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ARTICLE

No seed zone effects on the survival, growth, and stem form of Pacific silver fir (*Abies amabilis*) in Britain

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Abstract: Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) was first introduced to Britain in 1830 but has not been widely planted and occupies a minute part of the forest estate. The results of six experiments established in the uplands of Britain examining material from 30 collection sites in 14 seed zones clearly demonstrate that its potential has not been recognised. The trials were assessed after 28 years and show that Pacific silver fir has the potential to be as productive as other common species options. There was little variation in performance between the 14 seed zones, and future seed collections could be carried out within a wide geographical range, including mainland British Columbia and Vancouver Island and the Olympic Mountains and western Cascades of Washington. The silvicultural characteristics of the species mean that it could be used more widely to diversify forests in Britain both as a plantation species and in the wider use of continuous cover management. More work is justified to determine its susceptibility to Annosum root rot (*Heterobasidion annosum* (Fr.) Bref), confirm its productivity on sites with rainfall below 800 mm·a^{-1} and (or) with a high peat content, and provide more detail on its wood properties.

Key words: seed zone, *Abies amabilis*, silviculture, genetics.

Résumé : Le sapin gracieux (*Abies amabilis* Douglas ex J. Forbes) a été introduit en Grande-Bretagne pour la première fois en 1830 mais n'a pas été beaucoup planté et n'occupe qu'une infime partie du domaine forestier. Les résultats de six essais établis sur les hautes terres de la Grande-Bretagne pour étudier le matériel récolté à 30 endroits dans 14 zones de semences démontrent clairement que son potentiel n'a pas été reconnu. Les essais ont été évalués après 28 ans et montrent que le sapin gracieux peut être aussi productif que les autres espèces potentielles. La performance variait peu entre les 14 zones de semences et les futures collectes de graines pourraient être faites à l'intérieur d'une vaste étendue géographique, incluant la Colombie-Britannique, l'île de Vancouver et l'ouest des Cascades dans l'État de Washington. Les caractéristiques sylvicoles de l'espèce indiquent qu'elle pourrait être plus largement utilisée pour diversifier les forêts de la Grande-Bretagne soit en plantations ou plus abondamment dans l'aménagement du couvert continu. Davantage de travaux sont justifiés pour déterminer sa sensibilité à la carie de racines causée par *Heterobasidion annosum* (Fr.) Bref., pour confirmer sa productivité dans les stations où la précipitation est inférieure à 800 mm·an^{-1} ou dont le contenu en mousse est élevé et pour fournir plus de détails sur les propriétés de son bois. [Traduit par la Rédaction]

Mots-clés : zone de semences, *Abies amabilis*, sylviculture, génétique.

Introduction

Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) is native to Pacific north–west America, and the major portion of its range lies between the latitudes 43°N and 56°N (Fig. 1). Within this, it occupies a wide range of elevations, being narrowest in Alaska, 0–300 m, and greatest in the western Cascade region of Washington, 240–1830 m. It generally occupies sites with a maritime climate with cool summers, winter temperatures seldom lower than –9 °C, and annual rainfall that varies from 965 mm on the eastern coast of Vancouver Island to 6650 mm on the western coast of Vancouver Island (Crawford and Oliver 1990). A summer dry season is characteristic of much of its range, but Pacific silver fir is dependent on adequate soil moisture during the growing season and is most abundant on sites where drought is minimal. Despite its extensive range and tolerance of a wide range of soil types, Pacific silver fir has been noted to be "not a highly variable species" (Zavarin et al. 1973).

The species was first introduced to Britain by David Douglas in 1830, and his journal of his travels (Douglas 1914) records that it is a tree that "justly merits our further consideration". However, many of the early introductions were not successful, and the tree was "rediscovered" in 1882 when a large seed lot arrived from Oregon (Elwes and Henry 1909). Based on a survey of early plantings, Elwes and Henry (1909) concluded that the species "appears to be a failure in cultivation". This may have prejudiced early thinking on its likelihood of success; for example, authorities such as Edlin (1949) stated that "being an alpine tree, it is unlikely to be of forest value here [in Britain]". However, based on a visit to the Pacific Northwest, Wood (1955) was more positive and commented that "*Abies amabilis* would appear to be a species more suited to Britain", and Lines (1979) thought it was one of the most promising species that had not been fully tested in Britain. In addition, Mitchell (1972) concluded "Growth: very variable indeed, the general pattern being slow and thin in south-east England and vigorous and luxuriant trees in the far north and west, but the

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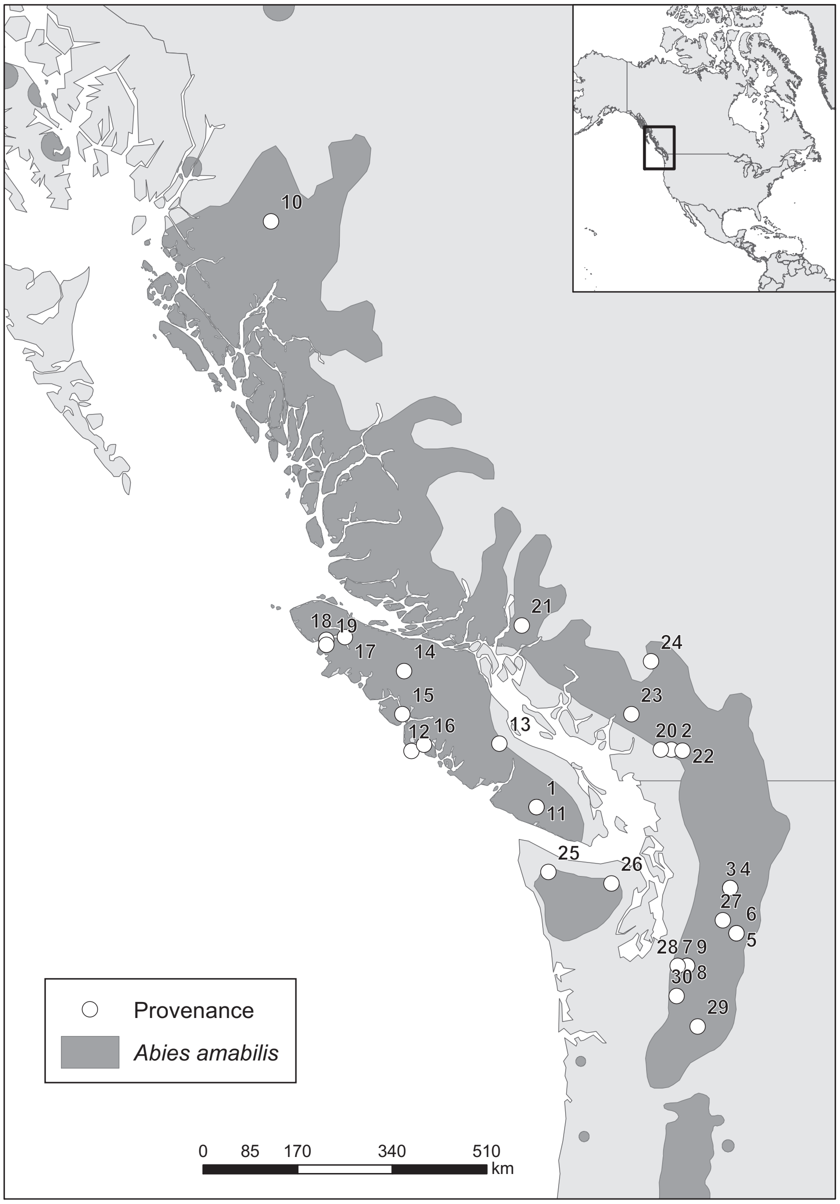
Fig. 1. The natural range of *Abies amabilis* and the location of the seed collections.

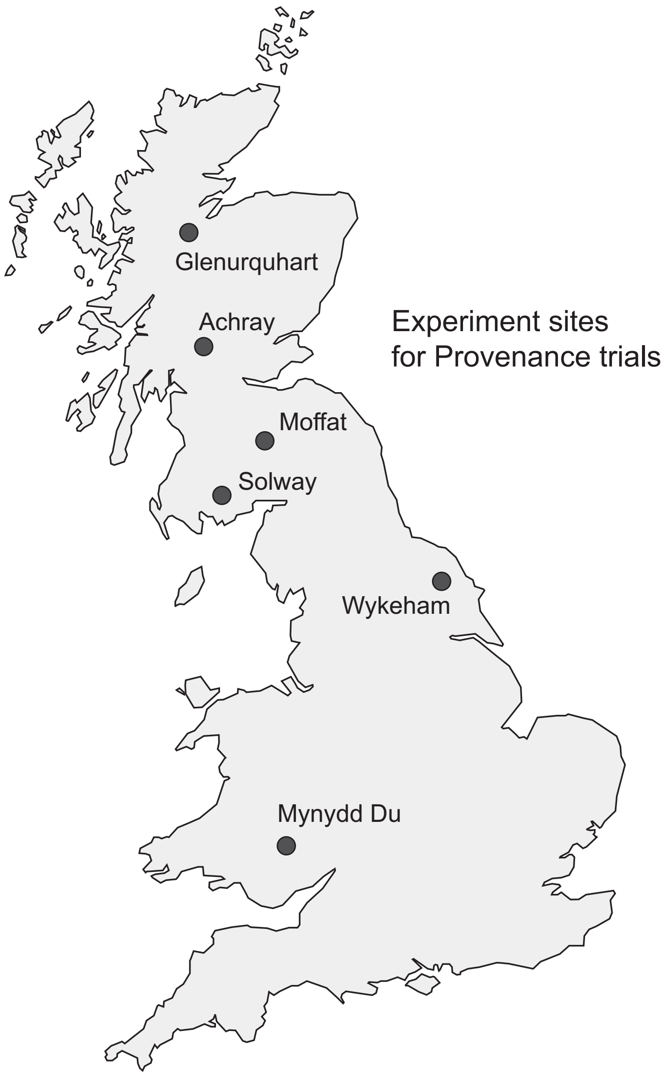


origin of the seed (unknown in all cases) may be important". However, despite this growing body of evidence of the potential of the species, it has never been widely planted in Britain (MacDonald et al. 1957). One of the main reasons for this, in common with other species of *Abies* spp., is what Lines (1960) attributes to "the impatience of nineteenth century foresters who preferred the much faster-starting conifers such as Douglas-fir, and the well tried Norway spruce". Recent work by Mason (2013) has shown that, in 2010, only a tiny area of the species was recorded in the National Forest Inventory, being so small that it was not identified separately as an individual species and is shown as part of 57 ha of "other silver firs". This term refers to silver firs that are not *Abies grandis* (Douglas ex D. Don) Lindl. (5207 ha), *Abies procera* Rehder (3008 ha), or *Abies alba* Mill. (402 ha).

In recent years, there has been growing recognition that the optimism of Wood (1955), about the prospects for good growth of Pacific silver fir in Britain, may be justified. Lines (1979) comments that there are many fast-growing individuals in arboreta and notes very good growth at one forest plot on the west coast of Scotland. Mason et al. (1999) has measured the forest plots at the Kilmun Forest Garden (Forestry Commission 1931) and recorded a mean annual increment of 24 $m^3 \cdot ha^{-1} \cdot a^{-1}$. The work of Read et al. (2009; tables 6.5 and 9.1) also indicates the potential role that *A. amabilis* could play in a climate change adaptation strategy for British forestry. Diversification is a major theme of forest policy in Britain, and it is now timely, once again, to review the potential contribution of a range of different species. The main drivers of this are the increasing impacts of pests and pathogens on a forest estate dominated by just five species (Forestry Commission 2011), and the need to diversify forests through the use of a wider range of silvicultural systems (Kerr 1999); central to this latter point is the need to identify a range of shade-tolerant conifers (Paterson 1990).

An increase in North American interest in the species in the late 1970s prompted the British Columbian Forest Service and the Weyerhaeuser Company in Washington to carry out a seed collection in 1978, some of which were made available to the Forestry Commission in 1980. A series of six experiments was planted in Britain in 1985, testing material from 30 collection sites in 14 seed zones on sites in Scotland, Wales, and England. These experiments

Fig. 2. Map of Britain showing the locations of the experiment sites.



represent a unique opportunity to provide scientific information to guide future seed collections based the natural range of Pacific silver fir in the Pacific Northwest. This information is important as the planted area in Britain is so small and there are no registered seed stands. In addition, the experiments can be used to objectively re-evaluate the potential of *A. amabilis* in Britain. Hence the objectives of this study are to (*i*) examine the effect of seed zone on the survival, growth, and stem form of Pacific silver fir on a range of sites in Britain and (*ii*) re-evaluate the potential of Pacific silver fir based on previous published information and experience gained from the seed zone experiments.

Methods and materials

The objective stated in the experiment plan was "to study the pattern of variation among up to 33 seed origins of *A. amabilis*, so as to select those most suitable for wide-scale planting". The six sites were selected in Scotland, England, and Wales to represent a range of upland site conditions (Fig. 2; Table 1). When the experiments were established, material from 30 collection sites were available, and these were mainly from the central part of the native range of the species (Fig. 1; Table 2). Not all collections were planted at all sites; plots of 23 were planted at most sites (21 at Solway and 22 at Wykeham) with four replicate blocks at each site (3 at Solway).

The sites were planted in 1985 (Table 3). Each experiment was a randomised block design with collection site as the treatment. Each plot contained 16 trees (4 trees × 4 trees), planted at 2m × 2 m spacing (there were slight variations to this spacing at Achray and Solway, see Table 3). There was a two-row surround around the boundary of each experiment, and excess plants were used for this so that different seed collections were used at each site.

All the plants for these experiments were raised at the Forestry Commission nursery at Fleet in southwestern Scotland. They were planted out in the experiments as 4-year-old stock having been transplanted twice. Notes from the planting indicate that the quality of the planting stock was very good although the plants were small; records show a mean height of 20 cm.

All experiment sites were either situated in a large fenced research enclosure or were fenced against animals that had been identified as a risk of causing damage to newly planted trees. Competing vegetation was controlled using a combination of hand weeding and the application of herbicides. Dead trees were replaced with those of the same collection at all sites except Mynydd Du in April 1986; numbers of trees replaced were generally low (for numbers of trees replaced, see Supplementary Table S1[1]). Dead trees were also replaced in April 1987 at Moffat and Solway, but again, the number of trees replaced was low. Fertilizer was applied at Glenurquhart and Moffat in the early phase of establishment due to concerns about nutrition and the colour of foliage. Full details of establishment and other maintenance operations can be found in Supplementary Tables S1 and S2[1]. No thinning was carried out in any of the plots. Subsequently, each site was assessed in terms of the ecological site classification (ESC) of Pyatt et al. (2001) and Ray (2000).

Survival and height of all plants at each site were recorded at regular intervals during the establishment period and at the end of the sixth growing season (Supplementary Table S3[1]). In winter 2012–2013, 28 years after planting, all existing plots were reassessed. The number of trees per plot (survival), diameter at breast height (1.3 m) of all trees, and heights of the trees with the two largest diameters in each plot were measured (the mean of these was used as an estimate of top height). The form of each tree was also recorded using a simple scoring system: 1 = single, straight clear stem and leader ("potentially excellent timber tree"); 2 = single stem and leader but some kinks in main stem and (or) heavy branching ("potential timber tree"); and 3 = neither 1 nor 2 ("candidate to remove in early thinning"). All 2012–2013 measurements were carried out by the same assessor on five of the sites; however, at Mynydd Du, three assessors were involved in the assessment, but the main assessor validated this assessment.

Two approaches were used to give an indication of volume productivity. Firstly, the general yield class (GYC, the maximum mean annual increment in $m^3 \cdot ha^{-1} \cdot a^{-1}$) for each seed collection at each site was estimated from top height–age relationships for noble fir in Edwards and Christie (1981). The guidance of Matthews and Mackie (2006; table A7.1) was followed to select appropriate alternative species to estimate GYC; *A. procera* is recommended for all *Abies* species listed. For all plots where the estimated top height exceeded that for the maximum value of GYC for *A. procera* (22), values were recorded as GYC > 22.

Secondly, a volume index (VI) was calculated for a representative tree in each plot by using the following formula:

$$\mathrm{VI} = D^2H$$

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0303.

Table 1. Summary of the experiment sites.

	Experiment site					
	Achray	Glenurquhart	Moffat	Mynydd Du	Solway	Wykeham
Site factor						
Grid reference	NN 557 012	NH 415 290	NT 065 234	SO 274 256	NX 837 624	SE 945 865
Latitude, longitude	56.18°N, 4.33°W	57.32°N, 4.63°W	55.50°N, 3.48°W	51.92°N, 3.06°W	54.92°N, 3.82°W	54.27°N, 0.55°W
Elevation (m)	90–100	229–247	380–405	420	46	168
Aspect	SE	N	SE	W	WSW	SW
Rainfall ($mm \cdot a^{-1}$)	1200	1100	1400	1400	1200	800
Exposure	Moderate	Moderate	Very exposed	Moderate	Moderate sheltered	Moderate
Slope	12°	12°	5°	7°	5°	Flat
Geology	Lower old red sandstone (75)	Moine (8, 9, 10, 12)	Silurian greywacke (70–74)	Devonian old red sandstone (75)	Granite, syenite–intrusive (34)	Lower cretaceous grit (81)
Soil	Brown earth (1d)	Podzolisic brown earth (1z)	Peaty iron pan (4p)	Upland brown earth (1u)	Stony brown earth (1ds)	Brown earth (1d)
ESC parameters						
Suitability, Pacific silver fir GYC	Very suitable, 20	Marginal, 6	Suitable, 10	Suitable, 10	Marginal, 6	Suitable, 20
AT5	1309	1054	943	1082	1533	1380
CT	5.4	4.6	7.1	8.6	5.7	8.1
DAMS	**11.7**	11.2	14.9	**16.3**	12.6	**14.0**
MD	113	73	51	67	143	157
SNR	Medium	Poor	**Poor**	Poor	Poor	Medium
SMR	Fresh	**Slightly dry**	Fresh	Fresh	**Slightly dry**	Fresh
Sitka spruce GYC	22	16	16	18	22	20

Note: The exposure is as recorded in the experiment file. For geology, the figures in parentheses show lithology codes used in ecological site classification (ESC) analysis. The soil characteristics are according to Kennedy (2002). For the ESC parameters, see Pyatt et al. (2001) and Ray (2000): AT5, accumulated temperature above 5 °C; CT, continentality; DAMS, detailed aspect method of scoring, which is used in Britain as a method of estimated relative windiness of upland sites (Quine and White 1993, 1994); MD, moisture deficit; SNR, soil nutrient regime; SMR, soil moisture regime. General yield class (GYC) is a classification of the rate of growth in terms of potential maximum mean annual volume increment per hectare; the numbers in the table show ESC estimates for *Abies amabilis* (Pacific silver fir) and *Picea sitchensis* (Sitka spruce) at each site. Bolding indicates the main constraining factor according to ESC at each site.

where *D* is the quadratic mean diameter of the tree (m), and *H* is the mean height of two largest diameter trees per plot (m).

Statistical analysis

As early year assessments were compromised by the replacement of dead trees, it was decided to concentrate analysis on data collected at the end of year 6 and year 28. Because the number of trees replaced was so low (see Supplementary Table S1[1]), this was not taken into account in the analysis.

Given the unbalanced distribution of material from the 30 collections across sites, the response variables *H*, *D*, and VI were analysed by linear mixed models using the method of residual maximum likelihood (REML). Survival and form scores were analysed by generalised linear mixed models (GLMM), fitting a binomial error distribution and logit link function to the survival data and a multinomial error distribution and cumulative logit link function to the form data. In both GLMM models, the dispersion parameter was estimated as part of the model-fitting process.

The structure of the data for modelling was that there were six experiments (sites) each with four blocks (blocks), and the 30 collection sites (collection_sites) were treated as samples of the seed zones (seed_zones) within which they were located as described in Table 2. In each model, the effects of sites, seed zones, and their interaction were defined as fixed (constant + site + seed_zone + site.seed_zone). The random effects were blocks within sites and collection sites within seed zones (site.block + seed_zone.collection_site).

Linear regression was used to examine relationships between growth (year 28 height) and the latitude, longitude, and elevation of each seed collection.

All statistical analyses were undertaken using Genstat 13 (Payne et al. 2009).

Results

Establishment phase

Results at the end of year 6 show that survival was generally high, with all seed zones having > 90% survival, and there were no significant differences (Table 4). There was a significant difference in mean survival between sites ($p = 0.037$) (Table 5), and only Achray had < 90% survival. Across all sites, mean height was 142 cm after 6 years, indicating an annual height increment of 20 $cm \cdot a^{-1}$ as the initial height of planted trees was 20 cm (Table 4). There were no significant differences between seed zones for early height growth.

Final assessments at age 28

There were no significant differences between seed zones for survival or any of the measures of growth (*H*, *D*, and VI) or form score (Table 4). In general, survival was still high at 83%, probably attributable to the shade tolerance of the species in competitive situations. Mean height was 16.4 m, indicating a higher annual growth increment of 60 $cm \cdot a^{-1}$ compared with 20 $cm \cdot a^{-1}$ during the establishment phase. Diameter and VI ranged between 17.0 cm and 0.48 m^3 for seed zone 1070, respectively, and 21.4 cm and 0.77 m^3 for seed zone 221, respectively. Mean form score showed very little variation and ranged between 1.8 and 2.0, indicating that trees were of generally good form.

Results for the different experiment sites showed that there were very significant differences for *H*, *D*, and form score (Table 5), and sites ranked differently for these assessments. For example, Achray had the highest rank for *H* and *D* but the lowest form score, and Solway had a mid-rank *H* and *D* but the best form score. These results may partly have been influenced by initial spacing, which was higher at Achray and lower at Solway (Table 3), but this would mainly have affected *D*. However, in terms of GYC of the different collections, all were above GYC16, showing that *A. amabilis* has the potential to be a productive species in Britain

Table 2. Details of the seed collections present at each site.

ID code	Seed identification no.	Description of seed collection from experiment file	North American seed zone	Latitude (°N)	Longitude (°W)	Elevation (m)	Experiment site					
							Achray	Glenurquhart	Moffat	Mynydd Du	Solway	Wykeham
1	78(7116)500	Loup Creek, Gold River, Vancouver Island	1010	48.72	124.43	520	Y	Y	Y	Y	Y	Y
2	78(7117)4	Lord Creek, Mission	1050	49.33	122.25	450	Y	Y	Y	Y		Y
3	78(7974)501	Name not recorded	411	47.85	121.3	406		Y		Y		Y
4	78(7974)502	Name not recorded	411	47.85	121.3	600					Y	
5	78(7974)503	Name not recorded	412	47.36	121.2	620	Y	Y	Y	Y	Y	Y
6	78(7974)504	Name not recorded	412	47.36	121.2	760	Y	Y	Y	Y		
7	78(7975)500	Name not recorded	421	47.0	122.0	460	Y	Y	Y	Y	Y	Y
8	78(7975)501	Name not recorded	421	47.0	122.0	760	Y	Y	Y	Y	Y	Y
9	78(7975)502	Name not recorded	421	47.0	122.0	910					Y	
10	79(7114)500	Earlandson Creek, Skeena River	1140	54.58	128.72	225	Y	Y	Y	Y	Y	Y
11	79(7116)500	Loup Creek, south Vancouver Island	1010	48.72	124.43	560	Y	Y	Y	Y	Y	Y
12	79(7116)501	Naka Creek, north Vancouver Island	1020	49.32	126.46	375	Y	Y	Y	Y	Y	Y
13	79(7116)502	Qualicum River, east Vancouver Island	1020	49.5	124.83	1000	Y	Y	Y	Y		Y
14	79(7116)503	Woss Ridge, north Vancouver Island	1010	50.15	126.57	914		Y	Y	Y		Y
15	79(7116)504	Nootka Island, west Vancouver Island	1010	49.7	126.6	150	Y	Y	Y	Y	Y	Y
16	79(7116)505	Stewardson Inlet, west Vancouver Island	1010	49.38	126.25	825	Y	Y	Y	Y		Y
17	79(7116)506	Rupert Inlet (60), north Vancouver Island	1020	50.5	127.53	686	Y	Y	Y	Y		Y
18	79(7116)507	Rupert Inlet (80), north Vancouver Island	1020	50.47	127.83	686						Y
19	79(7116)508	Mahatta River, west Vancouver Island	1030	50.42	127.83	50	Y	Y	Y	Y	Y	Y
20	79(7117)4	Mission, Fraser River, mainland BC	1050	49.33	122.42	450				Y		Y
21	79(7117)500	Orford River, near Bute Inlet, mainland BC	1080	50.62	124.67	180	Y	Y	Y	Y	Y	Y
22	79(7117)501	East Norrish Creek, Lower Fraser River, mainland BC	1050	49.32	122.07	900	Y	Y	Y	Y	Y	Y
23	79(7117)502	Crawford Creek, Howe Sound, mainland BC	1050	49.7	122.9	1100	Y	Y	Y	Y	Y	Y
24	79(7118)500	Lizzie Creek, near Pemberton, mainland BC	1070	50.25	122.58	1380	Y	Y	Y	Y	Y	Y
25	79(7971)1	Forks, Olympics, Washington	012	48.08	124.33	305	Y	Y	Y	Y	Y	
26	79(7973)7	Bon Jon Pass, Sequim, Olympics, Washington	221	48.0	123.17	680	Y	Y	Y	Y	Y	Y
27	79(7974)4	Snoqualmie Falls, Cascades, Washington	412	47.5	121.42	910					Y	
28	79(7975)11	Voight Creek, Mowick, Cascades, Washington	421	47.0	122.15	835	Y				Y	
29	79(7975)3	Cispus River, near Randle, Cascades, Washington	430	46.33	121.83	835	Y		Y		Y	
30	79(7975)6	Mineral, near Ashford, Cascades, Washington	422	46.67	122.17	685	Y	Y	Y		Y	
Total no. of seed collections at each site							23	23	23	23	21	22

Note: The ID code is used only for clarity of presentation. For the seed identification number, see Forestry Commission (1965). For all instances of "name not recorded", only information on seed zone and altitude were available for these seed collections, and their locations are estimates based on the mid-point of the North American seed zone (see figure 24 in Fletcher and Samuel (2010)). "Y" means that the seed collection was planted at the site. BC, British Columbia.

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Table 3. Details of previous land use, establishment, and number of collections and blocks at each site.

Factor	Experiment site: Achray	Glenurquhart	Moffat	Mynydd Du	Solway	Wykeham
Previous land use	Mixed stand of European larch and Norway spruce planted in 1936 and felled in 1980	Pure stand of Sitka spruce planted in 1924 (GYC10) and felled in 1983	Rough hill grazing	Pure stand of Sitka spruce planted in 1950 and felled in 1984	Pure stand of Sitka spruce planted in 1930 and felled in 1981	Pure stand of larch planted in 1938 and felled in 1984
Planting date	April 1985	April 1985	April 1985	April 1985	April 1985	April 1985
Planting spacing	2.5 m between rows, 1.8 m within row, due to ploughing ridges	2 m × 2 m, on plough ridges	2 m × 2 m, just off the plough ridge	2 m × 2 m	1.7 m × 1.7 m due to space restrictions	2 m × 2 m
Vegetation before preplanting weed control	*Holcus mollis*, *Corydalis claviculata*, *Digitalis purpureum*, Sorrel, *Deschampsia flexuosa*, *D. caespitosa*, *Pteridium aquilinum*, *Cytisus*, *Rubus*, and *Calluna*	Almost no ground vegetation, occasional *Digitalis*, and small clumps of grasses.	*Calluna vulgaris*, *Molinia caerulea*, *Eriophorum vaginatum*, *Erica tetralix*, *D. flexuosa*, *Vaccinium myrtillus*, *Chamerion angustifolium*, and *Agrostis* sp.	Bare ground	*P. aquilinum*, *Rubus* spp., grasses, and seedling *Betula*	*P. aquilinum*, *Rubus* spp., grasses; hardwood coppice, mainly sycamore
No. of collections (and blocks)	23 (4)	23 (4)	23 (4)	23 (4)	21 (3)	22 (4)

Note: For planting date, details of site preparation treatment can be found in Supplementary Table S1. Authorities of the species follow Stace (1991).

(Table 5). Achray, Glenurquhart, and Solway were better sites, and a high proportion of collections were GYC > 22. This indicates very high productivity compared with other species, including Sitka spruce (*Picea sitchensis* (Bong.) Carrière); the likely productivity of Sitka spruce on these sites has been estimated using ESC in Table 1. The ESC-predicted mean GYC for each of the sites (see Table 1) is very different from the actual values measured and indicates that the ESC model for this species, which was developed on very little data for species such as *A. amabilis*, can be recalibrated now that objective data on growth on a range of sites have become available.

No significant interactions between site and seed zone were found for any of the seven measures considered in Table 4. This means that plants from the different seed zones did not vary in terms of their relative performance at each of the six experimental sites.

Results of the analysis between growth and latitude and between longitude and altitude failed to show any significant relationships.

Discussion

The two objectives of this paper were to (*i*) examine the effect of seed zone on the survival, growth, and stem form of Pacific silver fir on a range of different sites in Britain and (*ii*) re-evaluate the potential of Pacific silver fir based on previous published information and on experience gained from the seed zone experiments.

Seed zone

The decision to use seed zone as the primary factor in the data analysis was driven by the anticipated future need to identify the best areas for seed collections. The seed zones were delineated primarily on local evaluation of differences in environment, climate, and vegetation in 1966 and were intended initially for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) but were revised in 1973 for wider usage (Tree Seed Zone Map 1973; Johnson et al. 2004). The seed zone system is widely used in forest management in the Pacific Northwest to define areas in which seeds or plants can be transferred with minimal risk of maladaptation. Alternatives to this were considered, including using the major seed collecting regions of northwestern America shown in Forestry Commission (1965) and the individual collection locations. The use of either of these could have led to very different results, and some consideration concerning why they were not used is justified. The major seed collecting regions in Forestry Commission (1965) are large, heterogeneous areas and were judged to be less useful than the smaller, more homogenous seed zones for guiding future seed collections. Use of the actual locations of the seed collections was ruled out because there can sometimes be uncertainty about the precise locations of seed collections. In addition, precise locations may not be available for future collections because of access, ownership, or a wide range of other factors. Therefore, the decision to use seed zones in the analysis was based on the pragmatic need to inform future seed collections.

The main result from the study was that there were no significant differences in terms of survival and growth between the seed zones. In addition, the relative performance of planting material from different seed zones did not vary between the sites where they were planted, i.e., the seed zone × site interaction was not significant. One reason for this may be that most of the collections included in the study were from the middle latitudes of the species native range (Fig. 1), with 29 of the 30 seed collections coming from between 46°N and 50°N, with only one seed collection (from Earlandson Creek on the Skeena river) originating from a more northerly latitude, and it is notable that this performed well. However, it is perhaps not surprising that most of the seed collections came from this area, as this is where the species reaches its greatest development and commercial activity (Handley 1982; Grier et al. 1981). Wilson (2011) advises that provenances from coastal

Table 4. Summary results and analysis for seed zones.

	Region and seed zone															
	Olympics, Washington		Western Cascades, Washington					British Columbia mainland and Vancouver Island							Mean	Probability
Seed zone	012	221	411	412	421	422	430	1010	1020	1030	1050	1070	1080	1140		
Year 6																
Survival (%)	95	93	94	94	96	95	98	95	91	94	93	94	91	95	94	0.591
Height (cm)	159	149	130	143	147	166	147	150	146	139	143	136	127	159	142	0.415
Year 28																
Survival (%)	83	81	84	84	86	89	83	86	79	81	80	84	84	83	83	0.559
Height (cm)	16.7	16.6	16.0	16.3	16.7	16.4	15.8	16.9	16.6	16.7	16.3	15.7	16.3	16.7	16.4	0.372
Diameter (cm)	20.8	21.4	18.8	19.7	20.7	18.7	18.6	20.6	20.0	19.4	18.9	17.0	18.1	20.8	19.5	0.080
VI (m^3)	0.74	0.77	0.58	0.65	0.72	0.59	0.56	0.73	0.68	0.64	0.60	0.48	0.54	0.74	0.64	0.104
Form score	1.9	1.9	1.8	2.0	2.0	1.9	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.9	1.96	0.473

Note: The regions are as used in Fletcher and Samuel (2010), but they did not classify seed zones 221 and 1140 into the regions shown above. Probabilities for site × seed zone interaction were 0.169, 0.078, 0.362, 0.216, 0.512, 0.344, and 0.140, respectively; all are not significant. Height, diameter, and volume index (VI) were analyzed using REML; survival and form score were analyzed using GLMM, as described in Methods.

Table 5. Summary of results for experiment sites.

	Survival (%) year 6	Height (m) year 28	Diameter (cm) year 28	Form score year 28	No. of individual collections of each GYC				
					22	22	20	18	16
Site									
Achray	89	18.3	20.4	2.1	21	2			
Glenurquhart	94	17.5	18.8	2.0	20	3			
Moffat	97	14.4	17.4	2.1		3	7	9	4
Mynydd Du	95	15.5	19.5	1.8		11	8	4	
Solway	94	16.7	19.3	1.7	9	9	3		
Wykeham	94	15.8	20.7	2.1		10	12		
Mean	94	16.4	19.4	2.0					
Probability	0.037	<0.001	<0.001	0.020					
SED	1.52	0.394	0.498	0.062					

Note: Modelled means are presented with back-transformed means and standard error of the differences (SEDs) where appropriate. GYC, general yield class.

Washington State are likely to be best suited to Scottish conditions, but the evidence base for this recommendation is unclear. The results presented here indicate that the area for future possible seed collections is much wider and includes all the seed zones shown in Table 4, i.e., mainland British Columbia and Vancouver Island and the Olympic mountains and western Cascades of Washington.

Unfortunately, there is a dearth of information on provenance variation on Pacific silver fir when planted outside its native range; only one "grey literature" reference to some work in Germany has been traced (Hau 1991). However, within the natural range, some work has investigated provenance variation and genetic diversity of the species. For example, Worrall (1983) examined five provenances of *A. amabilis* planted at four sites covering an altitudinal range of 1330 m and demonstrated that those from higher altitudes had adapted to the shorter growing season. Work by Funck et al. (1990) examined two provenances from southern Vancouver Island and two provenances from the mainland (all four seed origins were from about 49°N) and found very few differences between them for leader growth, leader diameter, needle length, and internode length of 5-year-old trees. Any assumption from these studies of low provenance variation in the species is also supported by the work of Zavarin et al. (1973), Leadem (1986), Davidson et al. (1996), Davidson and El-Kassaby (1997), and El-Kassaby et al. (2003) and is a general conclusion from the review by Crawford and Oliver (1990).

In terms of interpreting the results of this study for forestry practice, the message is clear. First, so long as seed is collected from the seed zones included in this study (Table 4), it is likely that it will perform well when planted in upland Britain. Second, it is not necessary to recommend different seed zones for planting on the range of sites covered by this experiment, i.e., northern and western sites with predominantly mineral soil and rainfall greater than 800 mm·a^{-1}.

Silviculture

The main finding of this study is that *A. amabilis* is equally productive as many of the other conifers planted in Britain from the Pacific Northwest. Despite the generally high productivity, there were significant differences in growth between the sites, and it is interesting to relate this to the edaphic and climatic conditions and the known characteristics of the species. On three of the sites (Achray, Glenurquhart, and Solway), a large number of the collections tested had top height–age relationships that suggested that they were more productive than GYC22. However, in general, productivity was good on all sites, and the least productive site (Moffat) had no seed collections that were below GYC16, which is respectable and, with all else being equal, would mean that *A. amabilis* would be a serious species to consider in any plan to diversity forests where *A. amabilis* is capable of good growth. There are two sources of possible error in these findings. The first is that the plots were small, each one being just 16 trees, and productivity may change when the species is planted on a larger scale. The second is that Jenkins et al. (2012) recommend the use of *A. grandis* top height–age relationships for *A. amabilis*; this has been examined and generally would reduce the GYC by 2.

Five of the six experiment sites were on some form of brown earth, and it is noticeable that on the peaty iron pan at Moffat, there is a reduction in productivity. Moffat was the only site where soil nutrient regime was identified by the ESC analysis as the most

Table 6. Summary of silvicultural characteristics of *Abies amabilis* and the current state of knowledge in Britain.

Silvicultural characteristics of *A. amabilis* based on the review of the scientific literature by Crawford and Oliver (1990)	Knowledge of species in Britain
1. Grows in a maritime climate with mean daily temperatures ranging from 13 °C to 16 °C and winter temperatures seldom < −9 °C	These observations have led to the conclusion that it is a tree best suited to the maritime climate on the west coast of Britain and in the north. However, there are a number of observations on a wider range of sites, and its range in Britain should be further tested.
2. Sites have a great range of annual precipitation from 965 mm to 6650 mm, but the species is most abundant on sites where the regions characteristic summer drought is minimized by high rainfall, seepage, or prolonged snowmelt.	
3. Present on a very wide range of soils developed from every type of parent material found in northwestern America.	Good growth is clearly linked with mineral soils and the ability of the species to tolerate soils with high peat content would be a logical next step for research. Mason (2013; table 2) reported only moderate growth of *Abies amabilis* on two sites (Kielder and Shin) with high peat content.
4. Grows at a wide range of elevations from 0 m to 300 m in Alaska in the north of its range to 240–1830 m in the south of its range in the western Cascade Range of Washington.	The sites reported here range from 46 m to 405 m and, more importantly, up to a DAMS score of 16.3, which is probably near the upper limit for optimum productivity.
5. Seed production starts when trees are 20–30 years old and good seed years occur every 3 years. It is not considered a good seed producer and seed viability has often been reported to be < 50%.	The study did not address this.
6. Seedlings are very shade tolerant; seedlings 50–200 cm tall have been reported to be 65–110 years old.	The study did not address this.
7. Early height growth is slow and 9 or more years are required to reach breast height; when grown in the open, young trees are often overtopped by western hemlock, Douglas-fir, and noble fir (but situation with western hemlock is often reversed after 100 years). Advance regeneration can quickly adapt and take advantage of canopy opening.	The study has confirmed the slow early growth of the species but, once established, can achieve fast growth.
8. The species is a good volume producer in pure and mixed stands with western hemlock and figures of 20 $m^3 \cdot ha^{-1} \cdot a^{-1}$ have commonly been recorded; Hoyer and Herman (1989) have produced height–age curves to classify the site index for the species.	The experiment described here has confirmed that similar levels of productivity are possible on a wide range of sites in Britain. Mason et al. (1999) reports GYC 24 at Kilmun Forest Garden on the west coast of Scotland.
9. Pacific silver fir is one of the most shade-tolerant trees in the Pacific Northwest.	This is a useful characteristic and makes the species well suited to diversification of forests and its use in continuous cover forestry.
10. The seedlings more closely resemble a true taproot system compared with western red cedar, Sitka spruce, and western hemlock, but there is little information on its relative stability in later life.	The study did not address this.
11. The species is damaged by a several types of animal including elk (browsing), bears (bark stripping), grouse and rodents (clipping terminal buds), and squirrels (cones and cone buds).	The study did not address this, but it is known to be a problem with most true firs growing in Britain.
12. The species is affected by a wide variety of insects and pathogens including *Armillaria mellea*, *Heterobasidion annosum*, and the alien balsam woolly adelgid (*Adelges piceae*). Some reports that it is more susceptible to *H. annosum* than western hemlock, Douglas-fir or Sitka spruce.	The study did not address this, but the possible susceptibility to *H. annosum* is a concern and a contrast to *Abies alba*, which is considered quite resistant (Kerr et al. 2015).
13. "Its beauty and ability to withstand or respond to human impact make it a suitable species for multiple-use management."	Observation of the trials clearly indicates that the tree could fulfil a similar role in northern Britain.
14. "Despite its extensive range, Pacific silver fir is not a highly variable species." It does not hybridize with other true fir species.	This is one possible explanation for the results outlined in this study.
15. Produces strong timber that has a light colour and has low odour; it is used in a wide variety of uses including construction, flooring, sheathing, pulp, and plywood.	The timber has a specific gravity of 0.36, modulus of elasticity of 11.3, and modulus of rupture of 69 and could make C16 strength grade or much higher (Ramsay and Macdonald 2013)

Note: DAMS, detailed aspect method of scoring; GYC, general yield class.

likely constraining factor on growth. Crawford and Oliver (1990) make a clear link between the productivity of Pacific silver fir and adequate moisture, but unfortunately, the six sites used in this experiment have not fully tested the relationship between growth and moisture availability. For example, the driest site in terms of rainfall and moisture deficit was Wykeham, which was a productive site.

The form of trees in this experiment is worthy of further consideration. In general, the mean form score was 2.0 and is interpreted as a "potential timber tree". This suggests that the form of trees is similar to those of *A. alba* in the experiment described by Kerr et al. (2015), where form scores ranged between 1.96 and 2.25 for three sites. However, based on informal observations of both series of experiments, the form of Pacific silver fir is superior to that of European silver fir and is probably best explained by the strict interpretation of the form scores by the assessor.

There are two possible risk factors to the conclusion that the species is productive in Britain. The first factor is that the experiments only contained 16 tree plots and were designed to have a 15 year life. No thinning had taken place, and on some occasions, it was difficult to measure total tree height because stocking density was high (generally basal areas were > 50 $m^2 \cdot ha^{-1}$; Supplementary Table S4[1]). However, the height of each tree was measured from two sides to reduce the risk of measurement error to an acceptable level. The second factor is that GYC has been assessed using the top height–age curves for noble fir, but the relationship between height, age, and productivity may be quite different for Pacific silver fir. However, from a comparison with Hoyer and Herman (1989), this was considered to be a low risk. One significant finding from the study is that it clear from a comparison of the ESC-estimated values for GYC (Table 1) and the actual achieved values (Table 5) that a significant recalibration of the ESC model is required for Pacific silver fir.

An attempt has been made in Table 6 to compare the main silvicultural characteristics of Pacific silver fir from the review by Crawford and Oliver (1990) with the present state of knowledge about its silviculture in Britain, incorporating the results of the trials described here. In summary, the view of Lines (1979) that *A. amabilis* is a very promising species in Britain has been shown to be correct. Results from these experiments after 28 years clearly show that Pacific silver fir is a productive species. It could be deployed in British forests as a component to diversify species composition and in the wider use of continuous cover forestry, as it has a high degree of plasticity in physiological and morphological characteristics and can survive both in deep shade and in large canopy openings (King 1997). More work is justified to determine its susceptibility to Annosum root rot (*Heterobasidion annosum* (Fr.) Bref), an important fungal disease affecting many conifers, to confirm to what extent it can maintain productivity on sites with rainfall less than 800 $mm \cdot a^{-1}$ and with a high peat content, and provide more detail on its wood-quality characteristics.

Conclusions

1. Pacific silver fir is a productive species that could be used more widely to diversify forests in Britain as a plantation species and in the wider use of continuous cover management.
2. On six sites in England, Scotland, and Wales, the estimated yield of the collections planted varied between GYC 16 and GYC > 22 at age 28.
3. It should be planted on predominantly mineral soils, including peaty gleys, where moisture will not be limiting to growth and exposure is not extreme. Evidence from these experiments suggests that the detailed aspect method of scoring (DAMS) should be < 16, but the species may be able to maintain productivity above this.
4. There was little variation in performance between the 14 seed zones included in the experiments; therefore, future seed collections should be carried out within the geographical range of the zones, i.e., mainland British Columbia and Vancouver Island and the Olympic mountains and western Cascades of Washington.
5. There is no evidence from the experiments described to select material from different seed zones to suit climate and edaphic conditions.
6. More work is justified to determine its susceptibility to Annosum root rot, confirm to what extent it can maintain productivity on sites with rainfall less than 800 $mm \cdot a^{-1}$ and with a high peat content, and provide more detail on its wood-quality characteristics.

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