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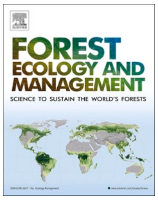

A comparison of the early growth and survival of lesser-known tree species for climate change adaptation in Britain

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ABSTRACT

Globally, climate change is altering both seasonal climates and the occurrence of extreme climate events, resulting in a drive to ensure our forests are resilient to these changes and the challenges they will bring. In Great Britain (GB), there has been a reliance on a limited number of species grown in monospecific plantations and concerns over the resilience of these forests is leading to a growing recognition of the need to diversify tree species composition. However, evidence of the relative growth rate and survival of alternative tree species and provenances during the critical establishment phase (typically within five or six years of planting) is often limited, hampering consideration of the wider adoption of many potentially suitable species. To address this knowledge gap, we compared tree height and survival data six years after planting from 34 provenances across 18 tree species at five experimental sites established across GB in 2012 in monospecific plots. For coniferous species, we found that *Larix decidua*, *Larix* x *marschlinsii* and *Pinus radiata* (on drier sites) were consistently amongst the tallest species, but survival could be variable. *Pseudotsuga menziesii* and *Pinus pinaster* also showed good early growth, matching the growth rate of *Picea sitchensis* (the most widely planted conifer in GB) when co-occurring and often exhibited good survival. In contrast *Picea orientalis* was slow to establish and amongst the smallest species at all five sites after six years, with *Cedrus atlantica* also performing poorly where planted. Surprisingly, we found very few differences in both mean tree height and survival between most provenances of the same species across all experimental sites, though more obvious differences may emerge as these trees mature. Only a small number of broadleaf species were available for analysis at age six in this study, but as expected *Betula pendula* generally performed well, while *Acer macrophyllum* often had very high mortality. While there are concerns around the susceptibility of pine species to *Dothistroma septosporum* and the future use of larch species in GB forestry is currently limited by the disease *Phytophthora ramorum*, our results highlight the potential for these species to establish well and exhibit good initial growth and survival on drier sites, with the same true of *P. menziesii* on moister sites. Future work should aim to understand whether further differences between species and provenances emerge with age and explore the potential of these emerging species as components of mixed-species stands to increase GB forest resilience to climate change.

1. Introduction

Across much of the world, climate change induced shifts in both local and seasonal climate, and the characteristics of extreme climate events have already been documented (Arias et al., 2021; Williams et al., 2007). Recent extreme climate events have now been linked to increases in tree mortality (Gazol and Camarero, 2022; van Mantgem et al., 2009), shifts in forest community composition (Suarez and Kitzberger, 2008), declines in tree vitality (Mundo et al., 2010; Rodríguez-Catón et al., 2016) and decreases in forest productivity (Martinez del Castillo et al., 2022; Treml et al., 2022). These changes are expected to intensify as our climate continues to warm (Arias et al., 2021; Shukla et al., 2019), leading to concerns over the declining resilience of forest ecosystems (Forzieri et al., 2022) and the vulnerability of the ecosystem services they provide (Anderegg et al., 2013; Mauri et al., 2023). The rate of these climatic changes will be particularly challenging for long lived, immobile organisms such as most tree species which may be well adapted to current site and climate conditions but maladapted or fail to acclimate to future conditions at the same site (Périé and de Blois, 2016). As a result, future shifts in site suitability and current species

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distributions for several key European tree species are expected to have wide ranging ecological and economic consequences (Buras and Menzel, 2019; Hanewinkel et al., 2013; Takolander et al., 2019). In turn, this has resulted in a pressing need to understand how vulnerable our forests and different tree species are to different stressors, and how we can increase the resilience of these systems to deal with a range of future conditions.

In Great Britain (GB), increases in the frequency of extreme heat events and the co-localisation of multiple extreme climate events has already started (Dodd et al., 2021), with further increases in the risks of droughts, wildfires and floods predicted under a range of future climate change scenarios (Arnell et al., 2021). In addition to shifts in the occurrence and characteristics of extreme climate events, future changes in seasonal climate are expected to vary considerably across the different regions GB (Yu et al., 2021), meaning that the suitability of some sites for the establishment of historically productive tree species will change, with some regions becoming more, and others less favourable for productive forestry (Ennos et al., 2019; Ray, 2008a, 2008b; Ray et al., 2010; Reyer, 2015). Issues surrounding appropriate species selection for productive, resilient forests are compounded where a historic over-reliance on a limited number of species has been common and a detailed understanding of the growth rate, form, survival, timber properties, site requirements and silvicultural characteristics of alternative species is limited. This issue is particularly pronounced in GB, where a very small number of species have been widely planted and grown commercially for many decades (Forest Research, 2022).

While Scots pine (*Pinus sylvestris* L.) is native to Scotland, it is the only native conifer with the potential to be grown for timber and so a large proportion of productive forestry in GB is reliant on non-native conifer species. More than two thirds of all current coniferous forest area in GB is represented by just two species, Sitka sprue (*Picea sitchensis* Bong. Carr.) and Scots pine (Forest Research, 2022), leaving the forest sector vulnerable to the anticipated shifts in the frequency and severity of abiotic and biotic events such as drought, insect outbreaks, and their compound interacting effects. The risks posed by these events is no longer confined to the future, with impacts on the productivity and survival of key commercial conifer species having already been documented in mainland Europe (e.g., *Picea abies*) (Boden et al., 2014; Obladen et al., 2021) and in Great Britian (e.g. *P. sitchensis* and *P. sylvestris*) (Green et al., 2008; Ovenden et al., 2022, 2021). In turn, this vulnerability poses a challenge for the effective delivery of productive, climate resilient forests (FCCWG, 2018, 2015) and achieving national tree planting targets (Committee on Climate Change, 2020; Tew et al., 2021), as the currently recommended species, provenances or silvicultural practices may no longer be appropriate under predicted future climates. These challenges, coupled with the desire to ensure productive forests are multi-functional and provide a range of goods and services has led to a growing interest in tree species diversification as one way to increase the resilience of these forests to the risks posed by global change (Messier et al., 2021). While there is an appetite for species diversification, evidence on the performance of alternative species and provenances under a range of GB soils and climates is currently limited (Stokes et al., 2022), presenting a barrier to the adoption of other species or provenances at meaningful scales. Equally, in a rapidly warming world one of the key challenges for forest managers is to ensure that species choice is suited to both the existing climate and anticipated future climates on the same site (Xu et al., 2024). To meet this challenge and address these knowledge gaps, five long-term experimental sites were established in 2012 across GB to explore the comparative growth and survival of a range of potential alternative species and provenances that might be suitable under a range of current and future climates. These five experimental sites were latitudinally distributed across GB to give an indication of how well each species and provenance is growing under both current and potential future site conditions.

Understanding which species show good initial survival and growth is important as the establishment phase partly sets the initial trajectory for the following decades of stand development, with consequences for both short-term and long-term forest productivity. For example, high mortality can result in significant additional costs for forest managers to achieve a desired stocking density, while slow initial height growth can leave trees vulnerable to browsing for longer. In this study, we evaluated mortality and height growth data from 34 provenances across 18 species (between 1 and 3 provenances per species) in all five experimental sites (spanning England, Scotland and Wales) to investigate which of these species and/or provenances show early signs of good performance during the crucial establishment phase and could contribute to the diversification of the limited number of tree species grown commercially in GB. Specifically, we aimed to investigate the following questions:

1. Which species show the fastest initial growth six years after planting both within and across a range of sites?
2. How does average tree height six years after planting vary between provenances of the same species and across experimental sites?
3. Which species show the greatest survival rates six years after planting, and how does survival differ between provenances of the same species?

2. Methods

2.1. Study sites and experimental design

This study uses individual tree height (cm) and survival data collected six years after planting from five experimental sites across GB (Fig. 1 and Table 1). These five experimental sites were established following a fully randomised block design with three replicated 49 tree plots of each provenance (one 49 tree plot of each provenance randomly allocated to each of the three blocks in each experimental site). All five experimental sites were fenced to exclude deer. Each of the 49 tree plots were established as a 7×7 tree square grid at two-metre spacing but due to constraints in the area available for planting, it was not possible to establish a tree buffer around any of the plots. All trees were between one and two years old at the time of planting. Four of the five experimental sites were established on re-stock sites, while the fifth site (Glentress96) was planted on open land which had previously been grazed by sheep. All five sites were chemically weeded for at least the first two years following planting and Westonbirt32 was weeded in year four to release the experimental trees from the competition of surrounding vegetation.

While all five of these sites were set up in 2012, initial species selection was matched to each site based on site conditions (e.g., soil and climate), meaning that while there is considerable overlap in the representation of species between sites, not all 18 species or 34 provenances considered in this study (Table 2 and S1) are represented at all five sites (Fig. 1 and Table 1). Provenances were initially selected to give as broad a representation of each species distribution as possible, however limitations with seed supply meant that this was not always possible. For more information on the provenances used, see Orazio et al., (2013) and Table S1. Any dead trees were replaced in all plots in the first two years following establishment; however, we restricted our analysis to only include survival and height data for those trees that were initially planted (i.e. replacement trees were not included in the analysis) to ensure comparisons of survival and height were as consistent as possible (i.e., to avoid including trees in our analysis that had been growing on site for less than six years).

Survival and height measurements (cm) were collected for each tree in every plot at all five sites in the sixth year after planting, reflecting the common timescale for tree establishment in GB forestry. In a small number of cases, some trees were recorded as dead but later showed signs of re-growth in subsequent years. For the purposes of comparing survival at age six, any trees which were identified as being ‘dead’ during a field assessment but were later found to be re-sprouting or alive during subsequent assessments were re-coded as ‘alive’. As no height data was collected for dead trees, any trees noted as ‘dead’ in year six

Fig. 1. Map showing the location of the five experimental sites considered in this study.

Table 1
Details of the five study sites including: full site name and site abbreviation in parentheses, Latitude (Lat), Longitude (Long), Mean annual Temperature (MAT), Accumulated Temperature > 5°C (AT5), Soil type and Ground preparation used during establishment. Soil Moisture Regime (SMR) and Soil Nutrient Regime (SNR) are the default values extracted from the Ecological Site Classification (ESC) tool (Reynolds et al., 2021).

	Mull17 (Mull17)	**Glentress96 (Glen96)**	**Llandovery52 (Llan52)**	**Westonbirt32 (West32)**	**Bramshill61 (Bram61)**
Lat/Long	56.540, −6.009	55.647, −3.108	52.022, −3.723	51.604, −2.240	51.380, −0.777
Elevation (m) a.s.l	50–100	170–210	175	140	95
Aspect	SSE	SE	NW	Nil	Nil
Slope	Steep-gentle	Steep	Moderate	Flat	Flat
MAT (°C)	9.0	8.2	8.9	9.4	9.7
AT5 (°C)	1356	1232	1651	1690	1797
Precipitation (mm)	1400	892	1351	824	665
SNR	Medium	Rich	Medium	Carbonate	Poor
SMR	Fresh	Fresh	Very moist	Moderately dry	Very moist
Ground preparation	Mounded	Ploughed	Mounded	Mulched	Mulched and scarified
Soil type	Basic brown earth	Typical brown earth	Surface-water gley/Peaty gley	Argillic brown earth/Typical surface-water gley	Podzolic surface-water gley

were removed from the comparative height analysis.

2.2. Tree survival and height comparison

To assess differences in the survival of each *Provenance* within *Species*, and between *Species* both within and between *Experimental sites*, we fitted two Binomial Mixed-Effects Models using the *lme4* package in R (Bates et al., 2015). In both survival models the proportion of trees that were alive or dead at age six was used as the response variable. The first survival model followed Eq. (1) to investigate the effect of *Species*, *Experimental site*, and their interaction on the probability of survival. In Eq. (1), p_{ijkl} represents the probability of survival for the ith tree, in the jth plot, in the kth block in the lth experimental site, $\beta0$, $\beta1$,… $\beta3$ are coefficients corresponding to the fixed effects and their interactions (donated by the *), $b0j$ and $b1jk$ are random intercepts for the nested experimental structure including *Block* nested within *Experimental site*,

Table 2
Summary of the species included in the analysis presented in this study and the four-letter code used for each species. Numeric values represent the number of provenances of each species considered at each experimental site. All species included in this study were non-native, except for *Pinus sylvestris, Quercus robur* and *Betula pendula.*

Species	Species code	Bram61	Glen96	Llan52	Mull17	West32
Acer macrophyllum	ACMA	1	-	2	2	1
Betula pendula	BEPE	1	1	2	1	1
Cedrus atlantica	CEAT	1	1	-	-	-
Cryptomeria japonica	CRJA	-	-	2	2	3
Larix decidua	LADE	1	1	1	1	1
Larix marschlinsii	LAEU	2	1	2	2	-
Pinus nigra subsp. laricio	PINI	-	-	1	1	-
Picea orientalis	PIOR	1	1	2	2	2
Pinus pinaster	PIPT	3	3	-	-	-
Pinus radiata	PIRA	2	2	2	2	2
Picea sitchensis	PISI	-	2	2	2	2
Pinus strobus	PIST	2	2	-	-	-
Pinus sylvestris	PISY	3	3	3	3	3
Pseudotsuga menziesii	PSME	3	3	3	3	3
Quercus pyrenaica	QUPY	-	-	1	1	1
Quercus robur	QURO	-	-	1	1	2
Quercus rubra	QURU	1	1	-	-	-
Thuja plicata	THPL	-	-	1	-	1

and of *Plot* nested within *Block* nested within *Experimental site*, while $\epsilon ijkl$ represents the residual error.

$$logit\left(p_{ijkl}\right) = \beta 0 + \beta 1 Experiment + \beta 2 Species + \beta 3 Experimental\ Site * Species + b0j + b1jk + \epsilon ijkl \tag{1}$$

The second survival model followed Eq. (2) to investigate the effect of *Provenance* on the probability of survival by including *Provenance* nested within *Species* and *Experimental site* as an additional third order interaction, and the same random effects structure as Eq. (1).

$$logit\left(p_{ijkl}\right) = \beta 0 + \beta 1 Experimental\ site + \beta 2 Species + \beta 4 Experimental\ site * Species + \beta 5 Experimental\ site * Species * Provenance + b0j + b1jk + \epsilon ijkl \tag{2}$$

Two models were necessary to fully investigate differences in survival as some provenances only occurred at a single experimental site, and so had to be removed from the provenance survival analysis ($n = 28$ provenances, $n = 12$ species) (as retaining them caused problems for model fitting) but retained for comparison in the species survival analysis ($n = 34$ provenances*,* $n = 18$ species). Model diagnostics and overdispersion was checked for both models using the *performance* (Lüdecke et al., 2021) and *DHARMa* (Hartig, 2022) packages in R.

To compare the height of each *Species* and *Provenance* within *Species*, both within and across each *Experimental site* (when a species and/or provenance was established in more than one experiment) we fit a linear mixed-effects model, again using the *lme4* package in R (Bates et al., 2015) following Eq. (3).

$$H_{ijkl} = \beta 0 + \beta 1 Experimental\ site + \beta 2 Species + \beta 4 Experimental\ site * Species + \beta 5 Experimental\ site * Species * Provenance + b0j + b1jk + \epsilon ijkl \tag{3}$$

In Eq. (3), H_{ijkl} refers to tree *Height* (the response variable) of the *i*th tree, in the *j*th plot in the *k*th block in the *l*th experimental site and was square root transformed to improved model fit, while the fixed and random effects structure are the same as those described for Eq. (2). We checked the normality and linearity of model residuals, homogeneity of variance (Figure S1), calculated both the conditional and marginal R^2 using the *performance* package in R (Lüdecke et al., 2021) and calculated both Leverage and Cook's distance values to ensure extreme values were not disproportionately influencing our models. Pairwise comparisons between *Species*, *Provenances* and *Experimental sites* were performed using estimate marginal means (aka least-squared means) in the *emmeans* package (Lenth, 2023), with the False Detection Rate (FDR) method (a Bonferroni-based method) used to adjust *p-values* for varying numbers of multiple tests. The *emmeans* package also detects the nested structure of Provenance within Species and provides appropriate means and comparisons. All analyses were conducted in the R programming environment (R Core Team, 2023).

Due to practical limitations during the experimental setup, a small number of plants spent an additional year in the nursery prior to planting (i.e., were one year older at establishment). To test whether this had any effect on our results, we also included *Tree age* at establishment as a separate fixed effect, but this was not significant ($p > 0.89$) and so was dropped from the final model following standard model selection procedures.

3. Results

3.1. Intraspecific differences in survival at age six

In both binomial mixed-effects survival models (the provenance model and the species model), all predictor variables and their nested interactions were significant ($p < 0.0008$ in all cases, Tables 3 and 4). However, only eight significant differences in the predicted probability of survival were detected between provenances of the same species using pairwise comparisons of estimated marginal means, four of which were for *P. sylvestris*. At Glentress96, the Spanish provenance from the Iberian Peninsula (PISY-VALS) showed significantly lower survival (48 %) than the other two provenances from Poland (PISY-POLA – 98 %) and Scotland (PISY- SCOT – 93 %, $p < 0.0003$ in both cases, Fig. 2**d**). Survival of the Polish provenance of *P. sylvestris* (PISY-POLA) at Llandovery52 (97 %) and Westonbirt32 (93 %), showed significantly greater survival than both other provenances ($p < 0.03$ in both cases, Fig. 2**d**), however it is worth noting that survival of all provenances of

Table 3
Analysis of Deviance summary of the binomial mixed-effects '*provenance'* model comparing mean survival between *Provenance* nested within *Species* and *Experiment.* Interactions are denoted by the ×, with *df* = degrees of freedom.

	Chisq	*df*	*p-value*
Experiment	34.97	4	< 0.0001
Species	257.78	11	< 0.0001
Species × Provenance	39.87	16	< 0.0008
Experiment × Species	253.48	31	< 0.0001
Experiment × Species × Provenance	73.97	33	< 0.0001

Table 4
Analysis of Deviance summary of the binomial mixed-effects '*species*' model comparing mean survival between *Species* nested within *Experiment*. Interactions are denoted by the ×, with *df* = degrees of freedom.

	Chisq	df	p-value
Experiment	52.20	4	< 0.0001
Species	246.80	17	< 0.0001
Experiment × Species	226.09	41	< 0.0001

this species was still relatively good except for PISY-VALS at Glentress96 mentioned above, and all Scots pine provenances at Mull17 (range 35–57 %, Table S2). At Llandovery52, the provenance of *B. pendula* (BEPE-NOR2) from the north of France had lower survival (73 %) than the Welsh provenance BEPE-UNIT (93 %, $p < 0.04$, Fig. 2**a**) and the *P. orientalis* provenances from the USA (PIOR-P2) exhibited lower survival (67 %) than the Turkish provenance PIOR-TURK (95 %, $p < 0.004$, Fig. 2**b**). Finally, the Oregon coast provenance of *P. menziesii* (PSME-ORCO) had lower survival (61 %) than the Oregon Siskyou (PSME-ORSI) provenance (91 %) at Westonbirt32 ($p < 0.01$, Fig. 2**e**). The conditional and marginal R2 for the provenance survival model were 0.41 and 0.39 respectively. See Figure S2 and Table S2 for all provenance survival comparisons.

3.2. Interspecific differences in survival at age six

For comparisons of species survival within each experimental site (averaged across provenances), several results are worth highlighting in more detail. All initially planted *C. atlantica* died at Glentress96 (Table S2), while *Acer macrophyllum* (ACMA) generally showed very low survival at Bramshill61 (7 %), Llandovery52 (19 %) and Westonbirt32 (39 %) compared with other species (Figure S3a**, c and e**), and most species showed lower survival at Mull17 than at other sites (Figure S3d). In contrast, other than *A. macrophyllum,* survival of most species was high at Bramshill61 (range 60–98 %). High survival was particularly evident for most pine species at Bramshill61, Glentress96 and Llandovery52 (Figure S3a, **b** and **c**), except for *P. radiata* (PIRA) which only appeared to show good survival at Bramshill61 (86 %) compared with other sites (range 16–54 %, Figure S3a). The conditional and marginal R2 for the species survival model were 0.37 and 0.36 respectively.

3.3. Inter and intraspecific comparison of tree height at six years old

The linear mixed-effects model results for tree height showed that all predictor variables and their interactions were significant (Table 5), suggesting that differences between provenances varied depending on the species and the experimental site, while differences between species

Table 5
ANOVA summary of the mixed-effects model output comparing mean top height between *Provenances*, *Species*, *Experimental Site,* and the nested interaction between these two variables (denoted by the colons), with *df* = degrees of freedom.

	Chisq	df	p-value
Experimental Site	45.43	4	< 0.001
Species	1791.34	18	< 0.001
Experimental Site × Species	354.28	38	< 0.001
Experimental Site × Species × Provenance	95.76	48	< 0.001

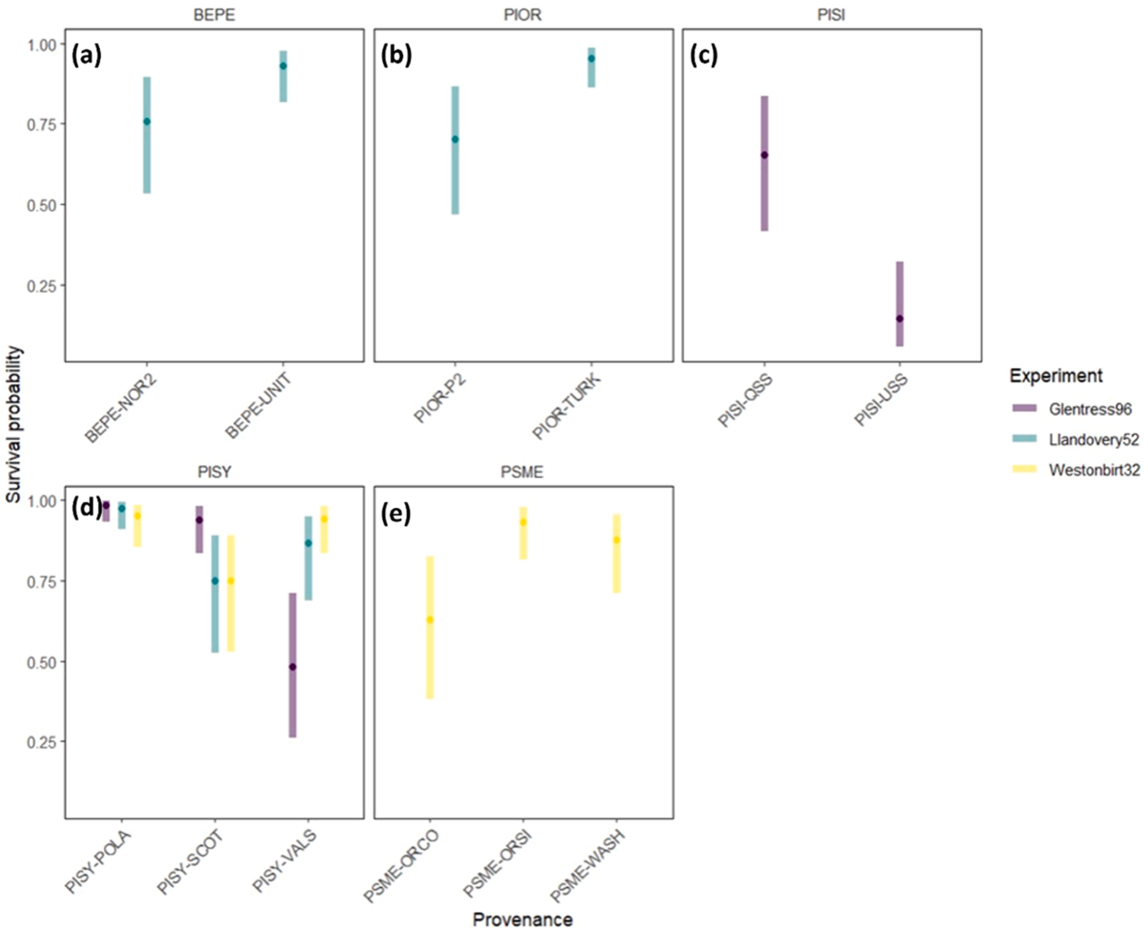


Fig. 2. Estimated survival probabilities and 95 % confidence intervals for provenances for which a significant difference was detected. See species and provenance codes from Table 2 in the main text. Species codes have been included above each sub-plot to aid comprehension.

also varied between experimental sites. We also tested the significance of all random effects in our model using the *lmerTest* package in R (Kuznetsova et al., 2017)($p < 0.001$ in all cases). The conditional and marginal R^2 were 0.78 and 0.68 respectively, indicating that collectively the fixed and random effects in our model explained c.78 % of the variability in tree height at age six. To explore these differences in mean tree height, we performed pairwise comparisons between species both within each experimental site (Figs. 3 and 4), between experimental sites (Figures S4 and S5), and between provenances within species (Fig. 5) using estimated marginal means. All comparisons between species are averaged across provenances of that species in each experimental site. To reflect slight differences in the species planted at the five experimental sites, we have graphically presented our results by grouping more easterly experimental sites (Bramshill61 and Glentress96) in Fig. 3 and more westerly experimental sites (Llandovery52, Mull17 and Westonbirt32) in Fig. 4.

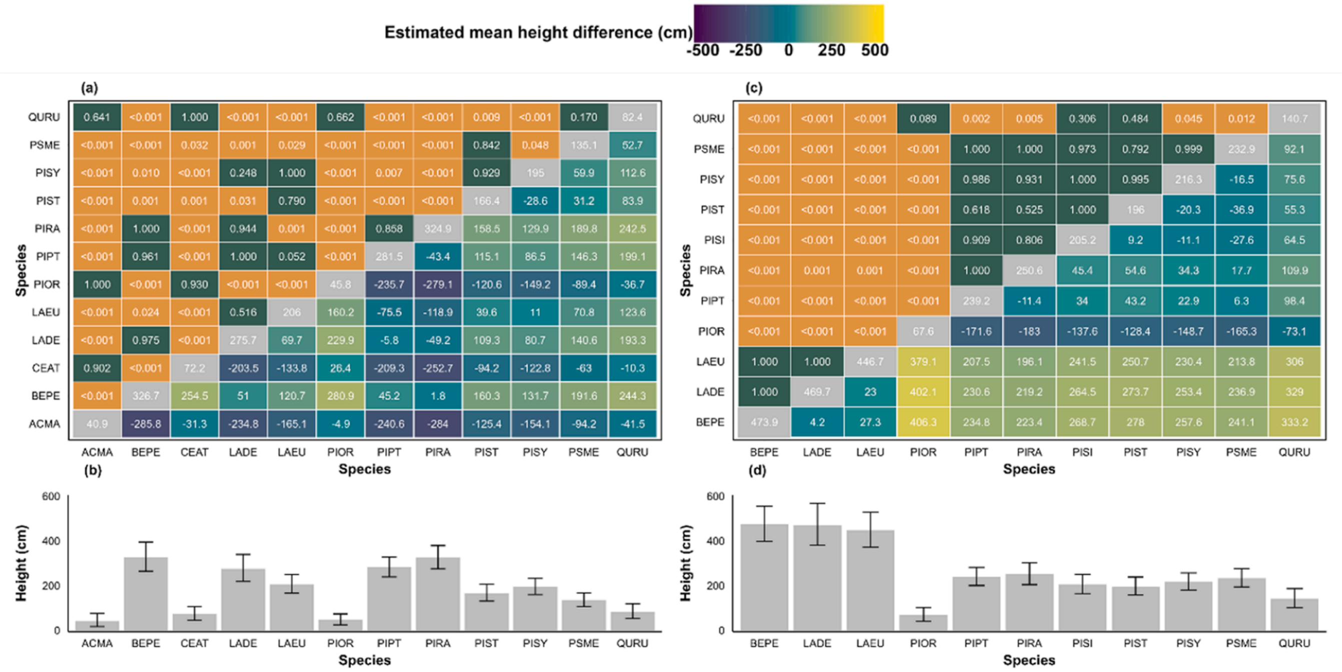
Where present, larch (*Larix decidua* – LADE and/or *Larix x marschlinsii* - LAEU) were consistently amongst the tallest conifer species (Figs. 3 and 4), with *Pinus radiata* (PIRA) at Bramsshil61 being the only example of a species that was significantly taller than *L. marschlinsii* (Fig. 3**a-b**). Conversely, no species other than *L. marschlinsii* was ever taller than *L. decidua* in any of the five experimental sites (Figs. 3 and 4). At Glentress96, both larch species were significantly taller than all other species (except for each other) while oriental spruce (*Picea orientalis* – PIOR) was significantly shorter than all other conifers (Fig. 3**c-d**). No other differences in height were detected between any of the other conifer species at Glentress96 after six years (Fig. 3 **c-d**) and this slow initial growth of *P. orientalis* relative to most other species was common across all five experimental sites (Figs. 3 and 4).

Differences in tree height between species was more variable at Bramshill61 than at Glentress96 (the two easterly sites), with *Pinus pinaster* (PIPT) and *Pinus radiata* (PIRA) amongst the tallest species. The latter species was significantly taller than seven of the nine other conifer species at Bramshill61 (Fig. 3**a-b**) and grew relatively well at all sites. Most of the pine species and Douglas-fir (*Pseudotsuga menziesii* – PSME) had reasonably consistent mean top height relative to each other at Llandovery52 and Westonbirt32 and were as tall as Sitka spruce (*Picea sitchensis* - PISI) six years after planting, though *P. radiata* (PIRA) was significantly taller than *Pinus sylvestris* (PISY) at both sites (Fig. 4**a-b** and **e-f**). Like most other species at Mull17, *Cryptomeria japonica* (CRJA) showed slow initial growth (Fig. 4**c-d**). This species was however statistically indistinguishable from *Picea sitchensis* (PISI), *Pinus sylvestris* (PISY) and *Pseudotsuga menziesii* (PSME) at Westonbirt32 (Fig. 4**e-f**) but was not growing as fast as *Pinus radiata* (PIRA) at Westonbirt32 (Fig. 4 **e-f**), or any of these four species at Llandovery52 (Fig. 4 **a-b**). *Cedrus atlantica* (CEAT) was only assessed at Bramshill61, where it showed very slow initial growth (Fig. 3**a-b**).

In terms of broadleaves, *B. pendula* (BEPE) was significantly taller than the limited number of other broadleaf species considered in this study at four of the five sites, likely reflecting the pioneer status of birch. However, the growth advantage of *B. pendula* over most other species was not apparent at Mull17, where all species except for *Larix x marschlinsii* showed relatively slow initial growth (Fig. 4**c-d**).

When comparing the estimated mean height of each species between sites, the growth of most species was not significantly different, however for a few species a notable pattern did emerge. Most of the significant differences between sites that were observed indicated that species tended to be shorter at Mull17 (Figures S4 and S5). However, the exception was for both *P. menziesii* and *L. x marschlinsii* which were both significantly shorter at Bramshill61 than at all other sites where they were planted, including at Mull17 (Figure S4) where these two species were the two tallest (Fig. 4 **c-d**). Both *Quercus pyrenaica* (QUPY) and *Acer macrophyllum* (ACMA) were more than twice as tall at Westonbirt32 than at any of the other sites where they were established (Figure S5), with Westonbirt32 also being the best site for *C. japonica* (Figure S4).

When comparing differences in mean tree height between provenances within each species and experimental site, only seven out of 61 pairwise comparisons were significant (Fig. 5). At Bramshill61, the second-generation seed orchard provenance of *Pinus pinaster* (PIPT-LAND) from Landes in France was significantly taller than the other two



(a)

Species	ACMA	BEPE	CEAT	LADE	LAEU	PIOR	PIPT	PIRA	PIST	PISY	PSME	QURU
QURU	0.641	<0.001	1.000	<0.001	<0.001	0.662	<0.001	<0.001	0.009	<0.001	0.170	82.4
PSME	<0.001	<0.001	0.032	0.001	0.029	<0.001	<0.001	<0.001	0.842	0.048	135.1	52.7
PISY	<0.001	0.010	<0.001	0.248	1.000	<0.001	0.007	<0.001	0.929	195	59.9	112.6
PIST	<0.001	0.001	0.001	0.031	0.790	<0.001	<0.001	<0.001	166.4	-28.6	31.2	83.9
PIRA	<0.001	1.000	<0.001	0.944	0.001	<0.001	0.858	324.9	158.5	129.9	189.8	242.5
PIPT	<0.001	0.961	<0.001	1.000	0.052	<0.001	281.5	-43.4	115.1	86.5	146.3	199.1
PIOR	1.000	<0.001	0.930	<0.001	<0.001	45.8	-235.7	-279.1	-120.6	-149.2	-89.4	-36.7
LAEU	<0.001	0.024	<0.001	0.516	206	160.2	-75.5	-118.9	39.6	11	70.8	123.6
LADE	<0.001	0.975	<0.001	275.7	69.7	229.9	-5.8	-49.2	109.3	80.7	140.6	193.3
CEAT	0.902	<0.001	72.2	-203.5	-133.8	26.4	-209.3	-252.7	-94.2	-122.8	-63	-10.3
BEPE	<0.001	326.7	254.5	51	120.7	280.9	45.2	1.8	160.3	131.7	191.6	244.3
ACMA	40.9	-285.8	-31.3	-234.8	-165.1	-4.9	-240.6	-284	-125.4	-154.1	-94.2	-41.5

(b)

(c)

Species	BEPE	LADE	LAEU	PIOR	PIPT	PIRA	PISI	PIST	PISY	PSME	QURU
QURU	<0.001	<0.001	<0.001	0.089	0.002	0.005	0.306	0.484	0.045	0.012	140.7
PSME	<0.001	<0.001	<0.001	<0.001	1.000	1.000	0.973	0.792	0.999	232.9	92.1
PISY	<0.001	<0.001	<0.001	<0.001	0.986	0.931	1.000	0.995	216.3	-16.5	75.6
PIST	<0.001	<0.001	<0.001	<0.001	0.618	0.525	1.000	196	-20.3	-36.9	55.3
PISI	<0.001	<0.001	<0.001	<0.001	0.909	0.806	205.2	9.2	-11.1	-27.6	64.5
PIRA	<0.001	0.001	0.001	<0.001	1.000	250.6	45.4	54.6	34.3	17.7	109.9
PIPT	<0.001	<0.001	<0.001	<0.001	239.2	-11.4	34	43.2	22.9	6.3	98.4
PIOR	<0.001	<0.001	<0.001	67.6	-171.6	-183	-137.6	-128.4	-148.7	-165.3	-73.1
LAEU	1.000	1.000	446.7	379.1	207.5	196.1	241.5	250.7	230.4	213.8	306
LADE	1.000	469.7	23	402.1	230.6	219.2	264.5	273.7	253.4	236.9	329
BEPE	473.9	4.2	27.3	406.3	234.8	223.4	268.7	278	257.6	241.1	333.2

(d)

Fig. 3. – Pairwise comparisons of estimated marginal mean tree height between species (see Table 2 for species codes) in the sixth year after planting at (a-b) Bramshill61 and (c-d) Glentress96 (the two more easterly experimental sites). The top left triangle of matrices (a) and (c) indicate which pairwise comparisons between species are significant (orange) where $p < 0.05$ and non-significant (green). The values in the bottom right tringle of matrices (a) and (c) indicate the difference in mean height (cm) between the species on the y-axis relative to the species on the x-axis, while the grey diagonal details the estimated mean height for each species. Grey bars in (b) and (d) indicate mean tree height while error bars are the 95 % confidence interval.

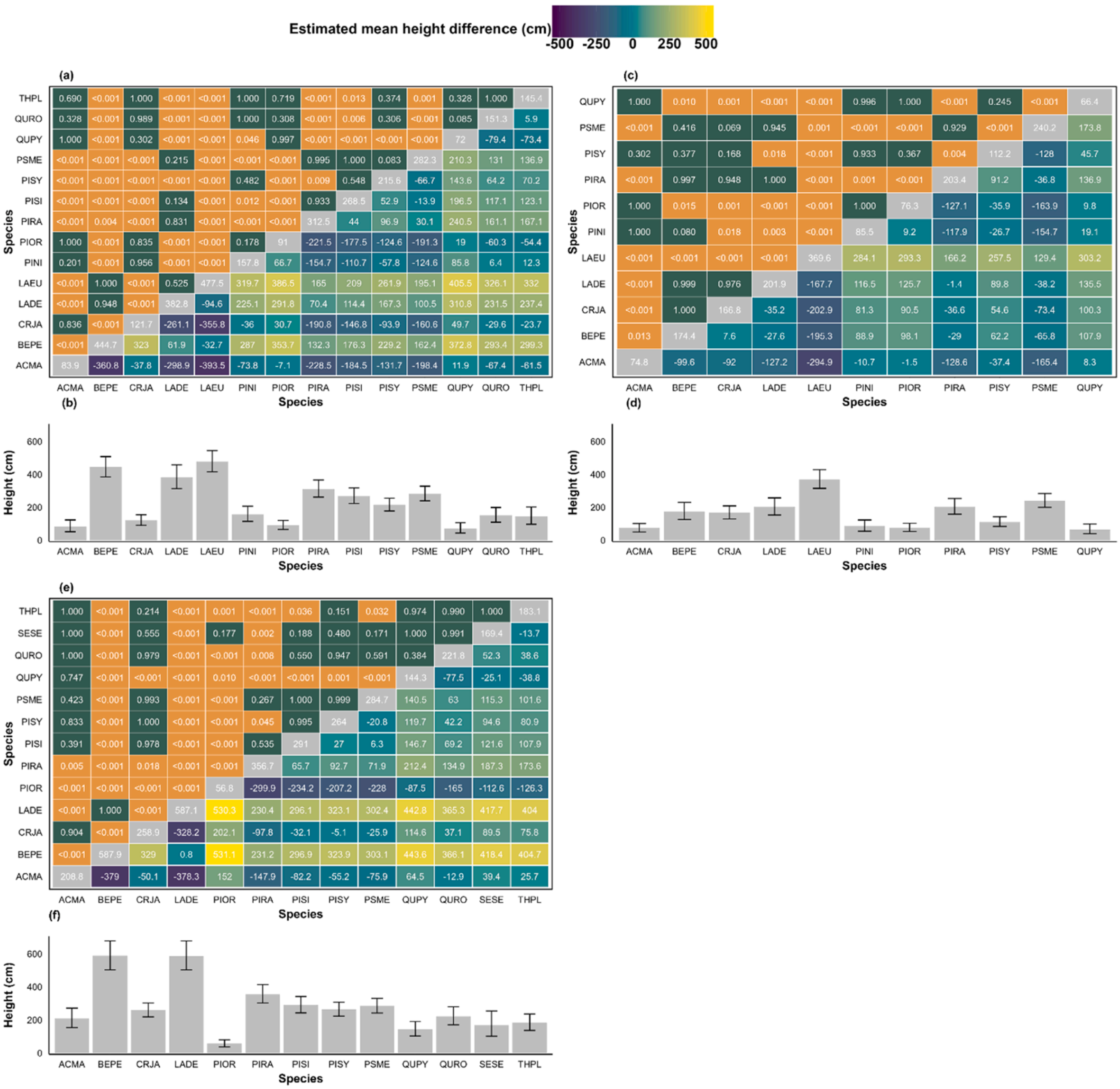


Fig. 4. – Pairwise comparisons of estimated marginal mean tree height between species (see Table 2 for species codes) in the sixth year after planting at (a-b) Llandovery52, (c-d) Mull17 and (e-f) Westonbirt32 (the three more westerly experimental sites). The top left triangle of matrices (a), (c) and (e) indicate which pairwise comparisons between species are significant (orange) where $p < 0.05$ and non-significant (green). The values in the bottom right tringle of matrices (a), (c) and (e) indicate the difference in mean height (cm) between the species on the y-axis relative to the species on the x-axis, while the grey diagonal details the estimated mean height for each species. Grey bars in (b), (d) and (f) indicate mean tree height while error bars are 95 % confidence interval.

provenances ($p < 0.003$ in both cases, Fig. 5**a**). Interestingly the Oregon coast provenance of *P. menziesii* (PSME-ORCO) was significantly taller than the Oregon Siskyou provenance at Bramshill61 ($p < 0.006$, Fig. 5**b**), but significantly shorter than the Oregon Siskyou provenance at Westonbirt32 ($p < 0.01$, Fig. 5**e**). At Llandovery52, the Polish provenance of *P. sylvestris* (PISY-POLA) was significantly taller than both other provenances ($p < 0.05$ in both cases, Fig. 5**d**) and the provenance of *Picea orientalis* from the USA (PIOR-P2) was significantly taller than the Turkish provenance of this species (PIOR-TURK) ($p < 0.05$, Fig. 5**c**) at Llandovery52. No significant differences between any provenances were detected at Glentrees96 or Mull17.

4. Discussion

In this study, we compared the early growth and survival of a range of species and provenances growing in monospecific plots that may help diversify British forestry under a changing climate. Of all the coniferous species considered, *P. orientalis* consistently showed very slow early growth across all five sites. While no species can be excluded as a potentially productive species after six years, an inability to establish quickly across a range of sites and climates will make this species both vulnerable to browsing pressure and require longer term and more costly maintenance (e.g., vegetation control) than all other coniferous species considered in this study. This will likely limit the attractiveness

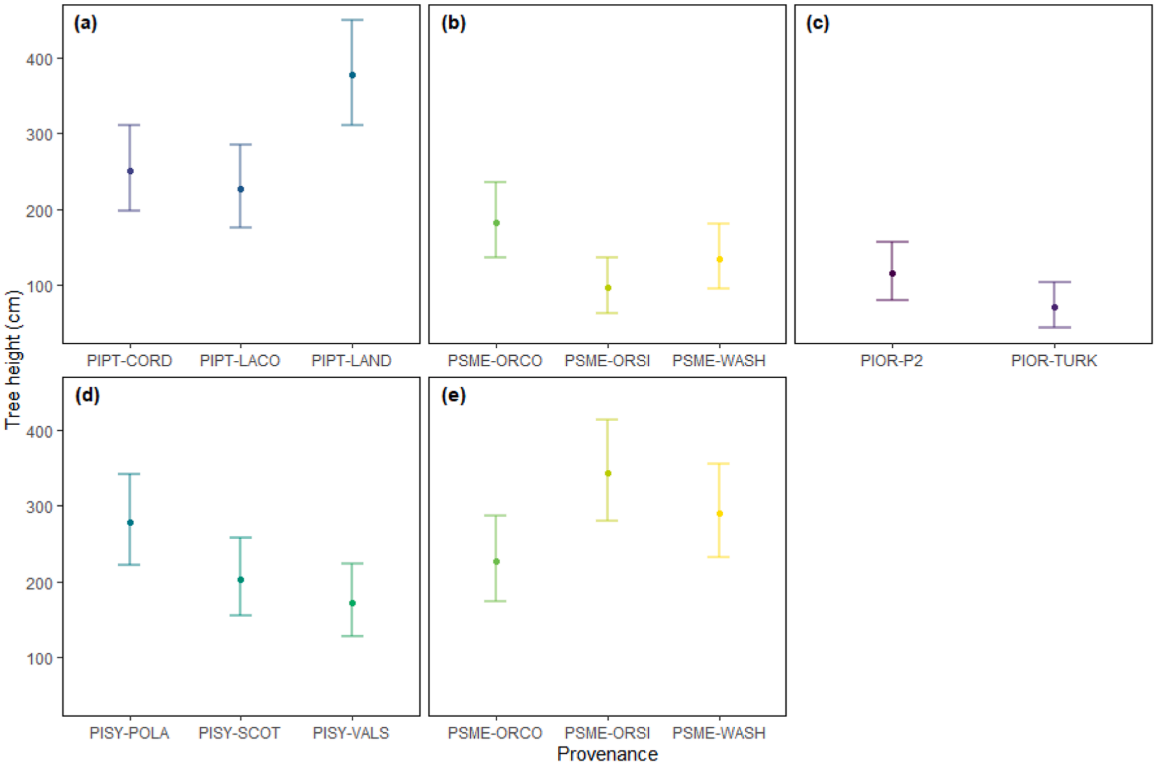


Fig. 5. – Pairwise comparisons of estimated mean tree height (coloured dots) and 95 % confidence intervals (error bars) between provenances for (a) *Pinus pinaster* (PIPT) and (b) *Pseudotsuga menziesii* (PSME) at Bramshill61, (c) *Picea orientalis* (PIOR) and (d) *Pinus sylvestris* (PISY) at Llandovery52 and (e) *Pseudotsuga menziesii* (PSME) at Westonbirt32 six years after planting. To aid comprehension, only species where significant differences existed between provenances are displayed.

of this species to forest managers looking to diversify species composition, even if its growth later accelerates. *C. atlantica* survival and growth was also poor, with all trees of this species dying at Glentress96. In contrast we found evidence that across a range of GB sites, *L. decidua* and *L.* x *marschlinsii* were consistently amongst the tallest conifer species six years after planting, however larch survival was sometimes variable (Table S2 and Figure S3). While the timber properties of British larch have been studied less than for spruce or pine, the limited studies that do exist suggest larch wood can be denser, stronger, and stiffer than other softwoods grown in Britain (depending on the species compared) (McLean et al., 2024). The productivity of larch species under GB conditions and their aesthetic value in softening the visual appearance of uniform blocks of often monospecific conifer in the landscape has been known for some time and has seen these species form a minor component of British forestry for many years (Savill, 2019), representing approximately 8 % of the GB's coniferous forest area (c. 100,000 ha) in 2021 (Forest Research, 2022). Unfortunately, in 2009 and 2010 *Phytophthora ramorum* was detected on *Larix kaempferi* in both England and Scotland, resulting in shoot dieback and the rapid, widespread mortality of both mature and juvenile trees (Brasier and Webber, 2010). By 2022, > 65 % of Scotland's larch resources (approximately 40,000 ha) fell within a 'Priority Action Zone' where the immediate felling of infected trees is currently still ongoing (Scottish Forestry, 2022). While anecdotal observations have suggested that *L. decidua* may be less affected by *P. ramorum* than *L. kaempferi,* recent work failed to detect any differences in lesion development between the two species, or find any evidence of greater resistance to infection in *L. decidua* compared with *L. kaempferi* (Dun et al., 2022).

The ongoing challenge of *P. ramorum* on larch species in GB means that these species are currently considered highly undesirable for planting across large parts of the country. However, we currently know very little about the productivity and disease resistance of larch growing on drier, compared with much wetter sites, or in mixed species stands. The limited evidence of larch productivity in mixtures compared with monocultures in GB that we do have is of *L. kaempferi* in mixture with *Pinus contorta* (both light demanding species) (Mason and Connolly, 2021) which suggests that the productivity of both species can be similar in mixed compared with monospecific stands. While both stocking proportion and relative contribution to total stand basal area remained relatively consistent throughout the first 50 years of stand development, these results are from only a single experiment in the north-east of England (Mason and Connolly, 2021). Numerous studies have shown the beneficial effects of mixtures compared to monocultures for increasing forest resistance to insect damage, mammalian herbivores and soil-born fungal diseases (Jactel et al., 2017), and in reducing the risk of tree mortality from pests and pathogens, partially due to reduced access to host trees (Roberts et al., 2020). To our knowledge no direct evidence of increased disease resistance in larch in mixed compared with monospecific stands yet exists. However, recent work has linked greater tree species diversity with a reduction in disease risk from *P. ramorum* (Haas et al., 2011), and the diversification of forest composition away from monocultures of many species may reduce the risk of catastrophic loss of the entire stand to a pathogen such as *P. ramorum* (Ennos et al., 2020), assuming the admixed species are not also susceptible. This evidence, coupled with the clear suitability of larch species to a range of GB conditions presented here suggests that the future role of larch as a component of more diverse, mixed-species forests (and the resistance of larch to *P. ramorum* in these mixtures) is a much-needed area of future research (alongside efforts to identify genetic resistance and inoculation trials) before larch species are abandoned entirely, particularly on drier sites where the risk from this pathogen might be lower.

Of the other conifer species considered in this study, *P. radiata* performed relatively well in terms of initial height growth compared with other species across most sites, reflecting this species ability to show rapid growth and its success as a plantation species in temperate regions (Mead, 2013). Observed differences between *P. menziesii* and *P. radiata* or *P. pinaster* likely reflect the different climatic requirements of *P. menziesii* and these two pine species, which are both better suited to drier Mediterranean climates (Romanyà and Vallejo, 2004; Savill, 2015) while *P. menziesii* prefers moist soils with an annual rainfall > 800 mm. *P. radiata* and *P. pinaster* were both amongst the fastest growing species with high survival at Bramshill61, the driest site with 665 mm mean annual precipitation, but Bramshilll61 was clearly the worst site for early *P. menziesii* growth. To date, *P. radiata* has been of relatively low importance in Britain, primarily due to its high susceptibility to red band needle blight (*Dothistroma septosporum*) (Savill, 2013; Watt et al., 2009). *P. radiata* trees are however rarely killed by *D. septosporum*, is often considered to be resistant by age 15 (Brown and Webber, 2008; Mead, 2013), and any impact on stand growth is proportional to the level of infection (Mead, 2013). Commercial plantations of *P. radiata* require a minimum of c. 600–750 mm annual rainfall but *D. septosporum* often emerges as a problem where rainfall is > 1000–1200 mm per year (Mead, 2013), providing a window within which *P. radiata* may be more safely planted as levels of infection might be lower. While no differences between *P. radiata* provenances were detected in this study, the inclusion of a *Dothistroma* resistant provenance will be of particular interest as these experiments continue to mature. The use of these resistant provenances in higher rainfall areas, coupled with the trend towards a warmer and drier climate across much of GB may expand the area within which this species could be planted, and would be a good candidate for the focus of future work. *Pinus pinaster* is also considered moderately susceptible to red band needle blight and planting of this species has declined elsewhere in Europe in favour of *P. radiata,* but it will again be interesting to see if any provenance differences later emerge as there has been limited provenance testing of this species in Britain to date (Savill, 2015).

Previous work on the provenance suitability of *P. menziesii* in GB suggests that the Washington Cascades provenance of *P. menziesii* (PSME-WASH) would be superior to both Oregon coast (PSME-ORCO) and Oregon Siskyou (PSME-ORSI) provenances (Fletcher and Samuel, 2010). However, the results from our study suggest that all three *P. menziesii* provenances were performing similarly after six years, with only one significant difference in mean tree height noted between these provenances at Westonbirt32, where there was some evidence that Oregon coast (PSME-ORCO) provenance was slightly shorter. Early survival of the different provenances of *P. menziesii* within each experimental site was also relatively consistent, and future assessments of these experimental sites should monitor whether any differences between these provenances and those of other species emerge as the stands mature, as we detected very few differences between provenances of most species after six years. It is worth noting that the number of provenances compared in this study for each species is relatively small compared with some provenance trials (Nabais et al., 2018). However, the results from these trials will provide a useful indication as to which species may be good candidates for more extensive provenance testing, or which species show relatively consistent growth and survival irrespective of provenance choice.

At all three sites where a direct comparison between *P. menziesii* and *P. sitchensis* (the most abundant and widely grown commercial conifer in GB) could be made (Glentress96, Llandovery52 and Westonbirt32), no significant differences in mean tree height were detected six years after planting. Equally, both species showed similar rates of survival, depending on the provenance compared. Collectively these initial results reinforce other recent work highlighting the potential of *P. menziesii* to be more widely grown in GB under certain climatic and soil conditions (Stokes et al., 2022). Similarly, the co-existence of *P. menziesii* and *P. sitchensis* in their natural range make them good candidates for intercropping to diversify species composition, and recent work has predicted an increase in the climatic suitability of *P. menziesii* across much of England, Wales, Northern Ireland, and Eastern Scotland under several different climate change scenarios (Dyderski et al., 2018). Despite this clear potential as a productive conifer, *P. menziesii* currently makes up < 4 % of GB's total coniferous area (Forest Research, 2022) and very few replicated experimental trials have historically been established to measure the productivity of *P. sitchensis* and *P. menziesii* in mixed compared with monospecific stands. Globally, > 70 % of mixed-species forest plantations have been found to have a larger mean height, DBH and biomass than monocultures comprised of the same species of the same age and stocking density (Feng et al., 2022), with similar findings also documented in Britain (Mason et al., 2021; Mason and Connolly, 2021, 2014). This evidence, coupled with experiences from elsewhere in Europe that suggests *P. menziesii* can maintain relatively good growth under some drought conditions and is considerably more drought resistant than *Picea abies* (Vitali et al., 2017) provides further encouragement that this species could be more widely adopted to increase GB forest resilience under a changing climate.

A more limited number of broadleaves were available for comparison during six-year assessment presented here, with few differences in top height detectable at this age. The notable exception was *B. pendula*, which excelled at all sites except for Mull17. *B. pendula* is predicted to continue to be suitable under a range of climate change scenarios across much of GB, except for the Southeast (Dyderski et al., 2018). This consistently good survival (except for at Mull17), fast early growth, native GB status and ability to naturally regenerate across a range of sites will likely make *B. pendula* an attractive choice as a future broadleaf, including as a component of mixed broadleaf/coniferous forests.

While it was not possible to establish more than five experimental locations due to resource limitations, the sites used in this study do offer valuable insights as to the general performance of different species and provenances during the critical establishment phase across broadly representative site types. These early results can act as a “first filter” to help guide the design of future experiments, which could now look to trial a smaller number of species that show good initial height growth and survival at additional locations across GB, to provide some replication of these site types and to expand into other site conditions to more comprehensively assess the range of conditions under which these species might be best suited, both now and under future climate scenarios. Productive forestry in Britian has relied on non-native tree species for many decades, in part due to the lack of native conifers that can be grown productively. As our climate warms it will be important to remain vigilant about the future risks that might be associated with the adoption of a wider range of non-native species, but to also explore the opportunities these species present to diversify productive forestry and adapt to climate change.

5. Conclusions

Climate change is expected to alter the suitability of many sites for species that have historically been planted for timber and other forest products across much of Europe (Dyderski et al., 2018; Takolander et al., 2019). However, it is also likely that some sites will start to become favourable for a range of species that were previously unsuitable, with both species range expansions and contractions predicted under different climate change scenarios (Dyderski et al., 2018; Ray, 2008b). While these shifts present significant challenges, changes in the species or sites where timber can be grown commercially also represents an opportunity for the forest sector to diversify species composition and in doing so, simultaneously increase forest resilience to the challenges posed by climate change.

The results presented here provide evidence for the early growth and survival during the critical establishment phase for a range of potential species that may help diversify and adapt GB forests to climate change. While we cannot make any definitive recommendations on the long-term performance of these species after six years post-planting, some species showed both clear signs of good initial growth and survival, whilst others struggled to establish quickly, if at all. Both larch species and *B. pendula* performed well across a range of sites, but the use of larch in British forestry is currently hampered by the ongoing challenge posed by the pathogen *P. ramorum*. More promisingly *P. menziesii, P. radiata* and *P. pinaster* exhibited both good growth and site-dependant survival, often growing as fast as *P. sitchensis* (the most abundant conifer grown in Britain), underlying the importance of matching species to both site conditions and current and future climates. In contrast, initial height growth for *P. orientalis* was consistently below average across all sites and *C. atlatica* survival was very poor, suggesting these species are slow to establish and unlikely to be attractive to foresters looking to diversify species composition for climate adaptation, even if the growth rate of these species later improves. Future work should aim to understand the comparative performance of these species and provenances, and the role these species (particularly larch and *P. menziesii*) may have as part of mixed species stands.

Authors contributions

TO was involved in the conceptual development and lead the methodological approach and data analysis as well as the production of the manuscript.

GK worked with RJ and CJ to establish, maintain, and assess the experiments and helped with the silvicultural interpretation of results from the experiments and the write-up.

WLM was involved in the original design of the experiments, the species and site selection and the initial establishment, and contributed to the production of the manuscript.

CRediT authorship contribution statement

Thomas S Ovenden: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Richard L Jinks:** Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **William L Mason:** Writing – original draft, Funding acquisition. **Gary Kerr:** Writing – original draft, Project administration, Formal analysis, Conceptualization. **Chris Reynolds:** Writing – original draft, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Thomas Ovenden reports financial support was provided by Forestry Commission England. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122340.

Data availability

Data may be avalaliable through request

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