Sixth Year Results from Four Ash *(Fraxinus excelsior)* Breeding Seedling Orchards

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Abstract

A series of four ash *(Fraxinus excelsior)* progeny trials were established as Breeding Seedling Orchards (BSOs) in 1993. The aim was to improve the form and vigour of Britain's second most widely planted broadleaved species. Four sites were planted, employing seed from 36 selected mother trees across Great Britain. By 1998 the average height of the trees in the best family, on the best site, was 2.7 m. Tree heights were first measured in 1996 and determined to be highly heritable. In July 1998 they were assessed for dbh, height, forking, straightness and branching. Analysis confirmed that height growth is strongly heritable with estimates of genetic gain from 2% to 25%. Heritability for height does not appear to be declining and comparisons with 1996 family rankings reveal a very strong consistency at all sites. These results suggest that juvenile – mature correlations may be strong in ash. The extent of branching is strongly heritable, although heritabilities for forking and straightness were much weaker.

Key words: ash, *Fraxinus excelsior,* progeny trial, heritability, genetic gain.

1. Introduction

Ash *(Fraxinus excelsior* L.*)* is the third most widely distributed broadleaved species in Great Britain, after the oaks and birches (Locke, 1987), and is currently the second most commonly planted broadleaved tree (Kerr, 1995). On the best sites, it has yield classes of 10 to 12 m^3 ha^{-1} year^{-1} (Evans, 1984).

Ash is very exacting and requires a highly fertile, well-oxygenated moist soil and little competition from weeds to produce fast-growing crops of high timber quality (Evans, 1984). Young ash trees are well known for their susceptibility to forking, caused by spring frosts and the ash bud moth *(Prays fraxinella)* (Evans, 1984; Savill, 1991; Kerr, 1995). In Britain, at least, ash is not regarded as a particularly variable species, unlike oak and beech. Its form is generally good, unless it is repeatedly damaged by the ash bud moth or frost. Early flushing trees are particularly vulnerable to late spring frost damage, and so the time of flushing can be an important selection criterion since it appears to be a heritable trait (Kleinschmit *et al.,* 1996).

In 1991, an improvement programme was started for ash under the auspices of what is now called the British Hardwoods Improvement Programme (BHIP) (Savill, 1998). This paper examines the results of assessments taken from four trials that were planted in the spring of 1993 and measured in July 1998, six growing seasons after planting. The locations of the trials are indicated in *table 1.* Roberts (1996) took several measurements at these trial sites before 1998, including a full measurement of height in 1996.

Table 1. – Abbreviations and locations of the four BSOs measured in July 1998.

Abbreviation	Location
1—LHF	Little Hidden Farm, Hungerford, Berkshire
2—MGE	Mulgrave Estate Office, Lythe, Whitby, North Yorkshire
3—LWT	Little Wittenham, Little Wittenham, Abingdon, Oxfordshire
4—SCH	Scarr Hill, Huntley, Gloucestershire

2. Materials and Methods

2.1 The Breeding Seedling Orchards (BSOs)

Barnes (1995) has described the methodology adopted as a Breeding Seedling Orchard (BSO). This is a compromise strategy that lies between the seedling seed orchard and the progeny test within a multiple population breeding strategy, as defined by Namkoong *et al.* (1980). The BSO allows estimation of genetic parameters, family ranking, seed production and the selection of founders for the next generation of improvement (Barnes, 1995). It is a simple, cheap and robust approach that, in the tropics, has provided gains of between 20% and 50% in recoverable volume, in the first generation (Kanowski, 1993). The structure of the trials is such that the identities of mother trees (families) are retained. The BSOs can, therefore, be considered half-sib progeny trials. The origins of the 36 mother trees included in the trials are indicated in *table 2.*

Table 2. – Ash families: seed collected in autumn 1991 and planted in spring 1993.

Family code	Location	Region
1	Tintern Woods, Newport, Monmouthshire	Wales
2	Tintern Woods, Newport, Monmouthshire	Wales
3	Lady Park Wood, Coleford, Gloucestershire	W. England
4	Lady Park Wood, Coleford, Gloucestershire	W. England
5	Lady Park Wood, Coleford, Gloucestershire	W. England
6	Oldstone Well Wood, Coleford, Gloucestershire	W. England
7	Highmeadow Woods, Coleford, Gloucestershire	W. England
8	Rossway Park Estate, Hertfordshire	S.E. England
9	Wytham Woods, Oxfordshire	S.E. England
10	Wytham Woods, Oxfordshire	S.E. England
11	Wytham Woods, Oxfordshire	S.E. England
12	Wytham Woods, Oxfordshire	S.E. England
13	Wytham Woods, Oxfordshire	S.E. England
14	Chestnut Coppice, Garnons Estate, Herefordshire	W. England
15	Chestnut Coppice, Garnons Estate, Herefordshire	W. England
16	Chestnut Coppice, Garnons Estate, Herefordshire	W. England
17	Bradleyhead Wood, Garnons Estate, Herefordshire	W. England
18	Tin Hill Woods, Garnons Estate, Herefordshire	W. England
19	Aconbury Wood, Guys Estate, Herefordshire	W. England
20	Wellbroor Wood, Guys Estate, Herefordshire	W. England
21	Aconbury Wood, Guys Estate, Herefordshire	W. England
22	Boughton Estate, Kettering, Northamptonshire	S.E. England
23	Overbury Estate, Gloucestershire	W. England
24	Overbury Estate, Gloucestershire	W. England
25	Overbury Estate, Gloucestershire	W. England
26	Overbury Estate, Gloucestershire	W. England
27	Sling, Gwynedd	Wales
28	Bulters Wood, Englefield Estate, Berkshire	S.E. England
29	Pallinsburn, Coldstream, Berwickshire	Scotland
30	Pallinsburn, Coldstream, Berwickshire	Scotland
31	Dunnottar, Kincardine Forest District, Banchory	Scotland
32	Bacheiddon, Mid Wales	Wales
33	Dunnottar, Kincardine Forest District, Banchory	Scotland
34	Settrington, Yorkshire	N.E. England
35	Settrington, Yorkshire	N.E. England
36	Grimsthorpe Estate, Lincolnshire	N.E. England

All families within a trial are represented as single tree plots in each unit (or replicate), and distributed randomly within the unit. A variable number of units (between 6 and 13 in the different experiments) are grouped into blocks. The area available at each site dictated the number of units within a trial. *Figure 1* provides a general idea of site layout at each BSO.

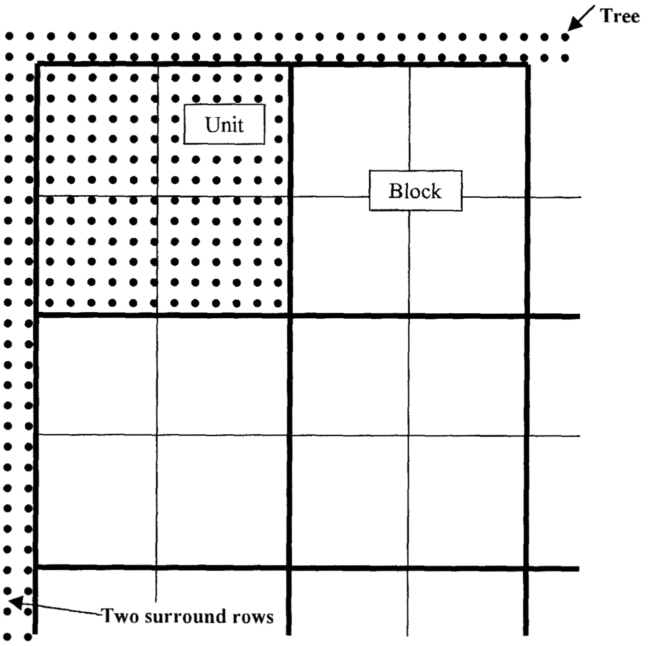

Figure 1. – Generalised layout of breeding seedling orchard, showing units (replicates), blocks and surround rows. Individual trees are represented by dots.

At the time of planting, the trials were balanced – all families within a trial were represented in each unit by one tree. Owing to some mortality and, in some cases, a lack of available replacements from the same family, the experiments became slightly unbalanced. Individual site details are provided in *table 3*.

2.2 Assessments

The following assessments were made in July 1998: diameter at breast height (dbh) to the nearest 0.1 mm, and height to the nearest 1 cm. Three measures of form were also recorded for each tree: forking, extent of branching, and straightness. As shown in *figure 2*, forking was categorised on a subjective scale from one (no forking) to three (repeatedly forked), branching from one (few branches) to six (many). Straightness was assessed on a six-point scale from one (excellent) to six (very poor). These measures were derived following experience with other broadleaved trials. Data were recorded in the field and transferred for analysis using a PSION Workabout.

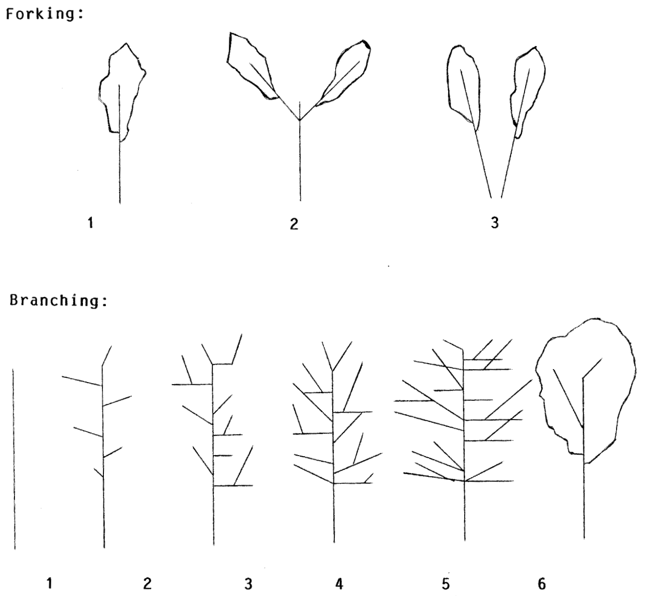

Figure 2. – Categories (scores) used for assessing forking and branching.

2.3 Analyses

Correlations, regressions and several analyses of variance were calculated using MINITAB (1998); depending on the procedure, single tree values or mean family values were used. In all of them, families with fewer than sixteen representatives were excluded.

2.3.1 Analyses of Variance

The possibility of grouping families by region, and analysing the performance of provenances derived in this way was rejected after some initial analyses. There was a large between-family variance within provenances, and provenance means were very similar, suggesting that between-provenance differences are small.

The analysis was divided into four stages.

Stage 1

The data sets for the four sites were first analysed separately. In the analyses of variance (using the General Linear Model), the first model treated the data set for each site as a completely randomised design recognising family as the only source of variation. TUKEY's multiple comparisons were employed to assess the significance of differences between means for height at each site. The model employed was:

$Y_{ik} = \mu + F_i + e_{ik}$

Where:

Y_{ik} is the observation on the k^{th} tree in the i^{th} family.

Table 3. – Site details of the BSOs.

Site	No. of units	No. of single tree plots in unit	No. of blocks	No. of units per block	No. of families represented in trial	Planting spacing (m)	No. of guard rows	Protection
LHF	24	30	8	3	27	2 x 2	2	Rabbit fencing
MGE	52	21	13	4	21	2 x 2	2*	1.3 m shelters
LWT	36	36	9	4	36	3 x 3	2	1.3 m shelters and deer fencing
SCH	36	36	6	6	32	2 x 2	2	Quills

*) Only present on north and west borders of site.

μ is the overall mean for the site.

F_i is the effect of the i^{th} family.

e_{ik} is a random error associated with the k^{th} tree in the i^{th} family which contains all the effects not included in F.

Stage *2*

The second analysis followed ROBERTS' (1996) strategy, where each data set was blocked to test family x block interaction. Details of the numbers of blocks at each site are shown in *table 3*.

Single tree plots of the same family within a block were treated as a non-contiguous plots. These provided an estimate of within plot variance (the error term or residual, which allows the significance of family variance to be tested). Only those families that displayed complete representation across the blocks were analysed. The model employed was:

$Y_{ijk} = \mu + F_i + B_j + e_{ijk}$

Where:

Y_{ijk} is the observation on the k^{th} tree in the i^{th} family in the j^{th} block.

μ is the overall mean for the site.

F_i is the effect of the i^{th} family.

B_j is the effect of the j^{th} block.

e_{ijk} is a random error associated with the k^{th} tree in the i^{th} family and the j^{th} block that contains all the effects not included in F and B.

As non-contiguous plot size varies between families and blocks, the General Linear Model (GLM) function was used, to provide an adjusted sum of squares.

The expectations of mean squares were calculated assuming that both families and blocks are random effects. They were used to calculate variance components and estimates of heritabilities. From these estimates, genetic gain for height was calculated using the following equation, which assumes mass selection:

$R = H^2 \times S$

Where:

R = response (genetic gain)

H^2 = heritability

S = selection differential (the difference between the population mean and the mean of the selected trees (top 15%)).

Since heritability is a property of the environment it was calculated separately for each site. Estimates of genetic gain are only valid when the improved seed is grown in a similar environment to that of the trial site.

Stage 3

The model used was identical to that employed in the second stage of the analysis. The families analysed were those analysed in stage two except that those not represented at all four sites were excluded. Family x block interactions were disregarded. Variance components and estimates of heritability were calculated for each site.

Stage 4

The pooled data set for the 20 families common to all four sites were also analysed to determine whether there were any family x site interactions. The families were assumed to come from one population in HARDY-WEINBERG equilibrium. The model employed was:

$Y_{ijk} = \mu + F_i + S_j + (FS)_{ij} + e_{ijk}$

Where:

Y_{ijk} is the observation on the k^{th} tree in the i^{th} family in the j^{th} site.

μ is the overall mean for all sites.

F_i is the effect of the i^{th} family.

S_j is the effect of the j^{th} site.

$(FS)_{ij}$ is the effect of family x site interaction for the i^{th} family on the j^{th} site.

e_{ijk} is a random error associated with the k^{th} tree in the i^{th} family and the j^{th} site that contains all the effects not included in F, S and (FS).

The model ignored blocks, so that, in effect each site was treated as a completely randomised design. Although there were some slight block effects, the block variance component was small in comparison to the residual variance component. Therefore, the inclusion of the block effect within the error term was considered not to distort the estimates of the genetic parameters sufficiently to forego the analysis.

The model recognised three sources of variation (families, sites and family x site interaction). This and the fact that the number of individuals within a family varies between families and sites meant that the General Linear Function was used on MINITAB to give an adjusted sum of squares.

The expectation of mean squares assumes that both families and sites are random effects, and a fully random model was used. Sites were assumed to be a random sample from all possible sites within England. The expectation of mean squares were used to calculate variance components and estimates of heritabilities. Sites were then regarded as fixed. Estimates of heritabilities were recalculated omitting the site variance component from the total phenotypic variation. The second estimate of heritability is appropriate for the estimation of genetic parameters that are to be applied to site-adjusted data for selection purposes. Standard errors for the estimates of heritabilities were calculated using the formula detailed by BECKER (1984). The standard error varies between the situation where site is assumed to be random and where it assumed to be a fixed factor because the intraclass correlation coefficient varies. The intraclass correlation coefficient is the between-family variance expressed as a proportion of the total phenotypic variance. When sites are a random factor, the site variance component is included in the total phenotypic variance. When sites are a fixed factor, the site variance component is not included in the total phenotypic variance.

2.3.2 Regression and Correlation Analyses

The twenty common families were ranked at each site according to family mean height. PEARSON rank correlation coefficients were calculated to test the null hypothesis that any similarities in ranking arose by chance.

Regression analyses were performed for each site on the rankings of mean family values for height in 1996 and 1998 to determine site consistency.

Correlations between rankings of mean family values for dbh, height, forking, straightness and branching were calculated for each site, and across sites using the PEARSON's correlation coefficient.

3. Results

3.1 Site Performance

Table 4 details the mean performance at each site for the five measured parameters. Comparisons with ROBERTS' (1996) data allowed mean height growth since 1996 to be calculated.

Table 4. – Mean site performance (numbers in brackets are standard deviations).

Site and p values	No. of single tree plots on site	Dbh 1998 (cm)	Height 1998 (cm)	Growth 1996-1998 (cm)	Forking (Scale 1-3)	Straightness (Scale 1-6)	Branching (Scale 1-6)
LHF	720	0.74	123	16	1.72	2.93	2.80
		(0.29)	(40.6)	(24.1)	(0.50)	(0.97)	(0.89)
MGE	1092	1.31	208	42	1.33	3.33	3.28
		(0.49)	(45.3)	(42.6)	(0.47)	(1.10)	(1.09)
LWT	1296	1.68	235	48	1.69	3.27	3.16
		(0.54)	(39.5)	(24.8)	(0.46)	(1.23)	(1.07)
SCH	1296	1.27	191	85	1.72	3.24	3.26
		(0.51)	(54.1)	(36.6)	(0.46)	(1.18)	(1.10)
P for family	-	<0.000	<0.000	<0.000	0.004	<0.000	<0.000
P site x family	-	0.004	<0.000	<0.000	0.014	0.097	<0.000
P for sites	-	<0.000	<0.000	<0.000	<0.000	<0.000	<0.000

The p values given in the bottom three lines of the table, are for combined analyses of the 20 families common to each site.

Little Hidden Farm was the poorest performer in terms of growth. Competition with herbs and grasses was severe and the lack of individual tree protection has led to damage from rabbits, hares and possibly deer on this site. It is likely that pesticide drift from a neighbouring wheat field has further compounded these effects. Mulgrave Estate has enjoyed careful weeding and tree shelters are of the flared rim type. At Little Wittenham, regular, straight edged shelters caused considerable damage to stems (cf. POTTER, 1991) and at Scarr Hill some quills were waterlogged. The Little Wittenham site has produced the largest trees although the Scarr Hill site has shown the greatest two-year growth. *Figure 3* illustrates the relative performance at two of the sites based on mean height for the twenty families represented at all sites.

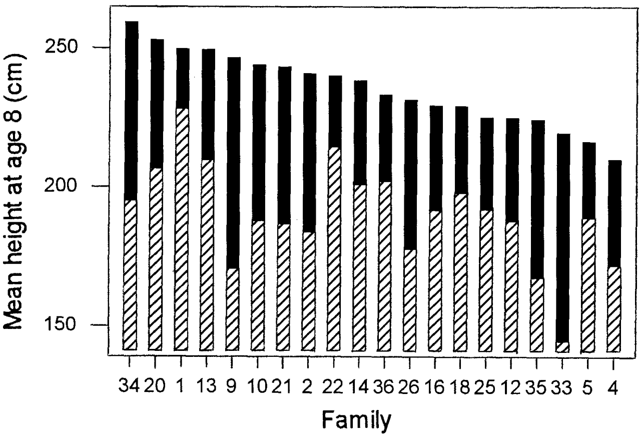

Figure 3. – Mean heights (cm) in 1998 of families occurring at both Little Wittenham (shown as black bars) and Scarr Hill (hatched bars), in decreasing order of height for the Little Wittenham site.

Forking is most common at Little Hidden Farm and Scarr Hill, slightly lower at Little Wittenham and least serious at the Mulgrave Estate. There is little variation in straightness between the sites apart from Little Hidden Farm, which shows better than average straightness results, largely as a result of the small size of the trees at that site.

3.2 Analyses of Variance

3.2.1 Family Variability

TUKEY's multiple comparisons for heights, which are presented in *table 5,* confirm that variability in family means is low. This is especially true of Little Hidden Farm and the Mulgrave Estate whilst Little Wittenham and, in particular, Scarr Hill show more variability.

Diameter at breast height – the significance of differences between family means at Little Hidden Farm, Little Wittenham and Scarr Hill for dbh indicates that there is a large genetic influence on the observed phenotype *(Table 6).* The Mulgrave Estate was an exception at all stages of the analysis, nor was dbh significant at Little Hidden Farm in the third stage of analysis.

Height – Height is under strong genetic control. This is demonstrated by the significance of differences between family means at all four sites *(Table 7).* Each analysis of variance showed height to be significant at least at the 0.005 level with only one exception: at the Mulgrave Estate height was only significant at the 0.01 level at stage two of the analysis of variance.

Forking – Differences between family means were not significant *(Table 8),* which suggests that forking is more influenced by environmental conditions, though a certain consistency across environments is evident in *table 8.* An interesting exception is provided by Little Hidden Farm at the third stage of analysis. This is examined further in section 3.2.2.

Straightness – Differences between family means were significant at all four sites in the first and second stages of genetic analysis at the 0.005 level with the exception of the Scarr Hill site. At the third stage of analysis of variance straightness was not significant at the Mulgrave Estate, Little Wittenham, or Scarr Hill. This suggests that straightness is not under strong genetic control.

Branching – Branching is under strong genetic control. This is demonstrated by the significance of differences between family means at all four sites. Each analysis of variance showed branching to be significant at the 0.005 level with only one exception: at Scarr Hill branching is only significant at the 0.05 level at stage three of the analysis of variance.

3.2.2 Genotype x Site Interactions

In terms of height, there was a strong genotype x site interaction (p=0.000) for height at age six *(Tables 4* and *6).* Though

Table 5. – Ranked mean family heights at all four sites with 1996 rankings (ROBERTS, 1996). Black lines indicate those families that are not significantly different according to TUKEY's multiple comparisons.

	Little Hidden Farm			Mulgrave Estate			Little Wittenham			Scarr Hill		
Rank 1998	Family	Rank 1996 Family	Height (cm)	Family	Rank 1996 Family	Height (cm)	Family	Rank 1996 Family	Height (cm)	Family	Rank 1996 Family	Height (cm)
1	23	2	150	1	2	226	19	2	270	23	1	233
2	11	1	147	22	1	221	23	1	261	1	3	228
3	16	5	140	9	3	221	34	3	259	15	2	225
4	22	4	140	20	4	215	30	16	255	22	5	214
5	34	3	136	36	7	215	20	8	253	13	10	210
6	20	6	136	14	9	212	1	12	250	28	7	208
7	26	7	136	2	8	211	13	7	249	20	4	207
8	9	8	134	26	6	211	9	11	247	17	6	204
9	18	11	132	10	5	210	17	4	247	11	11	202
10	12	10	125	13	11	209	15	9	245	36	15	202
11	36	18	125	12	10	208	10	5	244	14	13	201
12	35	9	124	18	17	208	21	6	243	24	9	199
13	17	16	122	25	12	207	2	24	241	18	27	198
14	1	19	122	21	18	206	7	13	241	34	20	195
15	2	14	122	16	15	206	22	10	240	25	18	192
16	21	13	120	30	14	204	14	17	238	16	14	192
17	13	22	119	35	16	203	8	14	235	5	8	189
18	5	15	118	33	13	203	36	19	233	10	16	188
19	10	12	117	34	19	200	28	18	233	12	21	188
20	33	21	114	4	21	190	26	15	231	21	19	187
21	4	23	113	5	20	186	6	25	231	7	17	185
22	14	20	110				16	21	229	2	22	184
23	25	17	109				18	29	229	29	12	182
24	30	26	106				24	20	229	26	23	178
25	29	24	105				11	32	226	4	28	172
26	3	25	100				31	27	226	9	29	171
27	27	27	95				25	28	225	35	26	168
28							12	23	225	32	25	166
29							35	30	224	3	24	164
30							3	22	224	31	30	154
31							29	26	223	27	31	149
32							33	31	220	33	32	145
33							5	33	217			
34							4	35	210			
35							32	34	208			
36							27	36	190			

Table 6. – Rankings for dbh (in cm) of the 20 common families in the trials. The 5 families with the biggest dbhs on each site are shown in bold type, and those with the smallest in small italic type.

Family	Overall Mean Dbh-98	Hungerford Dbh-98	Mulgrave Dbh-98	Wittenham Dbh-98	Scarr Hill Dbh-98
22	**1.44**	0.06	**1.43**	1.77	**1.46**
34	**1.42**	0.73	*1.26*	**2.00**	1.26
10	**1.41**	*0.62*	1.32	**1.93**	*1.09*
1	**1.40**	**0.78**	1.32	1.68	**1.38**
20	**1.40**	0.72	1.35	**1.82**	**1.36**
13	1.39	*0.64*	1.32	**1.92**	1.31
9	1.39	**0.93**	**1.43**	**1.82**	*1.09*
2	1.38	0.75	**1.37**	1.72	1.23
14	1.37	*0.58*	1.32	1.70	1.35
21	1.36	0.69	1.29	1.79	1.18
36	1.34	0.64	1.36	1.71	1.16
16	1.33	**0.88**	1.28	1.61	**1.42**
26	1.31	0.74	**1.38**	1.65	1.13
35	1.31	**0.86**	1.27	1.60	1.18
12	1.30	0.74	1.29	1.58	1.17
18	*1.28*	**0.83**	**1.36**	*1.56*	1.11
5	*1.23*	0.65	*1.09*	*1.41*	**1.39**
25	*1.19*	*0.50*	*1.22*	*1.48*	*1.09*
33	*1.19*	0.66	*1.19*	*1.47*	*0.98*
4	*1.16*	*0.58*	*1.18*	*1.37*	*1.08*
P=	0.000***	0.000***	0.122 ns	0.000***	0.000***

The p values shown are for the significance of differences between families, using appropriate ANOVAs.

many provenances retained reasonably similar rankings between sites, only family 20 was among the five best on all sites. The shortest two families (4 and 33) were among the five worst on all sites. Some others were markedly less stable: for example, family 34 was among the five overall best on four sites, but was among the five worst on the Mulgrave estate. Family 16 was the best at Little Hidden Farm, but in the lower half of the families on other sites. Performance in diameter at breast height, as might be exepected, showed similar trends.

Forking *(Tables 4* and *7)* showed a weaker (p=0.014) genotype x environment interaction. In general, except on the Little Hidden farm site, the families that were least forked overall, were well within the best 10 on the other three sites, and there was a similar consistency with the worst five families, except on the Scarr Hill site.

Branching showed highly significant interactions. For example, family 18 is one of the least branched on all sites, while 36 was among the best on the Mulgrave Estate, and one of the worst five on two of the other three sites.

3.2.3 Heritability

Heritability was calculated twice for dbh, height, forking, straightness and branching at all four sites using expected mean square values from stages two (taking into account blocks) and three (only families represented at all sites) of the analyses of variance. Details of heritability for each trait are presented in *tables 8* and *9*. ROBERTS' (1996) estimates for height are included to show changes in heritability estimates over time. At both stages of the genetic analysis, height was the most heritable trait in ash, followed by dbh.

Between 1996 and 1998 heritability of height increased at Scarr Hill from 0.50 to 0.58, and at Little Wittenham from 0.64 to 0.67 *(Table 9)*. At the other sites it decreased. In the third stage of analysis (common families), heritability decreased at

Table 7. – Rankings for mean height (cm) of the 20 common families in the trials. The tallest 5 families on each site are shown in bold type, and the shortest 5 in small italic type.

Family	Overall Mean Ht-98	Hungerford Ht-98	Mulgrave Ht-98	Wittenham Ht-98	Scarr Hill Ht-98
1	**215.8**	122.2	**226.3**	**249.7**	**228.0**
22	**210.5**	**139.8**	**221.0**	240.1	**214.4**
20	**207.4**	**136.3**	**214.9**	**253.0**	**206.6**
34	**202.2**	**136.5**	*200.1*	**259.4**	194.9
13	**199.1**	118.7	208.8	**249.5**	**209.6**
36	198.8	124.9	**214.6**	233.1	**202.0**
2	198.4	121.7	211.1	240.8	183.8
10	197.7	*117.2*	209.9	244.0	187.8
18	197.1	132.0	207.5	229.3	197.8
9	197.1	134.3	**220.7**	**246.6**	*170.7*
21	196.3	119.6	206.4	243.2	186.6
14	195.1	*109.7*	211.5	238.4	200.8
26	194.3	**135.5**	210.7	231.5	*177.7*
12	193.5	125.1	207.6	*225.0*	187.8
16	193.2	**140.1**	205.8	229.5	191.6
35	*186.4*	123.5	*203.2*	*224.5*	*167.5*
25	*186.2*	*111.7*	206.7	225.2	191.9
5	*182.1*	117.9	*185.7*	*216.7*	188.9
33	*178.4*	*113.6*	*203.1*	*219.7*	*144.7*
4	*177.4*	*112.9*	*189.6*	*210.2*	*171.9*
P=	0.000***	0.000***	0.002**	0.000***	0.000***

The p values shown are for the significance of differences between families, using appropriate ANOVAs.

Table 8. – Rankings for forking of the 20 common families in the trials. The least forked 5 families (those with the lowest scores) on each site are shown in bold type, and the most forked 5 in small italic type.

Family	Overall Mean Forking-98	Hungerford Forking-98	Mulgrave Forking-98	Wittenham Forking-98	Scarr Hill Forking-98
33	**1.503**	**1.542**	1.312	**1.629**	**1.531**
12	**1.530**	**1.480**	1.327	1.694	**1.618**
18	**1.558**	1.667	1.327	**1.562**	**1.676**
34	**1.577**	1.667	1.364	1.676	**1.600**
36	**1.594**	1.800	**1.226**	1.703	**1.647**
4	1.595	*1.818*	**1.273**	**1.556**	1.733
35	1.602	**1.643**	**1.266**	1.750	1.750
21	1.613	1.760	1.308	**1.611**	1.774
10	1.621	1.731	1.365	**1.541**	*1.846*
26	1.637	1.794	**1.235**	1.667	*1.853*
16	1.648	1.806	**1.235**	*1.838*	1.714
13	1.651	**1.455**	*1.451*	*1.857*	*1.842*
14	1.657	1.774	1.294	1.811	1.750
5	1.662	*1.885*	1.291	1.657	*1.816*
25	1.670	1.771	1.275	*1.829*	1.806
9	*1.674*	1.731	*1.477*	1.778	1.711
22	*1.684*	**1.640**	*1.426*	*1.861*	*1.811*
20	*1.694*	*1.889*	*1.404*	1.714	1.767
2	*1.700*	*1.846*	1.370	*1.811*	1.771
1	*1.712*	*1.833*	*1.440*	1.795	1.781
P=	0.004**	0.023*	0.192ns	0.019*	0.058ns

The p values shown are for the significance of differences between families, using appropriate ANOVAs.

Table 9. – Heritability (h^2) estimates (from stage 2 of analysis, taking blocks into account).

Site	Height 1996	Height 1998	Dbh 1998	Forking 1998	Straightness 1998	Branching 1998
Little Hidden Farm	0.61	0.36	0.23	0.12	0.16	0.25
Mulgrave Estate	0.12	0.07	0.02	0.01	0.11	0.14
Little Wittenham	0.64	0.67	0.07	0.06	0.09	0.20
Scarr Hill	0.50	0.58	0.48	0.06	0.05	0.10

Table 10. – Heritability (h^2) estimates (only families represented on all 4 sites considered).

Site	**Height 1996**	**Height 1998**	**dbh**	**Forking**	**Straightness**	**Branching**
Little Hidden Farm	0.20	0.16	0.07	0.18	0.02	0.22
Mulgrave Estate	0.13	0.09	0.04	0.02	0.10	0.13
Little Wittenham	0.37	0.31	0.31	0.09	0.05	0.27
Scarr Hill	0.34	0.52	0.21	0.04	0.00	0.08

all sites except at Scarr Hill where it increased from 0.34 to 0.52 *(Table 10)*.

The rather uniform height and dbh growth among families on the Mulgrave Estate, which leads to low calculated heritabilities, may be due to the high quality of the site and the care the trees received. Factors such as branching, which may be less site dependent show the similar levels of variation (hence heritability) at all sites.

Branching is, generally, the most heritable trait after height and dbh. At the Mulgrave Estate, however, it is more heritable than both height in 1998 and dbh, and at Little Hidden Farm and Little Wittenham it is more heritable than dbh (second stage analysis). In the third stage of analysis it is more heritable than both dbh and height at Little Hidden Farm and the Mulgrave Estate.

Forking and straightness are the least heritable traits with figures generally under 0.1, though at Little Hidden Farm they were slightly higher. This apparent anomaly may be explained in the following manner. The trees at Little Hidden Farm received no individual protection as they did at the other sites. It follows that any resistance to frost will be expressed more strongly than at other sites where tree shelters create a warmer microclimate which may reduce frost susceptibility (POTTER, 1991).

The genetic gain of the best 15% of families for height was calculated using the above estimates of heritability and assuming mass selection. Estimates are presented in *table 11*; figures provided are for the estimated gain in centimetres, and as a percentage of the population mean.

This gives an average genetic gain of 29 cm or 16%. This average figure is not genetically meaningful, however, since heritability is a site-specific property.

3.3 Site Consistency

There were no family x block interactions in the second stage of the analysis.

Regressions were calculated for each site, using 1996 and 1998 data, to identify any consistency in the performance of families over time. The regression model employed the ranking of mean family height values in 1996 as a predictor for 1998 values. A very strong relationship was found at all four sites between 1996 and 1998 family rankings. *Figure 4* demonstrates this relationship employing figures from the Mulgrave Estate. The R^2 figures from the regression are presented for each site in *table 12*.

Table 11. – Genetic gain estimates for height at all four sites. Figures in brackets are 1996 estimated.

	Site			
Genetic gain	LHF	MGE	LWT	SCH
cm†	23	5	41	48
%	19 (26)	2 (3)	17 (18)	25 (24)

†) height gain = mean height of top 15% of families – mean height of total population.

Table 12. – r^2 values showing the relationship between 1996 and 1998 rankings for mean familiy height values at each site.

Site	r^2
LHF	87
MGE	86
LWT	85
SCH	79

3.4 Trait Correlations

Two types of correlation were calculated to establish whether relationships exist between the rankings of dbh, height, forking, straightness and branching. The first examined each site separately (stage 1). The second stage looked for similarities in trait rankings across sites (stage 2).

3.4.1 Within Site Correlations

The most strongly correlated ranked traits were, expectedly, dbh and height, with r-values greater than 0.7 at all four sites. Correlations between forking and straightness were strong, with r-values ranging from 0.30 at Little Hidden Farm to 0.69 at Scarr Hill. Those for forking and branching were less strong, with r-values ranging from 0.24 at Little Hidden Farm to 0.52 at Scarr Hill.

3.4.2 Across Site Correlations

Height rankings provide the strongest across site correlation coeffcients. R-values range from 0.21 (Little Hidden Farm (LHF)/Scarr Hill (SCH)) to 0.58 (Mulgrave Estate (MGE)/Little Wittenham (LWT)). Rankings for branching also give strong

Figure 4. – Relationship between 1996 and 1998 familiy rankings for height at the Mulgrave Estate.

across site correlation coefficients. R is greater than 0.4 for the following combinations: LHF/SCH (0.44), LWT/SCH (0.54), LHF/LWT (0.56) and MGE/SCH (0.59). MGE and LWT show the strongest correlation for dbh family rankings (r-value = 0.49); other values ranged from 0.02 (LWT/LHF) to 0.26 (MGE/LHF). There was a correlation for straightness rankings between LHF and LWT (0.39) and to a lesser extent between LHF and SCH (0.32) and the MGE and SCH (0.25). Rankings for forking were not strongly correlated across sites.

4. Discussion

The results indicate that the Breeding Seedling Orchard is a useful and valid strategy for the improvement of broadleaved species in a temperate country. This is demonstrated by the fact that two of the four functions of a BSO: estimation of genetic parameters and family rankings, have been achieved at this preliminary stage. Selection of founders for the next generation and seed production will occur at a later stage and will build upon results detailed in this paper.

Genetic gain for height (which assumed careful mass selection) ranged from 2% at the Mulgrave Estate to 25% at Scarr Hill. Three of the sites showed a gain of more than 15%, which is better than the range of 10% to 15% quoted for ash by MARINOV (1990), though not of the order encountered with breeding programmes employing a similar strategy in the tropics, where genetic gain can range from 20% to 50%. It demonstrates, nevertheless, that significant results can be achieved in temperate regions for a financial investment that is little more than that required for establishing a new woodland (ROBERTS, 1996). Furthermore, the improved seed stock, which will be derived from these Breeding Seedling Orchards, should significantly reduce rotation time and, thereby, improve the economic attractiveness of broadleaf plantations in the UK.

Confirmation that vigour is under strong genetic control in ash is useful from a breeding point of view. This information, combined with the fact that, at this early stage, age-age correlations of family performance appear strong, means that early selection for breeding purposes may be viable, particularly in the context of micropropagation. These possibilities will be verified by further analysis when the trees are at a later stage in their development. Such work will confirm the degree of juvenile-mature correlation present in ash.

There are conflicting results regarding decline in heritability and genetic gain between 1996 and 1998. Heritability estimates and thus genetic gain estimates often decrease with age (e.g. ZOBEL and TALBERT, 1984). This is not so with the ash BSOs. At Little Hidden Farm and the Mulgrave Estate heritabilities and genetic gain drop slightly. At the Little Wittenham and Scarr Hill they increase slightly. This suggests that heritability is currently a constant property of the sites.

Several conclusions regarding the genetic control of form can be drawn from these results. Hopes that susceptibility to forking may be under a significant degree of genetic control, seem unfounded at this stage, though MARINOV (1979) established that stem form is highly heritable in Bulgarian ash. Forking and straightness are revealed to be the least heritable of the parameters measured. The anomaly at Little Hidden Farm regarding forking is interesting, however, and further trials should perhaps include more sites with no individual tree protection. This would allow a clearer examination of whether lack of protection has made differences between families more apparent.

Owing to the low heritability values calculated for straightness, it was not considered worthwhile calculating genetic gain, since any figure produced would have very low significance in practical terms. This is despite the fact that calculating genetic gain for straightness is common practice in conifer breeding programmes (ZOBEL and TALBERT, 1984). It is likely that significant differences between family means for straightness will increase as the trees get older. It may be viable, therefore, to calculate genetic gain from the next round of measurements.

Branching is revealed to be the most strongly heritable form parameter. Indeed, at the Mulgrave Estate it is more heritable than either dbh or height. This is important since degree of branching is a significant criterion when considering timber quality and utilisation. Correlation analysis did not, however, reveal any useful relationships between degree of branching and vigour. Significant correlations were revealed between branching and straightness and straightness and forking.

Defining these relationships is important since at a later stage it should be possible to create a selection index for the ash trials based on the procedure recommended in COTTERILL and DEAN (1990). Such an index would also require a subjective estimation of the economic weight to be awarded to each parameter. However these decisions have yet to be made in the context of the ash trials and will require wide consultation with the timber industry.

When considering TUKEY's multiple comparisons from the first stage of the genetic analyses it was apparent that, overall, there was little variation in the ash population represented by the Breeding Seedling Orchards, This may be accounted for in two ways. Either the ash population in the UK has emerged from a narrow genetic base, which would certainly account for its demanding site requirements, or, the mother tree selection procedure for these trials significantly biased the gene pool represented.

These speculations could be tested through modern genetic techniques such as isozyme analysis and RAPDs where one could determine the extent and distribution of diversity in the British ash population.

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Evidence for Long-term Heterosis Phenomenon in the *Alnus incana* x *glutinosa* F_1 Hybrids

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Abstract

This report gives the result of investigation carried out with hybrid progenies of the phenotypically negative dwarf *Alnus incana* tree, pollinated with a pollen mixture sampled from 12 plus trees of *Alnus glutinosa*. The experiment covers growth rate, branching type, stem form and morphological character of leaves. Through twenty-eight years of studies the mean height and diameter growth of tested hybrid progenies *A. incana* x *A. glutinosa* were much better than those of *A. glutinosa* paternal population. At age 12 interspecific hybrids showed superior growth-rate over the paternal population on 90%. At age 28 hybrids surpassed the black alder paternal population by 22% in diameter. The trunks were straight with the vital twigs settled at an acute angle. Heterosis was also demonstrated in the bigger leaf size and more abundant production of leaf proteins. Flowering and seed production of hybrids was classified as poor.

Key words: Alnus glutinosa, Alnus incana, hybrids, heterosis, growth.

Introduction

This paper presents results of 28 years of observations of the heterosis (or luxuriance) occurrence in the hybrids between two *Alnus* species: *Alnus incana* (L.) Moench. – gray (or speckled) alder and *Alnus glutinosa* (L.) Gaertn. – black alder. In this context heterosis and hybrid vigor are synonymous. The aim was to produce interspecific hybrids to see, if these would maintain hybrid vigor and if the nondesirable characters such as poor shape and slight diameter growth would be transmitted from mother to F_1 hybrid generation. Such unwelcome traits like poor shape and stunted growth are frequently observed on the trees growing far away from their range of the massive distribution.

Both alder species belong to the important European trees of the genus *Alnus* (Mill.) occupying two different ecological niches. In the Poland the gray alder has two regions of the occurrence. The main one in southern Poland where it frequently grows on the slopes of Sudeten and Karpathian Mountains, used in the past for the agriculture purposes, and the second location in the northern Poland all along the Baltic see-shore. Sporadically isolated trees of gray alder appear along the rivers throughout Poland, producing viable seeds, also following selfing. In opposite to many plants selfed progenies of some alder species in Chiba studies (1966), frequently didnít show apparent decrease of growth. Black alder is most abundant and commercially important alder species in Europe. It occupied moist sites in lowlands of Poland producing very valuable hardwood timber resistant to decay in moisture soil. Both species posses nonleguminous nitrogen-fixing root nodules that seem to be of considerable ecological significance on poor forest and farmland sites. This may contribute to the fertility of the forest soil and prevent erosion of soil suitable for agriculture.

The first controlled interspecific crosses in trees, that have yielded a progeny with heterosis, was probably done on alders by Klotsch (1854, after Svoboda, 1957). Luxuriance however was not always observed at the alder interspecies hybrids