among provenances for survival or height but showed a relationship between phenology and growth, whereby late-flushing and late-senescing sycamores had the highest growth rate. Lodewijk-Meulman (2019) described variation in growth and form among 16 (mostly Danish) provenances in three provenance-progeny trials growing in Denmark. There were significant differences in mean height and diameter values among provenances, although the range was small after 9 years (<1.2 cm for DBH; 1.2 m for height). Across the three trial sites, the best and poorest performing provenances were typically the same (Lodewijk-Meulman, 2019).

Early-stage tree improvement efforts in sycamore are in place in a few European countries (Krabel and Wolf, 2013). The most advanced of these is probably that of Germany, where a breeding population of ∼1000 individuals has been evaluated, genotyped and established in a clonal seed orchard, and where methods to select and propagate genotypes possessing highly prized 'wavy grain' timber are under development (Weiser, 1996; Krabel and Wolf, 2013; Bäucker and Liesebach, 2018; Neophytou et al., 2019). In GB and Ireland, the Future Trees Trust has been involved in selection of seed stands and plus trees for sycamore for around 20 years (Hubert et al., 2010). Qualified clonal seed orchards, comprising grafted copies of ∼200 plus trees have been established and half-sibling progeny trials are planned to enable provision of improved sycamore. Since sycamore is a versatile species for which multiple breeding objectives could be set (e.g. quality timber production, short rotation forestry for biomass

production, ecological restoration, specialist markets such as wavy-grain timber), it is important to explore any available opportunities to understand the variation within sycamore as it is distributed around England prior to finalizing the next steps of improvement. To this end, the objectives of this study were to assess variation in growth and form at one-third to half rotation age among populations of sycamore, using a series of provenance tests established on 'farm woodland' sites in England and Wales in 1992. The trials included six English/Welsh, two German, one French and one Danish seedlots. Early results showed little differentiation in growth among seed sources at 4 years (Cundall et al., 1998). Given that the ranking of entries in genetic and provenance trials is prone to change, especially in the early years (Worrell et al., 2000; White et al., 2007; Whittet et al., 2019), later evaluations are required to form conclusions about long-term field performance.

The experiments were designed to identify sources of seed that would provide well-adapted and productive sycamore for planting on farm woodlands. There are few provenances in the trials (8–10) and the inclusion within the design was based on an overall evaluation of the quality of the parent stand (Cundall et al., 1998). Due to the original motivation for the trials and our focus on growth and form traits, the primary motivation of the article is to identify factors of relevance to the sycamore tree improvement programme rather than to describe adaptive genetic variation, which we can only discuss superficially. We ask whether the breeding programme for sycamore ought to be subdivided into breeding zones prior to establishing half-sibling progeny tests, or indeed whether extending the composition of parents in the breeding programme beyond GB and Ireland, as it is currently established, is desirable.

Methods

Plant Material

Five experiments containing 8–10 sycamore seedlots were established in 1992 at 'farm-forestry' sites in England and Wales (Figure 1, Table 1). Trees were planted in single-provenance 36 (6 × 6) tree plots at 2 × 2 m spacing, in three randomized complete blocks. Seedlings were pit-planted, with competing vegetation removed where necessary. Trials were beaten up with replacement seedlings of the same provenances after the first growing season (Cundall et al., 1998).

Selection of British provenances was based on surveys of potential parent stands identified firstly from the Forestry Commission's sub-compartment database and secondly in private woods following a postal survey. A total of 71 woods were visited and scored based on their potential for use as parent stands. The six British provenances (Figure 1) ultimately used therefore underwent a round of phenotypic selection at stand-level in the field. Seed were collected by shooting or climbing. Seed of the four continental provenances were obtained from a commercial seed merchant. No details of the number of parent trees per provenance were recorded. Seed was precision sown in April 1991 at 100 seed per m^2 in the open at a Forest Research nursery in Alice Holt, Hampshire (lat 51.1, long −0.84). Germination of two of the continental seedlots (Ornsbjerg, Denmark and Zweibrucken, Germany; Figure 1) was so poor that there
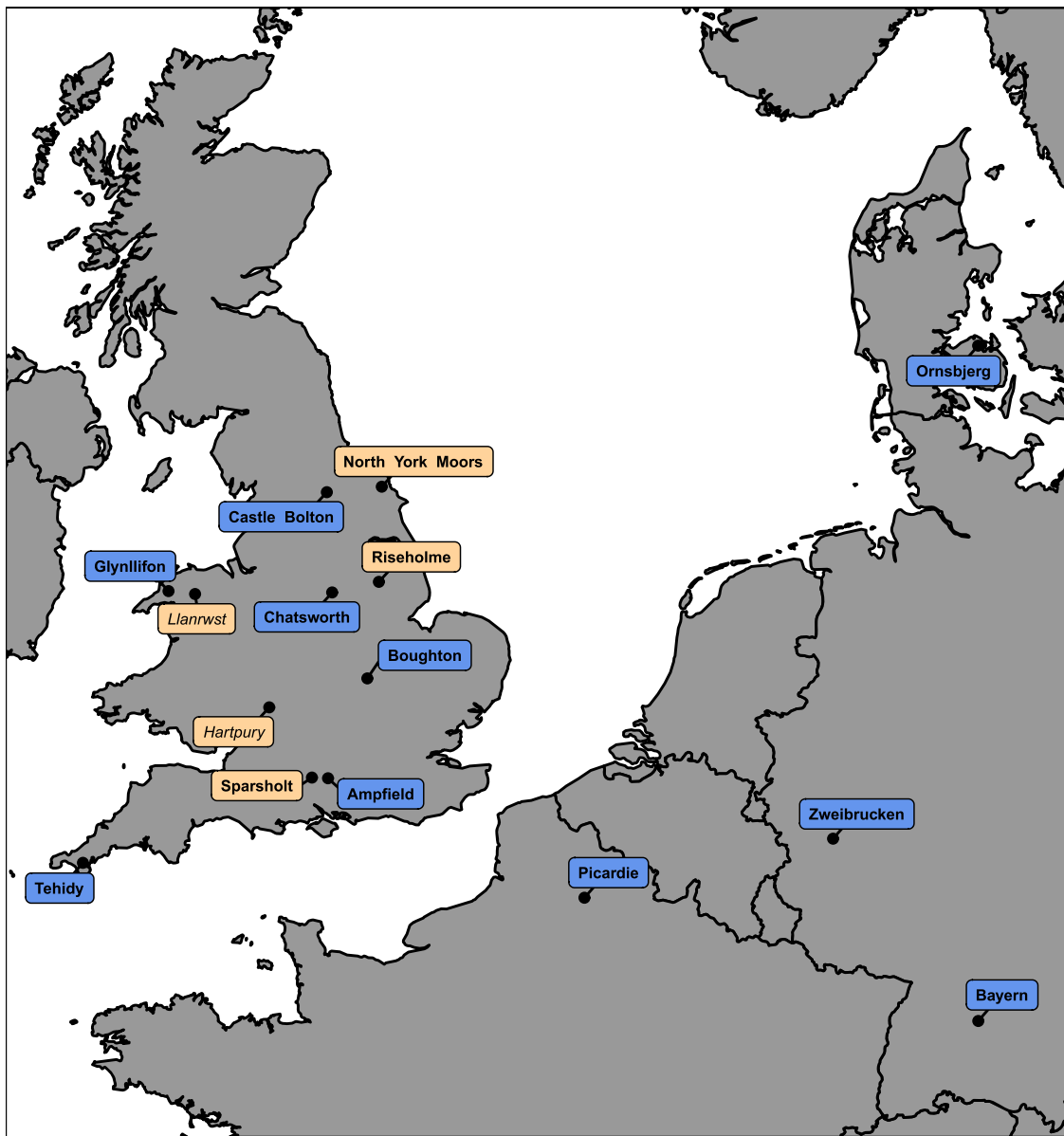
Figure 1 Sycamore provenances (blue) and trial sites (beige). The trial sites labelled in italic font (Hartpury, Llanrwst) were not assessed in 2019.

were only enough plants produced to establish in one experiment (Sparsholt). Full details of nursery production and trial establishment are provided in Cundall et al. (1998).

Assessments

The series of experiments originally contained five trial sites (Figure 1; Cundall et al., 1998). However, the experimental integrity of two of the five trial sites (Hartpury, Llanrwst) was determined to be so severely compromised due to invasion of other woody plants and unsystematic thinning that they were not assessed in 2019. The trials regarded as assessable had also undergone inconsistent management. Riseholme had been thinned following a chevron pattern at around age

12–15, removing ~55 percent of the original trees. Sparsholt had been thinned recently, removing ~65 percent of the original trees in a single episode, with the pattern of thinning relatively even throughout the site (Supplementary Data Figure S1). North York Moors has remained unthinned.

The assessment schedule followed in June 2019 involved measuring diameter, height and evaluating overall tree form with a four-point scale. Average diameter at breast height (DBH, 1.3 m) to the nearest 5 mm was measured using a calliper. The height of each tree present in the central 16 (4 × 4) trees in each plot was estimated using a Haglöf Vertex III laser hypsometer and recorded in 10 cm increments. At Sparsholt, where thinning had taken place recently and in a single operation, we

Table 1 Summary descriptions of three sites in England used for sycamore provenance trials, adapted from Cundall et al. (1998). Climatic information is taken from the Ecological Site Classification Decision Support System (ESC-DSS) (Forest Research, 2020), a full description of which is available in Pyatt et al. (2001).

	North York Moors	Riseholme	Sparsholt
English county	North Yorkshire	Lincolnshire	Hampshire
WGS84 Coordinates (N; E)	54.26; −0.55	53.27; −0.53	51.2; −1.52
Altitude (m.a.s.l.)	150	45	50
Previous land use	Forest nursery	Grassland	Grassland
Soil type	Brown earth	Surface water gley	Thin brown earth over chalk
Number of provenances	8	8	10
Management	Unthinned	Thinned at ~12 years	Recent first thinning
Accumulated Temperature	1400 (warm)	1687 (warm)	1868 (warm)
Exposure (DAMS)	13 (moderate)	13 (moderate)	11 (sheltered)
Moisture deficit	160 (moist)	195 (slightly dry)	188 (slightly dry)
Continentality	8 (neutral)	10 (continental)	10 (continental)

measured the diameter of cut stumps and diameter at stump height (~5 cm above ground level) on standing trees as well as the DBH of all standing trees. Since the number of standing trees was <50 percent of those planted, we opted to estimate height on every standing tree, rather than measuring only the central 4 × 4 which was done at the other sites. The pattern of thinning at Sparsholt was relatively even and *post hoc* data summaries of stump diameters of felled and standing trees suggest that thinning did not selectively remove large or small individuals (Supplementary Data Figure S2).

Form of all standing trees was evaluated independently of growth on an ordinal scale of 1–4. Greater emphasis in form scoring was placed on the lowest 6 m. Descriptions of values in the scale are:

1. **Plus tree.** A tree of outstanding form with a straight stem, fine branching and clear apical dominance.
2. **Good form.** A tree of good overall form with apical dominance and no major stem defects.
3. **Poor form.** A tree with multiple stem defects such as low forking, twisted or swept stem, heavy branching.
4. **Very poor form.** A tree with multiple serious stem defects and other trees not qualifying for categories 1–3, including multi-stemmed, shrubby, moribund or 'runt' trees which had failed to grow properly.

We opted not to include a category for trees of average or mediocre form as such trees are not of interest in selection programmes. Trees showing mediocre form were instead subsumed into score 3 (poor form). Form evaluation was site-specific; we reconnoitred each site to gauge the central tendency of form and scored individuals according to local standards.

Spring phenology was assessed on 12 occasions between April and May at 3–5 day intervals at the North York Moors trial in 2011. Nine trees in the centre of each plot were assigned an overall score based on an ordinal morphological scale (phenophases) representing the stage of bud burst. Description of the values in the scale is:

1. Dormant bud.
2. Bud elongating but remaining closed.
3. Bud scales broken. Leaves appearing but remaining fully upright.
4. Leaves partially unfolded.
5. Fully unfolded leaves.

Statistical Analysis

All statistical analyses were performed in the R statistical environment (R Core Team, 2019), with particular reliance on lme4 (Bates et al., 2015) for model fitting and ggplot2 for data visualization (Wickham, 2016).

Cross-sites analysis of growth traits were conducted by applying linear mixed models to plot mean data. Plot means were used in this case because of the sample size, which varied among thinned and unthinned experiments, and the randomized complete block design with single-entry 36-tree plots. The cross-sites analysis treated provenance and site as fixed effects and block within site and provenance x site interaction as random terms. The linear mixed model took the form:

$$Y_{ijk} = \mu + P_j + S_i + (I)_{ij} + B_{ik} + e^{ijk} \tag{1}$$

where Y^{ijk} is the plot mean trait value of provenance j in block k in site i, μ is an intercept, $(I)_{ij}$ is the interaction of provenance within site and e_{ijk} is an error term.

Variance components associated with the fixed, random and residual terms were extracted using functions within the R package 'insight' (Lüdecke et al., 2019). Calculating variance components for fixed effects followed the approach of Nakagawa and Schielzeth (2013).

Linear models for growth (height and diameter) were fitted separately for each site. The linear model took the form:

$$Y_{jk} = \mu + P_j + B_k + e_{jk} \tag{2}$$

where Y_{jk} is the plot mean phenotypic value for provenance j in block k, μ is an intercept, P_j is the fixed effect of provenance j, B_k is the fixed effect of block and e_{jk} is an error term.

Form scores were fitted to binomial generalized linear models based on plot summary data, taking as a response the number of trees per plot scoring 1 or 2 (good form) as a proportion of the total number of trees scoring 1–4. Cross-sites analyses of form scores were considered inappropriate due to variable thinning regimes. The generalized linear model took the form:

$$\text{logit}\,(Y_{jk}) = \mu + P_j + B_k + e_{jk} \qquad (3)$$

where Y_i is the proportion of trees scoring form scores 1 or 2 (good form) in plot, μ is an intercept, P_j is the fixed effect of provenance and B_k is the fixed effect of block and e_{jk} is an error term.

Least-square means and their standard errors were computed for each provenance using the 'emmeans' package within R (Lenth, 2019).

Spring phenology scores from North York Moors in 2011 were modelled using ordinal logistic regression, which fits an intercept to each provenance and is applied using the 'ordinal' package in R (Christensen, 2019). The model took the form:

$$\text{logit}\,(Y_j) = \mu + JD + P_j + e_j \qquad (4)$$

where Y_j is the phenological observation for provenance j, μ is an intercept, JD is the day of observation counting from January 1 (Julian date), P_j is the fixed effect of provenance and e_j is an error term.

The model fits a common slope meaning that each provenance has an identical curve but with a different intercept. Differences in time lags/leads which reflect the entire process of bud burst, in number of days between provenances were calculated from the beta coefficients returned by the fitted model (Vander Mijnsbrugge et al., 2015).

$$JD_{[Pj]} - JD_{[Pk]} = \left(\beta_{[Pj]} - \beta_{[Pk]}\right)/\beta_{JD} \qquad (5)$$

where $\beta_{[Pj,k]}$ are estimated beta coefficients for provenance j and k in the fitted model and β_{JD} is the estimated coefficient for time (expressed as Julian days JD since January 1). The fitted Julian date on which there was a 50 percent probability of the earliest flushing provenance having reached stage 5 was extracted manually from fitted values.

Results

Variation in Diameter and Height

Cross-sites analysis showed that variance associated with provenance was a very small portion of the total variance in diameter and height, explaining 4.3 percent and 1.9 percent of the total variance respectively (Table 2). Across sites, the only statistically significant difference among provenances for diameter was between the largest (Bayern) and the smallest (Tehidy) provenance (Figure 2). There were no significant differences among provenances for height. The variance associated with provenance x site interaction was 0.27 percent for DBH and 0.07 percent for

Table 2 Variance components and proportion of total variance in height and breast-height diameter at age 27 of eight sycamore provenances growing at three sites in England.

	Diameter	Height
Site	19.9 (72.6%)	15.2 (79.6%)
Provenance	1.18 (4.3%)	0.36 (1.9%)
Block within site	3.56 (13%)	1.76 (9.2%)
Provenance x site	0.07 (0.27%)	0.01 (0.07%)
Residual	2.69 (9.8%)	1.76 (9.2%)

height (Table 2), and the absolute ranking of provenances was reasonably consistent across sites.

Within sites, the only significant difference among provenances for either diameter or height was observed in plot mean diameter at Sparsholt, where the top two provenances (Bayern and Picardie) were significantly larger than the bottom two provenances (Tehidy and Glynllifon). There were no significant differences among provenances for height at any site or for diameter at North York Moors or Riseholme (Supplementary Data Table S1).

Variation in Stem Form

The four-point scale used to assess form produced a strongly skewed sample, dominated by score 3 (poor form) (Table 3). Proportions of trees scoring 3 were 0.70, 0.73 and 0.78 at North York Moors, Riseholme and Sparsholt, respectively. A total of 10 trees across the three sites were regarded as 'plus-trees', with form scores of 1. North York Moors had a larger proportion of score 4 (very poor) trees than the others, which may be due to an absence of thinning operations which would normally remove such trees.

No significant differences in the proportion of trees per plot with 'good' form scores (scores 1 and 2) were found among provenances. The absolute ranking of provenances was reasonably consistent across sites (Supplementary Data Table S1).

Spring Phenology

The process of bud burst took place from mid-April until mid-May of 2011 at North York Moors. The earliest provenance to develop was that of Glynllifon for which the 50 percent probability of having reached stage five (fully unfolded leaves) was on Julian date 108 (17 April, Figure 3). Glynllifon led the slowest provenance, Bayern, by 16 days. The latest British provenance to flush was Castle Bolton, which lagged behind Glynllifon by 8 days. Based on a very small sample size (n = 8), there was a marginally significant (P < 0.04) association between latitude of origin and timing of bud burst. This effect was largely driven by the much later flushing of French and German sycamore. While Castle Bolton was the only obvious exception to this trend, differences among British provenances were much smaller than differences between British and European mainland provenances (Figure 3).
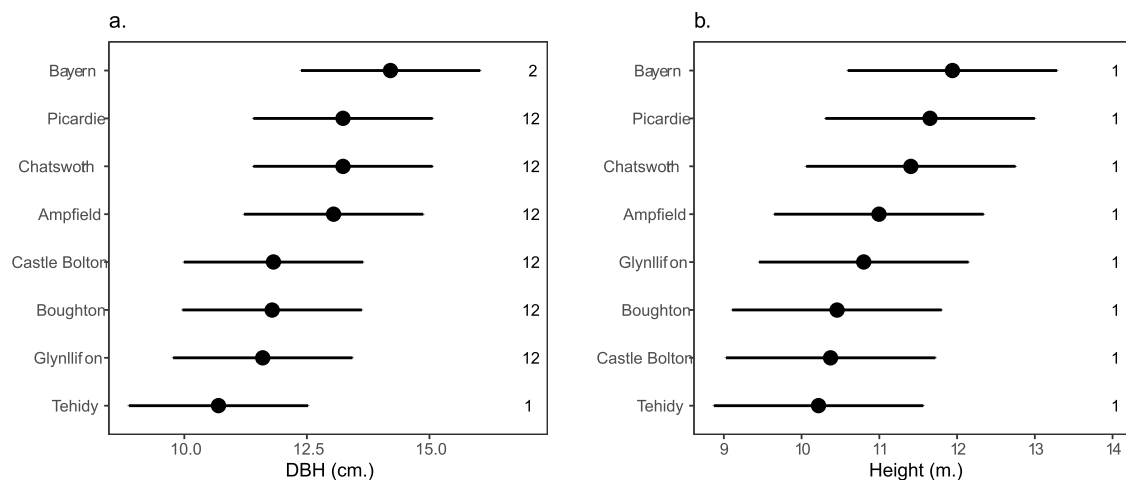
Figure 2 Least squares means and 0.95 confidence intervals for (a) DBH (diameter at breast height) and (b) height of eight sycamore provenances growing at three sites in England. Entries sharing a common numeral are not significantly different at $P < 0.05$.

Table 3 Unadjusted percentages of trees in 10 sycamore provenances with form scores 1 (plus tree), 2 (good), 3 (poor) and 4 (very poor). Zweibrucken and Ornsbjerg were only represented at one site (Sparsholt); the other eight provenances were represented at three sites (see Table 1). n.obs = number of observations.

| Provenance	n. obs.	Form score (%)			
		1	2	3	4
Chatsworth	196	1.0	27.0	65.8	6.1
Bayern	171	0.6	24.6	71.3	3.5
Ampfield	198	0	23.2	71.2	5.6
Boughton	182	2.2	19.2	67.6	11.0
Glynllifon	199	0.5	17.6	74.9	7.0
Castle Bolton	176	0.6	17.0	72.7	9.7
Picardie	182	0	11.5	78.6	9.9
Tehidy	171	0	9.4	78.4	12.3
Zweibrucken	*43*	*2.3*	*25.6*	*69.8*	*2.3*
Ornsbjerg	*36*	*0.0*	*16.7*	*83.3*	*0*

Discussion

Results suggest that variation in sycamore, for the measured traits, is mostly held within rather than among provenances, meaning that selection and testing of phenotypically superior 'plus trees' from a broad geographical range offers a route to improving sycamore. Performance was highly responsive to the combined effect of site type and management practices, which accounted for >70 percent of the variation in height and diameter in the cross-sites analysis. Therefore, opportunities to enhance silviculture of sycamore should be taken alongside genetic improvement through selection, testing and production of improved germplasm.

Geographical Scope

The trials described in this study are located in England. Two of the three sites represent lowland England. One site (North York Moors) can be considered intermediate between lowland and upland. The provenances evaluated are from central England (n = 4), oceanic areas in North Wales and Cornwall (2) and four continental locations (France, Denmark and two from Germany). Sycamore is controlled under Forest Reproductive Materials (FRM) but is not regarded as native to GB and so its deployment is voluntarily guided by British native seed zones which divide England, Scotland and Wales into four 'regions of provenance', with further subdivision into 24 seed zones (Herbert et al., 1999).

The breeding population for sycamore is composed of parents selected from throughout GB and Ireland. The breeding programme is approaching the stage of progeny testing and currently regards GB and Ireland as one breeding zone. There is no material or trial sites in this series of provenance trials from northern Britain or Ireland and so results cannot be used to predict performance in these regions. However, given the conservative intended use of the results (to identify whether substantial variation among provenances warrants subdividing the breeding zone), we feel comfortable generalizing results to lowland areas of GB and Ireland for this purpose.
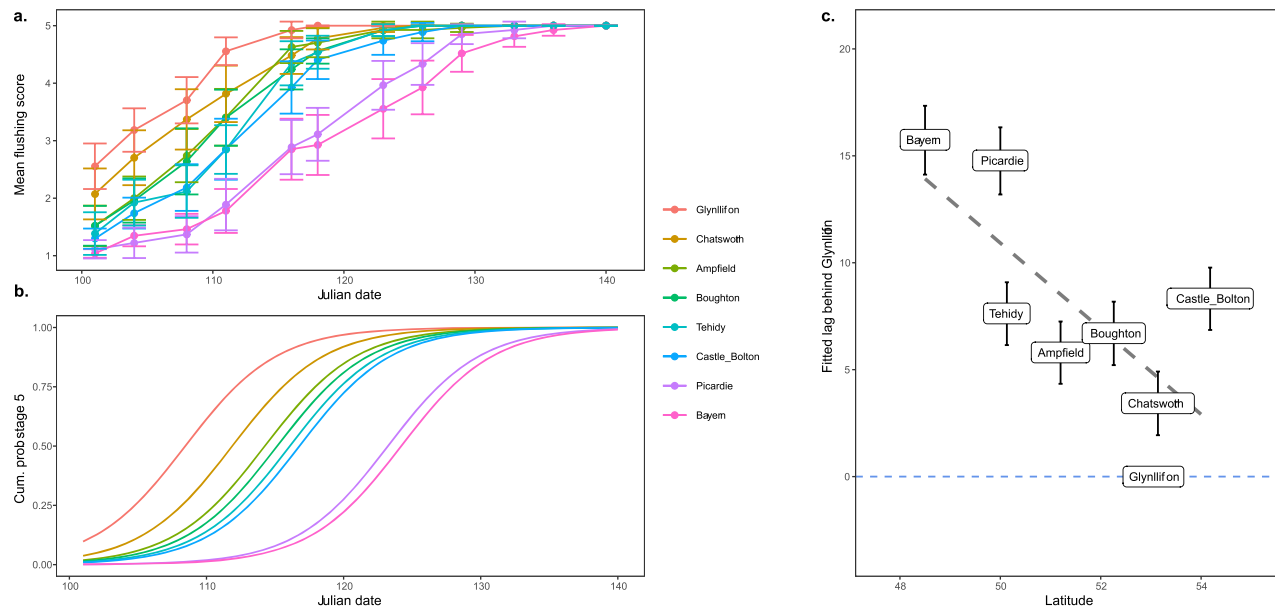
Figure 3 (a). Unadjusted mean flushing scores for each provenance (+/− 0.95 confidence intervals). (b). Fitted cumulative probabilities of a given tree having reached phenological stage 5, which represents complete unfolding of leaves. (c). Association between provenance latitude and the number of days' lag behind the earliest provenance to develop (Glynllifon).

Variation Among Sites

Growth and form of sycamore was strongly influenced by the combined effect of site type and management. Growth at North York Moors was much lower than at Riseholme and Sparsholt and there was substantial spatial variation within the site which had a non-contiguous plot layout (Supplementary Data Figure S1). The site at North York Moors is the coldest and wettest of the three trial sites and lies at 150 m above sea level (Table 1) in an exposed location near to the east coast of England. Cundall et al. (1998) regarded this site as a testing environment. Indeed, the growth of the sycamore experiment was conspicuously poorer than an immediately adjacent oak (both *Quercus petraea* and *Q. robur*) provenance experiment established in the same year (Hubert, 2005), which is contrary to the expectation that sycamore is a particularly fast-growing species. Although judicious thinning at around age 12–15, as took place at Riseholme, may have reduced competition and increased growth increment, an average height of ~6 m at 27 years is extremely poor and so we suspect that a particular stress episode has taken place which the trees have been very slow to recover from.

As opposed to North York Moors, which is located on a former Forestry Commission nursery site, Riseholme and Sparsholt are located on privately held land. There had been rather little scientific involvement in these trials following publication of early results (Cundall et al., 1998), and management has been inconsistent at these sites since that time. At Riseholme, chevron thinning had taken place between 2000 and 2006 and coppice regrowth was advanced, with stem diameters approaching those of the planted trees. Many trees had straight stems of good form to ~3–4 m but devastating grey squirrel damage above that height was common. Sparsholt is the warmest and southern-most of the three trial sites and has not suffered from

squirrel damage but was not thinned until much later than Riseholme.

Variation Among Provenances

Across sites, only one provenance (Bayern) was significantly larger in diameter than the smallest provenance (Tehidy) and no significant differences were observed among provenances for height nor form. Within sites, differences were observed at Sparsholt (which could be due to recent thinning) but not at either of North York Moors or Riseholme. The statistical power available to detect differences among provenances was low due to a small number of provenances, thinning, limited replication (n = 3) and the use of a randomized complete block design based on square single-entry plots. Qualitative comparisons can be made based on unadjusted means and absolute ranks which suggest that there was one consistently poor provenance (Tehidy) and three which were typically above the site average for all traits (Bayern, Chatsworth and Ampfield). Picardie was above average for growth but consistently below average in terms of form. The Danish provenance (Ornsbjerg) and one of the German provenances (Zweibrucken) were only present at Sparsholt. Early assessments found that these provenances showed the greatest growth (Cundall et al., 1998). The reason for under-representation of these two provenances across sites was low germination rate in the nursery (Cahalan et al., 1995), which may have led to the survival of only the most competitive genotypes within those seedlots. By age 27, these provenances showed no superiority over any other provenance for height and, in terms of DBH, were only significantly larger than the very smallest provenance.

Spring phenology data from the North York Moors site show later flushing of southern provenances, which is the only trait showing variation that can be obviously associated with environmental or geographical variation. The direction of this association runs contrary to the pattern that populations of other hardwoods (e.g. ash (Rosique-Esplugas et al., 2018) and oak (Ducousso et al., 1996)) from warmer environments flush earliest in common garden experiments (Soularue and Kremer, 2014; Whittet et al., 2019). Early flushing trees are typically likely to be more exposed to late spring frosts, which is often given as a reason to avoid non-local germplasm, as it can lead to mortality or serious stem defects such as forking (Whittet et al., 2019). However, in the case of sycamore, which is regarded as relatively frost-tolerant in any case (Joyce et al., 1998; Hein et al. 2008; Krabel and Wolf, 2013), this concern is likely to be unwarranted as similar, or superior growth rates were achieved by continental provenances despite later flushing. Vitasse et al. (2009) recognized an association between late flushing and greater height growth in sycamore. However, later flushing was also associated with later leaf senescence in autumn, so avoidance of late spring frosts may be achieved at the expense of greater exposure to early autumn frosts (Vitasse et al., 2009).

Understanding natural patterns of adaptive variation in sycamore was not a primary motivation for performing these trials (Cundall et al., 1998) and they do not provide compelling evidence that local land races have developed. Local adaptation evolves in response to successive generations of spatially variable selection across a species range (Kawecki and Ebert, 2004). The range of environmental variation covered by the few provenances included in these experiments is only a small proportion of the distribution of sycamore which is found throughout Britain and the environment of the lowland England seed sources are very similar (Supplementary Data Figure S3). Furthermore, the origin of the stands which provided seed for these experiments is unclear, and we have no reason to assume that the generation of trees from which seed were collected had naturally regenerated *in situ*. Indeed, estate records from Castle Bolton and Ampfield provenances show that the seed stands were 20th century plantations. Given the relatively small number of generations (compared with other tree species showing adaptive differentiation within Britain such as Scots pine, ash, birch, oak and rowan; reviewed in Whittet et al., 2019) over which sycamore has been present in GB, the narrow range of environments represented by the seed sources (Supplementary Data Figure S3) and the probability that not all seed sources had undergone seedling-stage selection pressures *in situ*, it is not surprising that differences among GB populations are small and difficult to interpret. To explore whether local adaptation has evolved in response to environmental variation within Britain would require replicated provenance-progeny experiments involving a larger number and wider range of seed sources known to have naturally regenerated in Britain. Were such trials to be established, evaluating variation in ecologically relevant phenotypic traits such as survival, spring and autumn phenology, reproductive characteristics or fungal infection of leaves may be better suited to detect responses to selection and inform deployment (for example by devising transfer rules) of unimproved sycamore than our assessments of growth and form. However, it is worth noting that trials are necessarily based on nursery-raised seedlings which reduces strength of early selection (especially considering the prolific reproductive output of sycamore *in situ*) and that survival was very close to 100 percent at the unfavourable site of North York Moors. Employing more robust statistical designs, greater replication and more consistent management in future experiments will greatly increase the ability to detect local adaptation with modern statistical methods.

Implications for Tree Improvement

Given the lack of differences among provenances, there seems to be no justification for identifying breeding zones or subdividing the existing breeding population of sycamore into regional subpopulations at this stage. Results do not preclude selection of additional plus trees from elsewhere in Northwestern Europe or including progeny from breeding programmes in other countries in half-sib progeny trials. Since variation among sites was substantial, testing on at least five sites representative of sycamore growing areas is recommended.

Despite sourcing seed from stands considered to be of high phenotypic quality, just under 20 percent (305/1554) of measured trees showed good form in the trials. The seedlings from the seed stand with the highest overall score at the time of seed collection, Castle Bolton, which is an estate with a long-standing history of growing quality sycamore (Bolton, 1949; Binggeli and Rushton, 1999; Dormor, 2002) ranked poorly in terms of proportion of good form trees. Historical records from Castle Bolton suggest that plantations may comprise trees grown from seed collected from a single plus tree purchased as a sapling from an ornamental nursery which is extraordinary enough to be granted the name 'old red stem' (Binggeli and Rushton, 1999). If this is indeed the case and the trial trees are very closely related, then inbreeding depression may be responsible for the relatively poor performance of that provenance. As demonstrated by Weiser (1996), sourcing seed from stands with a good average phenotype has not resulted in quality plantations, raising the possibility that the role of genetics in the overall quality of the selected parent stands was relatively small and calling into question the efficacy of selection at stand level in sycamore. While the provenance trials have largely been untended during the past 20 years, the owners of parent stands actively volunteered to have their sycamore woodlands surveyed for possible inclusion in trials. This implies a level of awareness of the quality of sycamore on the estates and the likelihood that parent stands were of good overall quality partly or mainly because of conscientious silviculture on favourable sites, rather than the intrinsic superiority of the genetic material.

The next step in sycamore improvement in GB and Ireland is to evaluate the performance of the progeny of selected 'plus trees' in progeny trials in contrasting environments to estimate breeding values for parents. The British and Irish breeding population is composed of ~200 plus trees which are maintained as grafts in seed orchards and clone banks. Increasing the size of the breeding population over time could provide opportunities for greater genetic gain. This could involve introduction of genetic material from outside GB and Ireland which shows late flushing, which may be linked to greater growth and frost avoidance in spring, with the caveat that later flushing may be

associated with later senescence, and in turn increased exposure to early autumn frosts (Vitasse et al., 2009). Evaluating spring and autumn phenology of individuals in existing clonal seed orchards or in planned progeny trials ought to be carried out routinely, to determine whether there is a trade-off between frost avoidance and growth. An important cause of forking in sycamore, less obviously associated with annual growth rhythm, is flowering of the apical shoot (Binggeli and Rushton, 1999). Understanding whether inflorescence position on individual trees is consistent across years and shows heritable genetic variation may provide a relatively simple proxy for selection against forking in sycamore.

Conclusion

The provenances of sycamore tested in the experiments show little differentiation for growth and form characteristics and conclusions from 27-year assessments validate the early findings published by Cundall et al. (1998). One provenance was consistently poor and three were typically above average across sites, although the absolute sizes and statistical significance of differences were small, and provenance accounted for a very small proportion of variation in the dataset. There was no evidence of superior performance of British provenances, although the configuration of the tests was not appropriate to explore local adaptation, so additional research is recommended to discover whether adaptation has taken place among British sycamore populations. The French and German provenances had later spring leaf-flushing than British provenances in the single year phenology was recorded at one site. Growth at the least favourable site was considerably lower than at two lowland sites although form was poor at all sites, despite attempts to source seed from quality stands. The next steps towards production of improved sycamore can be taken without identifying geographical breeding zones and subdividing the breeding population and we advise that testing is carried out in at least five locations covering a range of environments provided they are suitable for growing sycamore. In the interim, we make no recommendation about provenance choice for planting sycamore in England.

Supplementary data

Supplementary data are available at *Forestry* online.

Data Availability Statement

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

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