Variation among seed sources of silver birch in Scotland

R. WORRELL[1], E.P. CUNDALL[2], D.C. MALCOLM[1] AND R.A. ENNOS[1]

[1] School of Forestry, Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, Scotland
[2] Forest Research, Forestry Commission Northern Research Station, Roslin, Midlothian EH25 9SY, Scotland

Summary

The results of five provenance trials of silver birch (*Betula pendula* Roth.) in Scotland are described. These comprise: (1) two trials laid out in the 1970s and 1980s comparing improved Finnish stock with unimproved Scottish material, and (2) three recently established provenance trails of Scottish seed sources for which 1–2 year results are available. Use of planting stock of Scandinavian origin is not advisable in Scotland, or probably elsewhere in the UK, as it has poor survival and grows slowly (i.e. volume growth at years 16–22 is only 7–26 per cent of the Scottish controls). It is particularly prone to climatic damage due to late spring frosts. Recently established trials of seed sources from Scotland and Northern England showed significant variation among Scottish populations in growth and dates of flushing and senescence. Variation in 1-year height growth between the fastest and slowest growing provenances was about 30 per cent. Some geographic patterns of variation in early height growth and flushing were apparent among different seed sources at year 1, but equally there was considerable variation among sources which could not be simply attributed to location. A preliminary study of isozyme variation suggests that: populations are unlikely to have passed through severe population bottlenecks; that there is no consistent evidence for inbreeding within the populations; extensive gene exchange occurs between populations by pollen and/or seed flow; and there is no evidence for more than one postglacial origin for the nine populations tested. There is a need for more information on provenance performance among indigenous populations of birch in order to give useful guidance to nurseries, foresters and policy makers.

Introduction

Management of broadleaved trees has become increasingly important during recent years and broadleaves now constitute about 60 per cent of all forest planting in the UK. Silver birch (*Betula pendula* Roth.) is a widely planted species, particularly in upland areas, and is recognized as a species with timber production potential (Lorrain-Smith and Worrell, 1991; Cameron *et al*., 1995; Cameron, 1996; Worrell, 1999). In recent decades there has been widespread planting of continental origin broadleaved stock, including birch, and only in the last few years have indigenous sources become more widely available. This raises the question of the relative merits of different seed sources, both indigenous and foreign, for the production of planting stock.

Since about 1970, a small number of trials have been established in Scotland to test the performance of different origins of planting stock of silver birch. There have been three types of trial, namely:

1 *Scandinavian plus trees*. During the 1970s and early 1980s experiments were laid out to assess the suitability of improved Scandinavian planting stock using unselected Scottish material as controls.
2 *British and other plus trees*. During the late 1970s and 1980s a pilot tree breeding project based at Aberdeen University led to the establishment of progeny trials investigating the heritability of form and growth of selected individual trees from a range of sources, mainly from the north-east Scotland, but including some selections from England and Europe (Blackburn and Brown, 1988; Richardson, 1992).
3 *Provenance trials of Scottish seed sources*. Beginning in 1995 a series of provenance trials has been established to assess seed source variation among Scottish birch populations.

These trials do not represent a coherent research programme, but are the result of sporadic interest by a number of research institutions. Rook and Fletcher (1991) comment that the research effort has been 'fragmented, with very diverse aims, has lacked depth of effort in any one area and suffered from inadequate long term funding'. The trials represent a sequence where foresters wishing to plant silver birch looked first to material already available from foreign breeding programmes and only later began to consider British indigenous populations. The recent series of provenance trials of Scottish origin material, which might logically have been a first step, belatedly recognizes the importance of understanding variation among indigenous seed sources.

Previous accounts of some of these trials have shown that trees of Scandinavian origin, including improved stock from Finland, grow more slowly than Scottish birch, typically showing 3–10 year mean heights about 80 per cent of that of Scottish origin stock. The survival of the Scandinavian material is also about 80 per cent of that of the Scottish controls, though form is often better than that of the Scottish trees (Worrell, 1992; Samuel, 1996). Lines and Brown (1982) noted that foreign origin trees planted in north-east Scotland were more susceptible to early and late frosts and winter dieback of the crowns than indigenous seed sources. The few progeny trials of *B. pendula* and *B. pubescens* Ehrh. have demonstrated that there is significant variation in height, diameter and form among the progeny of selected individual trees at years 2–3 (Blackburn and Brown, 1988).

Studies on the genetic variation in silver birch in other northern countries have shown considerable variation between origins within a country. In Sweden this was closely related to latitude of origin and seed transfer rules have been developed based on this information (e.g. Eriksson and Johnsson, 1986; Rosvall *et al*., 1998; see also Ennos *et al*., 1998). However, in studies in south-east Norway, geographic patterns were less clear and considerable transfer of planting stock appeared to be possible, especially longitudinally, before maladaptation occurred (Langhammer, 1982). Currently there is no information on any geographic patterns of genetic variation in growth characteristics in silver birch populations in Britain. However there is some evidence of clinal variation in morphological characteristics, such as leaf size, of *B. pubescens* across Britain (Pelham *et al*., 1988).

The two older birch provenance trials in Scotland have now been assessed at ages 16 and 22 years, respectively, and the first assessments of the new series of provenance trials of British seed sources have been carried out (at age 1 year). In addition, a preliminary study on isozyme variation in Scottish silver birch populations, using material from the new series of trials, has been carried out.

The aims of this paper are therefore to:

- draw together information from all these trials and provide an updated account of the performance of different seed sources of silver birch, both domestic and foreign;
- provide some very preliminary information on patterns of adaptive genetic variation in British birch populations;
- provide a summary of patterns of variation at four isozyme loci in some Scottish birch populations. Such studies of selectively neutral variation provide insights into the postglacial origins of these populations and the extent of gene flow among populations.

Methods

Trial sites

Details of the types of trial and their locations are given in Table 1. The trials are mainly located in north-eastern Scotland which is the main area in the UK where silver birch is a major forest tree species.

The trials of Scandinavian material at Speymouth and Teindland (Morayshire) are only about 7 km apart, but on strongly contrasting sites. Speymouth 33 is on a hilltop fully exposed to the sea to the north and east and on a poor iron-pan soil with *Calluna vulgaris* heath as the dominant vegetation type. Teindland 113 is at 110 m elevation on a relatively sheltered site with a brown earth soil and the site was formerly used for arable agriculture. Dunkeld 21 (Perthshire) is a relatively testing site for *B. pendula*, being fairly high elevation (280 m) with a gleyed, stony soil and in an elevation zone known to be prone to snow damage. Moray 64 (Morayshire) is adjacent to Teindland 113 and is on a similar site. The University of Edinburgh trial is located in the university grounds and is therefore not strictly representative of forest sites in Scotland.

Planting stock type and origin

Speymouth 33 and Teindland 113

At Speymouth 33 and Teindland 113 improved Finnish material from breeding programmes was used, which comprised progeny from polycrosses between individual mother plus trees fertilized by mixed pollen from a number of plus trees. The Scottish controls were unselected material taken from individual woods and no information is available on how these were chosen or the exact locations of the parent trees. Whilst it is likely that they are from autochthonous populations, this cannot be established with certainty. Details of the Finnish crosses and the Scottish controls are given in Appendix 1.

Dunkeld 21 and Moray 64

The new series of provenance trials at Dunkeld 21 and Moray 64 included 36 seed sources of *B. pendula* from Scotland and northern England, together with one lot derived from a clonal seed orchard of plus trees (with origins around the Great Glen area in Inverness-shire). In addition, at Moray 64 one further lot of 'improved birch', obtained commercially under the name 'Elite

Table 1: Details of seed source trials of silver birch in Scotland

Name of trial	Trial type	Planting year	Location: Region	Lat. (°N)	Long. (°W)	Site type: Elevation (m)	Rainfall (mm a^{-1})	Soil type
Speymouth 33	Trial of Scandinavian plus tree progeny with unselected Scottish control	1975	Moray	57 40	3 05	175	830	Iron-pan soil
Teindland 113	Trial of Scandinavian plus tree progeny with unselected Scottish control	1983	Moray	57 40	3 12	110	820	Brown earth
Dunkeld 21	Provenance trial of 37 seed lots from Scotland and northern England	1997	Tayside	56 35	3 40	280	1200	Gleyed upland brown earth (stony)
Moray 64	Provenance trial of 38 seed lots from Scotland and northern England	1998	Moray	57 40	3 12	110	820	Brown earth
University of Edinburgh trial	Provenance trial of 8 Scottish and 1 Norwegian seed lot	1995	Midlothian	55 55	3 10	70	750	Loamy brown earth

birch' from Christie-Elite Nurseries, Forres, was included, which is derived from selected material from Scotland, England and Germany (three plots in each replicate at Moray 64 consisted of this planting stock). Two seed sources at Moray 64 (Glen Spean and Blaraidh, Glen Moriston) showed low survival, which may have been due to planting problems, and these have been excluded from the analysis of that experiment.

In both experiments several sources of *B. pubescens* were included, though these are not considered in this paper. Several of the *B. pendula* seed sources also included a small proportion of *B. pubescens* plants as a result of difficulties on the part of seed collectors in accurately telling the two species apart in the field. Five seedlots appeared to have considerable contamination (20–40 per cent *B. pubescens),* but these lots have been included in the 1-year analysis pending more certain identification to species as they get older.

The locations of the seed sources are shown in Figure 1 and a list of seed sources is provided in Appendix 2. It is highly unlikely that all these populations are autochthonous and at present there is no means of distinguishing which are of natural origin and which are of planted origin. Those from the central and eastern Highland region are most likely to be autochthonous, whereas those from the western Highlands, southern Scotland and northern England are most likely to have been planted in the past (Worrell and Malcolm, 1998).

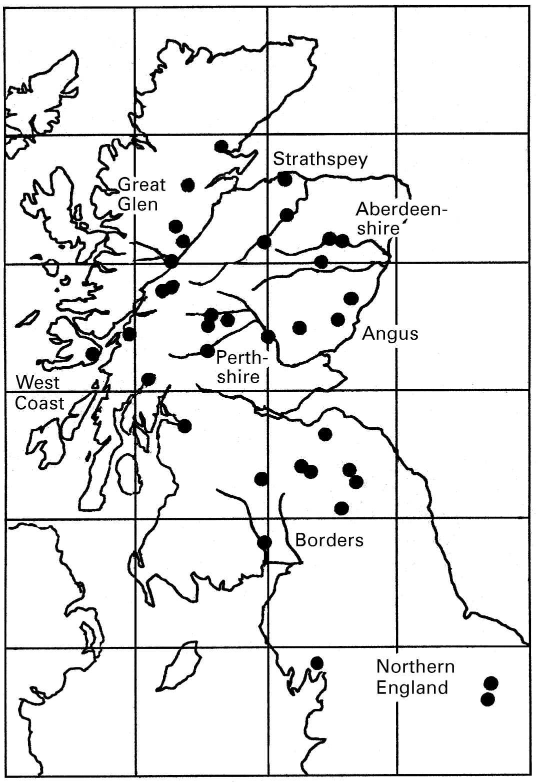

Figure 1. The locations of the seed sources of *B. pendula* included in the provenance trials at Dunkeld 21 and Moray 64.

The University of Edinburgh provenance trial

This comprises nine seed sources from several commercial nurseries (only two of these, Newtyle Hill, Perthshire, and Loch Creran, Argyll, were the same as those in the Dunkeld 21 and Moray 64 trials). Eight of the sources were Scottish and one Norwegian, and the stock were of diverse sizes and types. The trial was established mainly with a view to developing assessment techniques, but nevertheless yielded some useful data on early patterns of flushing and senescence. Details of the seed sources are provided in Appendix 3 and the same caveats about their autochthonous status apply.

Experimental design and assessment

All the trials were complete randomized block designs, with two to four replicates (see Appendix 1 for details). The variables assessed and the ages of the assessments reported in this paper are given in Table 2. Numerical scales used for assessing flushing and senescence were as follows.

- *Flushing stage*. Visual assessments of the progress of bud flushing were made using the following scale:
  1 = bud not swollen and still closed; 2 = bud swollen but still closed; 3 = bud opening; 4 = leaf starting to extend, but still bent back and wrinkled; 5 = leaf open but not full size; 6 = leaf fully open and full size.
- *Senescence stage*. Two variables were assessed on the top five leaves of the leading shoot: (1) number of leaves dropped (0–5); and (2) the percentage of the area of the leaves which were no longer green, i.e. yellow, brown or dropped

(scale from 0–100 per cent, estimated to the nearest 10 per cent).

The assessments of flushing and senescence were done during the spring and autumn (see Table 3 for dates).

Isozyme studies

Isozyme variation was studied in nine of the Scottish populations of *B. pendula* included in Dunkeld 21, chosen to represent the geographic range of the species in Scotland (i.e. Whitebridge, Glengarry; Tomich, Glen Affric; Baitlaws, Lamington; Cruach Ardura, Mull; Dall Mill, Black Wood of Rannoch; Glen Feshie, Kincraig; Delnapot, near Elgin; Birkhill, Alford; Pannanich Wood, Ballater – see Appendix 2 for details of locations). Subsequent tests showed two of these sources, Glen Feshie and Pannanich Wood, to have a considerable proportion of *B. pubescens* among the plants. Freshly expanded leaves were sampled from approximately 48 individuals from each population (range 40–58). Leaves were crushed over ice in extraction buffer, extracts were absorbed onto filter paper wicks, run on 11 per cent starch gels for 5 h at 60 mA, and stained for the enzymes leucine amino peptidase (LAP),

Table 2: Variables assessed and ages of assessment

Name of trial	Variables assessed	Units	Age of assessment (year)
Speymouth 33	Mean height	m	22
	Survival	%	
Teindland 113	Mean height	m	16
	Survival	%	
	Stem lesions	numbers > 4 cm long	
Dunkeld 21	Mean height	m	1
	Survival	%	
	Flushing stage	scale 1 (bud shut) to 5 (leaf open)	
Moray 64	Mean height	m	1
	Survival	%	
	Flushing stage	scale 1 (bud shut) to 5 (leaf open)	
University of Edinburgh trial	Mean height	m	1 and 2
	Survival	(%)	
	Flushing stage	1 (bud shut) to 6 (leaf fully open)	
	Senescence stage	% of leaves no longer green; no. of leaves out of top 5 dropped	

Table 3: Dates of assessments of flushing and senescence

University of Edinburgh trial		
Flushing	1995	8 and 28 April, 4 May
	1996	23 and 30 April, 8 May
Senescence	1995	3 and 20 October, 6 November
	1996	9 and 23 October, 12 November
Dunkeld 21		
Flushing	1998	22 March (an assessment of a subset of 17 of the seed sources by Donelly (1998))
Moray 64		
Flushing	1999	20 March (an assessment of a subsample of six trees per plot for all seed sources by Armstrong (1999))

phosphoglucomutase (PGM) and aspartate aminotransferase (AAT). For details of buffer systems see Brown (1999). Variation was scored at four polymorphic isozyme loci: LAP1, LAP2, PGM and AAT.

Analysis

For Speymouth 33 and Teindland 113, differences between the Finnish and Scottish seed sources in height growth, diameter growth and survival were analysed using ANOVA (Minitab). Survival data were transformed to arcsine values. At Teindland 113 differences in the presence of stem lesions were also analysed.

For Dunkeld 21 and Moray 64, differences among Scottish seed sources in height were analysed using ANOVA (Forestry Commission statistical package) and relationships between measures of growth and flushing stage and latitude and longitude of origin were determined by regression analysis (Minitab).

For the University of Edinburgh trial, differences among seed sources in flushing and senescence stage were analysed using ANOVA (Excel 5 General Linear Model). Data for senescence which were expressed as percentages were transformed to arcsine values. Height values were not included in the data because the wide variation in initial plant sizes masked any apparent differences in seasonal growth.

Isozyme study

Data analysis was carried out using POPGENE (Version 1.21). Diversity in each population was measured as percentage polymorphic loci (P) and gene diversity (H_e), and mean F_{is} over loci was calculated for each population to determine the level of inbreeding within populations. The extent of isozyme differentiation among populations was measured by calculating the value of G_{st}.

Results

Performance of Scandinavian material

The average height growth of the Finnish progenies was 74 and 83 per cent of that of the Scottish controls at Speymouth and Teindland, respectively, and the corresponding figures for diameter were 49 and 72 per cent (see Tables 4 and 5). The most striking contrast was in survival; the Finnish material showing levels of only 38 per cent (at Speymouth) and 61 per cent (at Teindland) of those of the Scottish controls. The volume production of the Finnish plots was only about 7 per cent of that of the Scottish material at Speymouth 33 and 26 per cent at Teindland 113. The Norwegian material (at Speymouth 33) appears to perform equally poorly, with height and diameter being 64 and 49 per cent, respectively, of the Scottish controls and survival being about half that of the Scottish material (plot volumes 8 per cent of the Scottish controls). This is a clear case of maladaptation of Scandinavian material to site conditions in this part of Scotland, even on the sheltered low elevation site at Teindland.

At Teindland 113 the two Scottish controls also differed considerably in performance, with one (Tummel) growing only marginally better than the average of the Finnish material in terms of

Table 4: Performance of Finnish, Norwegian and Scottish *B. pendula* at age 22 in experiment Speymouth 33

	Mean height		Diameter at 1.3 m		Survival	
Seed source	m	(% of Scottish control)	cm	(% of Scottish control)	%	(% of Scottish control)
Mean of Finnish progenies	6.2	(74)	5.2	(49)	36	(38)
Tangen, Stange, Norway	5.4	(64)	5.1	(49)	50	(53)
Banchory, Scotland	8.4		10.4		94	

The Finnish stock was progeny of plus trees in a breeding programme; the Norwegian and Scottish material was from unselected sources.

Table 5: Performance of Finnish and Scottish *B. pendula* at age 16 in experiment Teindland 113

Seed source	Mean height		Diameter at 1.3 m		Survival		Mean no. of stem lesions in lower 2 m of stem
	m	(% of Scottish controls)	cm	(% of Scottish controls)	%	(% of Scottish control)	
Mean of Finnish progenies	7.8	(83)	6.8	(72)	59	(61)	1.49
Tummel, Scotland	7.9		8.0		94		0.2
Glen Prosen, Angus, Scotland	10.7		10.9		100		0.1

The Finnish stock was progeny of plus trees in a breeding programme and Scottish material was from unselected sources. The values for the Finnish sources of percentage growth, survival and presence of stem lesions use the average of the two Scottish controls for comparison

height, though its diameter and survival were better than the Scandinavian material (see Table 5). There was also some variation among the Finnish progenies with one (seed source 8) performing relatively well. This had survival, height and diameter of 87, 97 and 85 per cent of the mean of the Scottish material, respectively (Armstrong, 1999).

At Teindland 113 a high proportion of the Finnish material had stem lesions (average 1.5 lesions over 4 cm long per tree in the lower 2 m of stem), with necrotic bark around them. The Scottish material was virtually unaffected (average 0.15 lesions per tree). The crowns of the Finnish material also showed considerable thinning, with a high proportion of dead twigs, particularly on the slower growing origins. These symptoms are interpreted as the result of late spring frost damage (D. Redfern, personal communication).

Variation among British seed sources

Growth and survival

There was significant variation in height growth at year 1 among seed sources from northern Britain at both Dunkeld 21 and Moray 64 (at Dunkeld $F_{2,36} = 2.29$, $P < 0.01$; at Moray $F_{2,37} = 2.95$, $P < 0.001$; see Table 6). The fastest growing seed sources at Dunkeld 21 and Moray 64 grew at 113 and 116 per cent of the experiment mean and the slowest growing at 89 and 80 per cent, respectively. The sources achieving high rankings (< 10) for growth rate in both experiments were: Killin (Perthshire), Montreathmont (Angus), Dunalastair (Perthshire), Locharbriggs (Borders), Castle Howard (N. England) and Sand Hutton (N. England). Those showing poor rankings (≥ 25) were: Leanachan (Inverness-shire), Birkhill (Aberdeenshire), Dall Mill (Perthshire), Achnatra (Argyll) and Cruach Ardura (Argyll).

The seed sources were allocated to geographic groups, and taken across the two experiments, southern groups (i.e. N. England, Borders and Angus) appeared to show faster growth than more northerly and easterly ones (i.e. Great Glen and Aberdeenshire) (see Table 6). The ranking of these groups was generally similar for both trials. This trend was confirmed by regression analysis at Moray 64, where a relationship was apparent between height at year 1 and location of origin, with southern and western origins being taller than northern and eastern ones:

$$\text{Height (cm)} = 146.0 - 1.81 \text{ latitude } (°\text{N}) + 1.21 \text{ longitude } (°\text{W})$$

($F_{2,31} = 8.80$, $P \geq 0.001$ (Armstrong, 1999)).

However, it is clear from Table 6 that there is considerable variation among sources within regions which cannot be attributed simply to location. Whilst there is some correspondence between the ranking of the sources between the two experiments, a considerable proportion have quite different rankings, suggesting that genotype × environment interactions were present. More detailed analysis of geographic variation at this early age was not considered worthwhile and is planned when the trials reach 3 years of age.

The material from crosses between plus trees in the Great Glen area showed only slightly higher growth rates than the experiment mean at Dunkeld 21 (103 per cent of experiment mean)

Table 6: Heights of seed sources and ranking in eight geographic groups at trials Dunkeld 21 and Moray 64

Seed source	Dunkeld Height (cm)	Dunkeld Rank (*group rank*)	Moray 64 Height (cm)	Moray 64 Rank (*group rank*)
Great Glen				
Leanachan	34.7	28	42.1	31
Glen Spean	30.3	–	–	–
White Bridge	36.1	22	46.5	24
Blaraidh, Glen Moriston	37.1	–	–	–
Tomich	38.3	12	45.2	26=
Strathgarve	35.3	24=	47.2	20
Kyloag	35.3	24=	48.1	15
Mean	**35.3**	(*8*)	**45.8**	(*7*)
Strathspey				
Straanruie	36.4	21	50.8	9=
Delnapot	38.6	11	48.6	14
Spindlemuir	39.4	5	42.8	29
Mean	**38.1**	(*3*)	**47.4**	(*5*)
Aberdeenshire				
Muir of Dinnet	37.9	16	39.4	34
Birkhill, Alford	34.5	29=	42.7	30
Invermossat	34.5	29=	47.4	19
Mean	**35.6**	(*7*)	**43.2**	(*8*)
Angus				
Montreathmont	40.4	3	52.1	6
Silvie, Alyth	37.3	17	49.0	13
Ingilsmaldie	38.0	15	46.7	22
Mean	**38.6**	(*1*)	**49.3**	(*3*)
Perthshire				
Dunalastair	38.8	8=	51.2	8
Dall Mill, Rannoch	35.0	26	40.7	33
Newtyle Hill, Dunkeld	32.9	34	46.8	21
Craiganour, Rannoch	38.2	13=	48.0	16=
Killin	41.9	1	53.0	5
Mean	**37.4**	(*4*)	**47.9**	(*4*)
West Coast				
Langbank	35.9	23	49.9	11
Achnatra	33.2	33	45.4	25
Creagan, Loch Crearan	41.2	2	45.2	26=
Cruach Ardura, Mull	34.8	27	43.8	28
Mean	**36.3**	(*6*)	**46.1**	(*6*)
Borders				
Glentress	39.0	7	41.2	32
Floors, Kelso	38.2	13=	54.9	4
Mellerstain, Kelso	33.9	32	49.7	12
Petersmuir	38.8	10	48.0	16=
Baitlaws	37.2	18	46.6	23
Wauchope	34.0	31	47.8	18
Locharbriggs	39.8	4	51.5	7
Elibank	36.7	20	56.6	2
Mean	**37.2**	(*5*)	**49.5**	(*2*)

Table 6: Continued

Seed source	Dunkeld Height (cm)	Dunkeld Rank (*group rank*)	Moray 64 Height (cm)	Moray 64 Rank (*group rank*)
N. England				
Finsthwaite	36.9	19	56.9	1
Castle Howard	38.8	8=	50.8	9=
Sand Hutton	39.3	6	56.2	3
Mean	**38.3**	(*2*)	**54.6**	(*1*)
Mean of all seed sources	**37.1**		**49.0**	
FC selected crosses from Great Glen	38.1		45.8	
'Elite birch' (mixed origin)	–		55.4*	

* Mean of three entries.

and showed lower growth rates at Moray 64 (93 per cent of experiment mean). This relatively poor growth is presumably a reflection of the slower growth of sources from the Great Glen area (the Great Glen group was ranked 7 and 8 for height growth in the trials). The 'Elite birch' grew faster than the experiment mean at Moray 64 (113 per cent of experiment mean) and only three of the sources at this trial exceeded it in height growth.

There was no significant variation in survival at Dunkeld 21 or Moray 64 and survival rates were generally very high (around 95 per cent) despite severe spring frost episodes at Dunkeld in 1997 and 1998.

The mean rates of annual height growth for the Scottish material over the lifespan of the two older trials at Speymouth 33 and Teindland 113 were 38 cm and 58 cm respectively; with the best origin (Banchory) growing at 67 cm a^{-1} at Teindland. These values probably represent the expected range of growth rates for unselected stock in this part of northern Scotland.

Phenology

There was significant variation among seed sources in flushing stage at the beginning of the second growing season at Dunkeld 21 and Moray 64 (Donelly, 1998; Armstrong, 1999). At Dunkeld, flushing stage was related to location of origin, with southern origins flushing earlier than northern ones (see Figure 2).

At the University of Edinburgh garden trial, significant variation among the seed sources in flushing and senescence was recorded on most, but not all, assessment dates during both years 1 and 2. The 2-year data were regarded as more reliable than the 1-year data because in 1995 (1) the plants had only been planted some 4 months prior to flushing and before that had experienced different conditions in the different source nurseries, which may have affected flushing; and (2) summer 1995 was exceptionally hot and dry and leaf-fall in 1995 was clearly affected by drought. The analyses of year 2 data demonstrated the following.

- Significant differences for flushing were found among Scottish seed sources on 23 April and 8 May ($F_{2,7}$ = 3.4, P = 0.024; $F_{2,7}$ = 3.3, P = 0.027) but not on 30 April ($F_{2,7}$ = 1.54, P = 0.23). Clear differences in senescence were found on both 23 October and 12 November ($F_{2,7}$ = 67.3, $P \geq 0.000$; $F_{2,7}$ = 24.3, $P \geq 0.000$, respectively). Differences were greater for time of senescence than for flushing; the progress of senescence between the earliest and latest seed sources averaged about 9 days, whereas for flushing this was 4–5 days.
- Early flushing Scottish seed sources tended also to senesce earliest in autumn and vice versa. The average growing season length was 181 days, with only a 7 per cent variation between the seed sources with the longest (187 days) and shortest (175 days) growing seasons (defined as the period between trees achieving

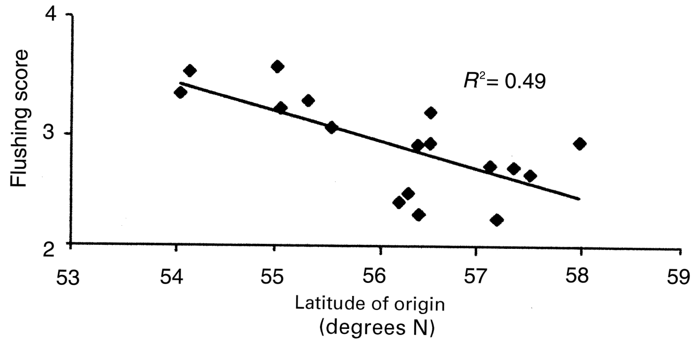

Figure 2. The relationship between flushing score and latitude of origin for 17 provenances at Dunkeld 21 scored in March 1998 (2 = late flushing, bud swollen but still closed; 4 = advanced flushing, leaf extended but not fully open).

a flushing score of 5 in spring and having lost ≥ 50 per cent of their green foliage in autumn). Flushing dates in 1996 varied for the different origins from 7–12 April and senescence dates ranged from 4 to 12 November.

- The Norwegian control was clearly different from all Scottish seed sources in growth rhythm, flushing some 15 days earlier and senescing some 16 days earlier than the average for the Scottish seed sources.
- There were no apparent geographic patterns in flushing. The seed sources showing earliest senescence appear to be those from the north west coast (Cluanie and Loch Creran) and from higher elevations (Blackmount and Glenlivet) compared with eastern and southern seed sources; for example the senescence scores (i.e. percentage of leaf area *not* green) for 12 November 1996 for these geographic groups were 64.5, 57.4 and 53.2, respectively. However, the trial has too few seed sources to be able to test adequately for geographic patterns.
- No significant differences were recorded in the numbers of leaves lost on the leading shoot during senescence and this is therefore not a good measure of the progress of senescence.

Isozyme studies

The four isozyme loci scored were polymorphic in most of the populations and the overall level of gene diversity within populations (H_e = 0.224) is similar to that found in other tree species with outcrossing breeding systems (Brown, 1999). Measures of diversity should be treated with caution since only four isozyme loci were used in their calculation. A significant excess of heterozygotes in comparison with random mating expectations was found in three populations, and a significant deficit of heterozygotes in two populations. However the mean value of F_{is} for all populations was very close to zero, suggesting no consistent, significant level of inbreeding within these *B. pendula* populations. The mean estimate of G_{st} over loci was 0.062, indicating that only 6 per cent of isozyme variation in Scottish *B. pendula* was found among populations (see Tables 7 and 8).

Discussion

These early results for the performance of different seed sources raise three questions which are critical for forest practice in Britain, namely:

- Are foreign sources acceptable as seed sources in the UK?
- Is it possible to identify particularly promising seed sources and how far may they be transferred before there is evidence of maladaptation?
- Do studies of genetic markers reveal aspects of the postglacial history of the species which need to be taken into account in choice of seed source or other aspects of genetic conservation?

Table 7: Summary of isozyme variation (% P, % polymorphic loci; H_e, gene diversity) and inbreeding (F_{is}) in nine Scottish populations of *B. pendula*

Population	n	% P	H_e	F_{is}
Glengarry	47	100	0.241	–0.154
Affric	58	75	0.194	–0.245
Lamington	40	75	0.234	–0.006
Mull	54	100	0.165	+0.058
Black Wood of Rannoch	45	50	0.219	+0.344
Glen Feshie	46	100	0.235	–0.102
Delnapot	49	100	0.299	–0.108
Alford	56	100	0.227	–0.222
Ballater	40	75	0.201	–0.005
Mean	48.3	86.1	0.224	–0.049

n = sample size.

Table 8: Proportion of gene diversity detected among populations (G_{st}) for Scottish *B. pendula*

Locus	G_{st}
LAP1	0.044
LAP2	0.059
PGI	0.042
AAT	0.101
Mean	0.062

Data are given for four individual isozyme loci, and the mean value over loci

Scandinavian sources

This study provides good evidence that the use of Scandinavian planting stock is not advisable in Scotland or probably elsewhere in the UK. In the two provenance trials described in this paper, the plots of improved Scandinavian birch only attained average volume production of between 7 and 26 per cent of that of unselected Scottish sources and were susceptible to climatic damage. Their performance had worsened since the assessment at age 10 reported by Worrell (1992) and Samuel (1996), suggesting that they had experienced continuing problems of maladaptation. The reason for the poor performance of the Scandinavian stock appears to be spring frost damage as a result of dehardening occurring too early during mild periods in late winter (D. Redfern, personal communication). Many of the Scandinavian trees had developed stem lesions suggesting death of the cambium, and thinning of the crowns was evident. Similar climatic damage has been reported for *Betula* in other north temperate regions following exceptionally warm periods in late winter (Braathe, 1957). Climatic damage on British *B. pendula* was also reported by Blackburn and Brown (1988), who attributed this to spring frosts and excessive cold and desiccation in a period of cold weather in late winter. There is some evidence that the poor performance of Scandinavian material in Scotland is mirrored when Scottish material is planted in Scandinavia; a Scottish seed source showed particularly low survival in a trial at Ås in south-east Norway (Langhammer, 1982). Thus the contrast in environments between Scotland and Scandinavia appears to be simply too great for *B. pendula* to cope with.

The particularly poor performance of the Finnish material on the exposed infertile site at Speymouth, as opposed to Teindland, suggests that maladaptation is worse on poor upland sites than on lowland ones. The variability in performance among the Finnish progenies at Teindland is interesting, as it suggests some variation in adaptability among the Finnish mother trees. However, it does not detract from the conclusion that use of Finnish origin planting stock is unacceptable. The results of these trials should dissuade any further attempts to cut short the improvement process for birch by importing improved foreign planting stock.

Variation among Scottish sources

There is clearly considerable variation among Scottish populations in growth and phenology.

This suggests that it is worthwhile to attempt to identify specific sources most suitable for planting, and that selection and breeding within the best populations could result in significant gains in volume production and quality. The scale of the differences in 1-year height growth between the fastest and slowest growing seed sources (from about 85 to 115 per cent of the experimental mean) is similar to that reported from regional scale trials of *B. pendula* in Norway (Langhammer, 1982).

There is some evidence of geographic patterns among the seed sources, especially at Moray 64, where southern and western sources initially appear to be relatively fast growing. This confirms the well-established pattern that northwards transfer of planting stock tends to lead to faster growth. However, there is considerable variation among sources within regions and the simplistic view that local sources inevitably perform better than sources from other regions of Scotland is not substantiated by these preliminary growth data. Part of this variation may be attributable to the fact that not all the populations sampled in the trial are autochthonous, and the inclusion of any planted sources will cloud the emergence of geographic patterns. Secondly, and more importantly, the provenance trials are only 1 year old, and this is very early to expect to observe differences, as the plants have only been subjected to one season's weather and are therefore unlikely to have encountered the sorts of extremes which lead to adaptive differentiation. More detailed analysis of growth patterns when the experiments are older is expected to cast useful light on the question of geographic variation among seed sources.

The issue is complicated by the fact that early growth rate alone is not a good indicator of overall performance, and slower growing seed sources which may be less prone to frost-related damage, could well turn out to be more desirable for timber production. The variation in flushing times recorded at the University of Edinburgh trial and at Dunkeld 21 is potentially important, as it suggests the possibility of increased risk of frost damage on the part of the earlier flushing seed sources. The Norwegian seed source in the University of Edinburgh trial flushed some 15 days earlier than Scottish material and if this is representative of Scandinavian material in general, then this scale of difference in flushing times leads to severe maladaptation. It remains to be seen whether the 4–5 day variation among Scottish sources in the same trial is enough to lead to significant variations in susceptibility to frost damage. In this respect there was somewhat contradictory evidence from the trials: at Dunkeld particularly severe spring frost events in 1998 did not appear to lead to significant damage; whereas at the University of Edinburgh trial there was considerable shoot dieback in some seed sources. Ongoing work testing resistance to frost and desiccation in a selection of Scottish seed sources will cast more light on this (Bruce and McKay, 1999).

There are increasing signs that some commercially available birch planting stock is susceptible to climatic damage, especially the so-called 'Elite birch' which was made available commercially when the Aberdeen University breeding work ceased (Richardson, 1992). In the more extreme cases this has led to death of trees in the sapling stage. This may be a result of the original plus trees containing a proportion of southern English or European material and/or of a tendency of plus trees to occur at low elevations and on sheltered sites. Such material would be most likely to experience problems when planted on poorer upland sites. In fact the reputation of silver birch as a hardy species is to some extent a misunderstanding, stemming from a lack of appreciation of the differences between silver birch, which is not particularly hardy, and downy birch, which is. This reinforces the need to be relatively conservative when recommending setting upper limits to transfer distances, at least until more information becomes available.

Isozyme study

The results of the isozyme study were largely as anticipated for a wide-ranging, outcrossing tree species with extensive powers of both pollen and seed dispersal. A high degree of polymorphism was detected for the small number of isozyme loci scored, indicating that none of these populations are likely to have passed through severe population bottlenecks. Genotype frequencies within populations generally conform to expectations under random mating. There was no consistent evidence for inbreeding within the populations. Differentiation was small, on the high end of the range expected for outcrossing tree species, indicating extensive gene exchange between populations by pollen and/or seed flow. There was no indication of substantial differentiation for particular groups of populations, and therefore no evidence for more than one postglacial origin for the nine populations (Brown, 1999).

The results reported in this paper still only provide a sketchy account of adaptive genetic variation in birch, despite this species having received some research attention over the last 25 years. There is clearly a need for more information on provenance performance in birch in order to give useful guidance to nurseries, foresters and policy makers. Some of this will become available from the series of provenance experiments now being established, but this still only includes seed sources from northern Britain, and similar trials located in England, with English and Welsh sources, would be useful.

Acknowledgements

The authors wish to thank the following people and organizations who contributed to this paper: staff of the Forestry Commission Forest Research including Sam Samuel and members of the Technical Support Unit; the following students at the University of Edinburgh: Linda Armstrong, Andrew Donelly and Nicola Brown; and the owners and agents who gave access to woods for seed collection.

References

Armstrong, L. 1999 *Provenance variation in silver birch (*Betula pendula *Roth.)*. Unpublished honours thesis, University of Edinburgh.

Blackburn, P. and Brown, I.R. 1988 Some effects of exposure and frost on selected birch progenies. *Forestry* **61**, 219–234.

Braathe, P. 1957 Is there a connection between the birch dieback and the March thaw of 1936? *For. Chron.* **33**, 358–363.

Brown, N. 1999 *Isozyme analysis of silver birch (*B. pendula *Roth.) in Scotland*. Unpublished M.Res. thesis, University of Edinburgh.

Bruce, J. and McKay, H. 1999 *A study of the frost hardiness status in silver birch seedlings of nine Scottish origins*. Unpublished Report to Scottish Forestry Trust, Edinburgh.

Cameron, A.D. 1996 Managing birch woodlands for the production of quality timber. *Forestry* **69**, 357–374.

Cameron, A.D., Dunham, R.A. and Petty, J.A. 1995 The effects of heavy thinning on stem quality and timber properties of silver birch. *Forestry* **68**, 275–286.

Donelly, A. 1998 *Provenance variation in silver birch (*Betula pendula *Roth.)*. Unpublished honours thesis, University of Edinburgh.

Ennos, R.A., Worrell, R and Malcolm, D.C. 1998 The genetic management of native species in Scotland. *Forestry* **71**, 1–23.

Eriksson, I. and Jonsson, A. 1986 A review of the genetics of *Betula*. *Scandin. J. For. Res.* **1**, 421–434.

Langhammer, A. 1982 [Growth studies on silver birch (*Betula verrucosa* Ehrh.) in Norway]. *Scientific Report of the Agricultural University of Norway* 14, 43 pp [in Norwegian].

Lines, R. and Brown, I.R. 1982 Broadleaves for the uplands. In *Broadleaves in Britain: Future Management and Research. Proceedings of a Symposium, University of Technology, Loughborough*. D.C. Malcolm, J. Evans and P.N. Edwards (eds). Institute of Chartered Foresters, Edinburgh, pp. 141–149.

Lorrain-Smith, R. and Worrell, R. [eds] 1991 *The Commercial Potential of Birch in Scotland*. Forestry Industry Committee of Great Britain, London.

Pelham, J., Gardiner, A.S., Smith, R.A. and Last, F.T. 1988 Variation in *Betula pubescens* Ehrh. (Betulaceae) in Scotland: its nature and association with environmental factors. *Bot. J. Linn. Soc.* **96**, 217–234.

Richardson, C.D. 1992 *A review of the methods and strategies for the genetic improvement of birch in Scotland*. Unpublished M.Sc. thesis, University of Aberdeen.

Rook, D.A. and Fletcher, A.M. 1991 Research on the genetics of birch in Britain. In *The Commercial Potential of Birch in Scotland*. R. Lorrain-Smith and R. Worrell (eds). Forestry Industry Committee of Great Britain, London, pp. 43–54.

Rosvall, O, Andersson, B. and Ericsson, T. 1998 *Species-specific guidelines for choosing forest regeneration material for northern Sweden*. The Forestry Research Institute of Sweden Redgorelse 1, 66 pp.

Samuel, C.J.A. 1996 Growth characteristics of locally grown native provenances compared with translocated and foreign stock. In *Native and Non-native in British Forestry. Proceedings of a Meeting, University of Warwick 1995*. P.R. Ratcliffe (ed.). Institute of Chartered Foresters, Edinburgh, pp. 100–111.

Worrell, R. 1992 A comparison between European and British provenance of some British native trees: growth survival and stem form. *Forestry* **65**, 253–280.

Worrell, R. 1999 *Birch Woodland Management*

Handbook. Highland Birchwoods, Timber Growers Association and Aberdeen University, 56 pp.
Worrell, R. and Malcolm, D.C. 1998 Anomalies in the distribution of silver birch (*Betula pendula* Roth.) in Scotland. *Bot. J. Scotland* **50**, 1–10.

Received 6 January 2000

Appendix 1

Details of planting stock origins and trial designs

Trial	Country of origin	Origin details		Trial design
Speymouth 33	Finland	Progenies are polycrosses involving Finnish plus tree pollen and female plus trees in Finland all south of latitude 62°30'N except KO8004which is latitude 67°30'N	KO6769*SV287 KO1007*SV287 KO1381*SV287 KO8004*SV287 KO1393*SV287 KO6771*SV287 KO1398*SV287 KO6776*SV287 KO6765*SV287 KO1383*SV287	2 replicates 8 plant line plots
	Norway	Open pollinated progeny from Tangen, Stange		
	Scotland	Open pollinated progeny of unselected parents, Glencommon Wood, Banchory		
Teindland 113	Finland	Progenies are polycrosses involving Finnish plus tree pollen and female plus trees in Finland	KO761448*SV288 KO761432*SV288 KO761405*SV288 KO761421*SV288 KO761429*SV288 KO771412*SV288*SV288 KO771421*SV288*SV288 KO771441*SV288*SV288 KO771404*SV288*SV288	4 replicates 8 plant line plots
	Scotland	Open pollinated progeny of unselected parents from Glen Prosen, Angus and Tummel, Tayside		
Dunkeld 21 and Moray 64	Scotland and N. England	Open pollinated, unselected progenies from semi-natural populations across the natural range of the species (see Appendix 2)		3 replicates 24 plant plots
Edinburgh	Scotland and Norway	8 Scottish and 1 Norwegian lots of plants from 5 commercial nurseries (see Appendix 2)		3 replicates 16 plant plots

Appendix 2

The locations of the seed of *B. pendula* included in the provenance trials at Dunkeld 21 and Moray 64

	Grid reference	Latitude (° min)	Longitude (° min)
Great Glen			
Leanachan	NN 222771	56 50	4 56
Glen Spean	NN 290808	56 53	4 48
White Bridge	NH 284007	57 03	4 50
Blaraidh, Glen Moriston	NH 376163	57 12	4 41
Tomich	NH 315283	57 18	4 47
Strathgarve	NH 408605	57 35	4 40
Kyloag	NH 662910	57 52	4 15
Strathspey			
Straanruie	NH 996154	57 13	3 40
Delnapot	NJ 169370	57 24	3 22
Spindlemuir	NJ 153648	57 39	3 25
Aberdeenshire			
Muir of Dinnet	NJ 433999	57 04	2 55
Birkhill, Alford	NJ 595163	57 14	2 40
Invermossat	NJ 495184	57 15	2 50
Angus			
Montreathmont	NO 569548	56 40	2 42
Silvie, Alyth	NO 273484	56 37	3 10
Ingilsmaldie	NO 665713	56 49	2 32
Perthshire			
Dunalastair	NN 733614	56 43	4 03
Dall Mill, Rannoch	NN 589568	56 40	4 18
Newtyle Hill, Dunkeld	NO 040423	56 33	3 34
Craiganour, Rannoch	NN 590580	56 41	4 18
Killin	NN 560310	56 26	4 19
West Coast			
Langbank	NS 490720	55 55	4 34
Achnatra	NN 110090	56 14	5 02
Creagan, Loch Crearan	NM 970440	56 33	5 18
Cruach Ardura, Mull	NM 680300	56 23	5 45
Borders			
Glentress	NT 286406	55 38	3 08
Floors, Kelso	NT 700280	55 32	2 28
Mellerstain, Kelso	NT 650380	55 37	2 33
Petersmuir	NT 490660	55 53	2 49
Baitlaws	NS 979308	55 33	3 37
Wauchope	NT 587075	55 21	2 39
Locharbriggs	NY 991810	55 06	3 34
Elibank	NT 355365	55 36	3 01
N. England			
Finsthwaite	SD 363865	54 16	2 58
Castle Howard	SE 705700	54 07	0 55
Sand Hutton	SE 689582	54 00	0 56

Appendix 3

Seed source locations at the University of Edinburgh experiment (the lots were bought in commercially and the exact locations are not all known)

Seed source	Location details
Berwick	Berwickshire, Borders
Newtyle Hill	Newtyle Hill, Dunkeld, Perthshire (see Appendix 2)
Banchory	Banchory, Aberdeenshire
Cawdor	Cawdor Estate, Moray
Glenlivet	Glenlivet, Moray
Blackmount	Blackmount Estate, Bridge of Orchy, Argyll
Loch Creran	Loch Creran, Appin, Argyll (see Appendix 2)
Cluanie	Cluanie, Glen Moriston, Inverness-shire
Norway	Unknown location in south Norway