species would be produced in it. Most of the plantations of this species in Pakistan are a mixture of hybrids of different species of Eucalyptus, which are generally of F2 and subsequent generations as well as of back crossing, and produce considerably variable material, which is not suitable for planting purpose. The stem form of trees from such seed is especially poor. About 100 kilograms of seed was collected from the test plantations of this study and supplied to field officers during 1977. Appreciable gain is expected as there is a 3 : 1 ratio in wood volume production of the fastest and slowest growing seed sources and only the best available trees were left in the test plantation to produce seed. The plantation is sufficiently large (1.5 hectares) for seed production purpose and planting of other species of *Eucalyptus* species in its vicinity which could hybridize with *Eucalyptus camaldulensis* is being avoided.

Conclusion

Large variations in the performance of 13 seed source of *Eucalyptus camaldulensis* have been observed in a 10-year old provenance study of this species at Peshawar. The observed differences of growth among various provenances are statistically significant, consistent with earlier observations and quantitatively large enough to warrant selection of the fast growing seed sources for planting. Any reduction in wood specific gravity of fast growing provenances was found to be more than compensated by increased wood volume production in them. The growth rate of the fast growing provenances in this study compares very favourably with the yield of shisham and babul plantations under similar site conditions.

Literature Cited

1. Ahmad, G. and S. M. Iqbal: Eucalyptus: An assessment of its performance in West Pakistan. Bureau of Agricultural Information, Lahore. 18 p (1964). — 2. Boden, R. W.: Eucalyptus in West Pakistan. Report to Government of Pakistan through Australian Department of External Affairs. Canberra, Australia. 20 p. (1967). — 3. Brockway, G. E. and M. I. R. Khan: Eucalyptus introduction and cultivation in West Pakistan. Pakistan Jour. For. 6 (4): 245—258 (1956). — 4. Burgess, I. P.: A provenance trial with Blackbutt: 9 year results. Australian Forest Research 7 (1): 1—9 (1975). — 5. Nawaz, M.: Introduction of fast growing tree species in West Pakistan. Government of West Pakistan, Lahore. 74 p. (1963). — 6. Hafeez, M. and M. I. Sheikh: *Eucalyptus camaldulensis* Dehn. Provenance trial in West Pakistan. Pakistan Jour For. 22 (4): 407—416 (1972). — 7. Karchon, R.: The relation of seed origin to growth of *Eucalyptus camaldulensis* Dehn. in Israel. Israel Jour. Agri. Research 23 (34): 159—173 (1974). — 8. Khan, M. I. R.: The Genus *Eucalyptus*, its past and future in West Pakistan. Pakistan Jour. For. 5 (4): 202—215 (1955). — 9. Pryor, L. D.: Past performance and future prospects for the use of *Eucalyptus* in West Pakistan. UNDP-FAO, Pakistan National Forestry Research and Training Project. Report No. 1 Peshawar. 20 p. (1967). — 10. Qadri, S. M. A.: The selection of Australian species for afforestation in West Pakistan: A rational approach. Department of Agriculture, Government of West Pakistan, Lahore, 144 p. (1968). — 11. Smith, D. M.: Maximum moisture content method for determining specific gravity of small wood samples. U.S. For. Serv. Rept. 2014. For. Prod. Lab. Madison, Wisc. 8 p. (1954). — 12. Wright, J. W.: Genetics of Forest Tree Improvement. F.A.O. Rome, Italy. 316—321 (1962).

A study of population variation and inheritance in sitka spruce

I. Results of glasshouse, nursery and early Forest progeny tests

By C. J. A. Samuel and R. C. B. Johnstone

Forestry Commission, Northern Research Station, Roslin, Midlothian, Scotland EH25 9SY

(Received November 1978 / January 1979)

Summary

The juvenile height growth of 116 families derived from open-pollinated seed collected from a random sample of trees in a 34-years-old plantation of Sitka spruce of Queen Charlotte Islands origin has been studied in a nursery, glasshouse and forest tests on three sites. Annual estimates of heritability up to the sixth year are not outstandingly high. The results are discussed in relation to the reliable interpretation of juvenile assessments, the gains to be expected from a number of methods of breeding and modifications to the breeding strategy for the species.

Key words: *Picea sitchensis*, Height growth, Progeny test, Variance components, Heritability.

Zusammenfassung

150 Einzelbaum-Nachkommenschaften aus einem 34 Jahre alten Bestand von *Picea sitchensis* (Bong.) Carr. in Schottland, in denen auch solche von sog. Plusbäumen enthalten waren, wurden sowohl im Gewächshaus als zugleich in der Baumschule sowie auf drei Waldstandorten auf die Entwicklung von Höhe, Durchmesser, Anzahl der Zweige und Zweiglänge hin untersucht. Die Nachkommenschaften der sog. Plusbäume zeigten im Alter 6 einen Wachstumsvorsprung von 4,1% gegenüber dem Mittel aus allen untersuchten Nachkommenschaften, wobei jedoch das Mittel aus den 5 wüchsigsten aller Nachkommenschaften 14,2% höher lag. Bis zu diesem Alter konnte nur eine relativ niedrige Heritabilität festgestellt werden. Die Ergebnisse werden im Zusammenhang mit dem aus einigen Züchtungsmethoden zu erwartenden genetischen Gewinn besprochen.

Introduction

A soundly-based breeding strategy for any species depends on reliable information on the underlying variation and pattern of inheritance of the characters for which selection will be made. When accurate estimates of genetic variances are available, it is possible to make realistic predictions of times and costs likely to be incurred under different breeding schemes and selection intensities.

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is the most widely used conifer for commercial forestry purposes in

Britain and accounts for more than half of the Forestry Commission's planting programme. Since the mid-1920's more than eight per cent of the seed used for plantation work has been imported from the Queen Charlotte Islands in British Columbia, Canada. It was important, therefore to study the inherent variation within a typical population derived from seed from this source. Ideally such a study should be completed before a selection and breeding programme begins. The need to progeny-test trees from all size classes within a population was recognized but early progress was hampered by the infrequency of very heavy seed crops. A suitable opportunity to collect seed from a stand in which cones were being produced on all size-classes of tree did not occur until 1969. By this time the main selection and progeny testing programme had already begun following traditional lines, but even so it was decided to attempt a detailed study to indicate the value of this programme and more importantly provide guide-lines for future development. The main aim of this study was to estimate genetic variances within a population of Sitka spruce which is representative of the material most commonly planted in Britain and which forms the basis of the main breeding programme. From the estimated genetic variances and from derived estimates of heritability the genetic gains from the current breeding programme and from alternative strategies can be compared. Progeny tests concerned with this study will be long-term and annual assessments of vigour are proposed for as long as practicable. The study of significant changes in family rank may enable the assessment and selection criteria used in the breeding programme to be refined. A number of detailed measurements were also made on the original parent-trees in the population and the relationships between these (or combinations of them) and the performance of their progeny under test will be investigated. Whilst the information on the parent trees was collected by destructive sampling, grafted material of each parent is available in a clone bank. This will afford the opportunity of controlled crossing programmes and subsequent progeny testing aimed to give estimates of non-additive genetic variances since only seed from open-pollinations collected from the parent-trees themselves formed the basis of the initial progeny tests.

The performance of open-pollinated families in an early glasshouse test and in forest experiments up to the sixth growing-season will be considered here, together with the early estimates of variance components and heritability which they afford. The detailed measurements made on the parent trees and their correlation with progeny performance will be considered in a subsequent publication.

Material and Methods

1. *Details of the parent population and site*

In 1969 an 8 hectare stand of 34-year-old Sitka spruce in South Strome forest in north-west Scotland was chosen for study. The stand has a latitude of 57° 12' N and longitude of 6° 32' W and occurs from 30 m to 130 m in altitude in a region with an average annual rainfall of 1780 mm. The soil is mainly brown earth with some surface-water gley, on Lewisian gneiss. The site has a south-westerly aspect and uneven topography with shallow gullies.

The stand was planted in 1935 with Sitka spruce from the Queen Charlotte Islands. The plants had been raised from two importations of seed from these islands in 1929 and 1930 which totalled over 1000 kg. Some thinning had been carried out to remove a proportion of the suppressed trees prior to the selection of trees for this study. This thinning had been very light due to the danger of wind-throw. During an initial survey of the stand, trees were subjectively classified as dominant, co-dominant or sub-dominant and the proportion of the crop falling into these classes was estimated. Selection of 144 trees for the study then took place. This selection was essentially random and aimed to reflect the distribution of dominance classes already noted in the stand as a whole. Six "plus-trees" which had been selected previously were also included. The final composition of the sample was: —

	Number	Percent
Plus trees	6	4
Dominant	48	32
Co-dominant	61	41
Sub-dominant	35	23
	150	

The mean total height of these 150 trees was 23.1 m and mean diameter at breast height was 33.9 cm.

In order that progeny tests based on open-pollinated seed could begin immediately, only trees bearing cones were included among the selections but, since the vast majority of the trees in the stand were coning, any bias was considered to be small. Likewise it was assumed that factors such as matched flowering-times were sufficiently favourable for random mating to occur in the population.

In the autumn of 1969 climbers collected approximately 100 wind-pollinated cones from each of the trees in the study. These were then kiln-dried and the seed extracted. All of the 150 trees produced seed in sufficient quantity for sowing in subsequent progeny tests. Progeny testing was carried out in two phases, an early-test in which plants were raised under intensive conditions in a glasshouse and a more traditional forest test on three sites. The glasshouse experiment was carried out in 1972 and the forest experiments were begun in 1970 when the material was sown in nurseries prior to planting out in the forest in 1972.

2. *Glasshouse test*

i. *Experiment conditions and design*

In February 1972 200 seeds of each parent tree were selected at random. They were pre-chilled for three weeks by soaking for 48 hours in water at a temperature of 3 to 5° C, drained, then placed in closed polythene containers at the same temperature for the remainder of the period. At the end of February the seeds were sown in John Innes seedling compost in covered seed trays. Six weeks after germination, 24 seedlings from each family were pricked out at random into 50 mm × 50 mm fibre pots arranged in a seed tray. In June, 20 seedlings from each family were chosen at random and were repotted into 125 mm × 125 mm plastic pots using a John Innes soil mixture of seven parts sterilised loam to three parts coarse sand.

From germination and throughout the main growing-season a minimum air temperature of 15° C and soil temperature of 20° C were maintained. From the end of September temperatures were gradually reduced until by the end of October only a minimum air temperature of 2° C was being maintained. Extended day-length through artificial lighting was provided to give a total day-length from germination up to the end of April of 15 hours then subsequently until the end of September of 18 hours. It was gradually reduced until switched off in mid-October. Throughout the whole experimental period watering, ventilation and nutrients were maintained at adequate levels.

Of the 150 lots sown, only 131 families provided sufficient plants to be included in the main phase of the experiment after the repotting. A randomised block design was used in which each family was represented by a single plant in each of 20 blocks.

ii. *Assessments and statistical analysis*

The following characters were measured during the dormancy period in December, height (mm); diameter at the root collar (mm); number of branches; length of longest branch (mm); stem form — 1 (good) to 6 (bad).

By December, 4 per cent of the plants had died. As these were distributed throughout most of the blocks the randomised block design was abandoned for the purposes of analysis in favour of an analysis of variance appropriate to a single classification of data.

The partition of the degrees of freedom and the derived expectation of the mean squares are: —

Item	d.f.	*Expectation (MS)*
Between families	130	$\sigma^2_t + 19.18\,\sigma^2_f$
Between plants within families	2382	${}^2\sigma_t$

where σ^2_t is the variance component between plants within families and σ^2_f is the variance component between families. The coefficient of the component between families was derived by the method given by SNEDECOR and COCHRAN (1967) which takes into account the unequal number of plants per family. The component σ^2_f is the covariance of half-sibs estimating one quarter of the additive variance σ^2_A and the component σ^2_t estimates the remainder of the genetic variance plus the environmental variance. Thus an estimate of heritability (narrow-sense) was obtained as

$$\hat{h}^2_N = \frac{4\,\sigma^2_f}{\sigma^2_f + \sigma^2_t}$$

3. *Forest progeny tests*

i. *Experiment conditions and design*

a. Nursery stage

In view of the large number of families to be tested and the intention to plant experiments with up to 49 plant plots on three sites it was necessary to use two nurseries, one at Newton near Elgin in north-east Scotland and one at Fleet in south-west Scotland. The system developed by FAULKNER (1967) was used. Following germination seedlings were lined-out in three randomised blocks, each family represented by up to six lines of 20 plants in each block.

b. Forest sites

Progeny tests were planted at three forest sites fairly typical of the sites in which Sitka spruce is commonly planted in Britain. Two of the sites at Wark and Garcrogo are in the Scotland/England Borders and the third at Tywi in mid-Wales. Site details are given in *Table 1* which shows that major differences in site type only occur between the Welsh and the other two sites where altitude and rainfall are lower.

After two years in the nursery, germination and subsequent losses had reduced the effective number of families from the original 150 and it was only possible to plant 134 families at Tywi and different sets of 125 families at Wark and Garcrogo. At each site the experiments were laid out in three randomised blocks and the plot size (the number of trees in a plot representing each family in each block) varied at the different sites as shown in *Table 1*. The trees were planted at a spacing of 1.8 m $\times$ 1.8 m.

Of the 150 families, 116 are common to all three sites and data from these form the basis of this study.

ii. *Assessments*

At the end of the second growing-season in the nursery, heights of the 40 plants comprising two lines from each family were measured in two blocks at each nursery. Following planting on the forest sites height was measured annually from the first growing-season. The data reported on are for the first six of these annual measurements. At Wark, with the exception of the third year when all 36 plants were measured, only the centre 16 plants were assessed in each plot. At Garcrogo the centre 25 plants and at Tywi the complete 25 plant plots were measured at each assessment.

Table 2. — Breakdown of degrees of freedom and expectations of mean squares for the main analysis of variance applied to the nursery and forest stage progeny.

Item	df	Expectation of MS
Families (f)	115 (114)	$\sigma^2_t + t\sigma^2_p + bt\sigma^2_{fs} + sbt\sigma^2_f$
Sites (s)	2 (1)	$\sigma^2_t + t\sigma^2_p + bt\sigma^2_{fs} + ft\,\sigma^2_b + fbt\sigma^2_s$
Families x sites (fs)	230 (114)	$\sigma^2_t + t\sigma^2_p + bt\,\sigma^2_{fs}$
Blocks within sites (b)	6 (2)	$\sigma^2_t + t\sigma^2_p + ft\sigma^2_b$
Families x blocks within sites (plots (t)	690 (228)	$\sigma^2_t + t\sigma^2_p$
Trees within plots (t)	T	σ^2_t

where f is the number of families = 116 (115), s is the number of sites = 3 (2), b is the number of blocks per sites = 3 (2) and t is the number of trees per plot (harmonic mean). Random effects model assumed. Figures in parenthesis are for nursery, others for forest tests. Values of the harmonic mean of the number of trees per plot (t) and the residual degrees of freedom within plots (T) are given below.

Year	Nursery	1	2	3	4	5	6
t	33.87	20.06	20.84	27.48	20.80	20.80	21.61
T	14993	21357	21686	28569	21635	21638	21633

iii. *Analysis of the Data*

The data from the 116 families common to all three sites were combined and subjected to an analysis of variance of the form shown in *Table 2*.

Due to the varying numbers of trees per plot the sum of squares for the first five items in the analysis were calculated on the basis of plot means and each was multiplied by the harmonic mean of the number of trees per plot. (The values of this for each of the six years are tabulated at the bottom of *Table 2*.) The mean square for the item for trees within plots in the analysis was calculated as the sum of the individual within-plot variances across all plots at all sites.

Because of the varying numbers of plants per plot the harmonic mean was again used as the coefficient t in the expectations of the mean squares shown in *Table 2* and the subsequent calculation of variance components. Narrow-sense heritabilities were estimated from variance components as

$$\hat{h}^2_N = \frac{4\,\sigma^2_f}{\sigma^2_t + \sigma^2_p + \sigma^2_{fs} + \sigma^2_f}$$

Results

1. *Glasshouse early test*

The analysis of variance for a single classification applied to the data showed that there were significant differences between families for all the characters measured. When the families were sub-divided into the different dominance

Table 1. — Details of forest test sites and experimental design.

Location	*Garcrogo* South-West Scotland	*Wark* North-East England	*Tywi* Mid-Wales
Latitude (°N)	55	55	52
Altitude (m)	220	200	440
Annual rainfall (mm)	1400	1220	2500
Length of growing season (days*)	195	179	181
Soil type	Shallow peat	Peaty gley	Deep peat
Blocks	3	3	3
Total families	125	125	134
Plot size	36	49	25

*Calculated by the method of FAIRBAIRN (1968).

Table 3. — Estimates of means, variance components and heritability for the characters measured in the glasshouse progeny test.

	Height (mm)	Diameter (mm)	Branch Number	Branch Length (mm)	Form
Plus trees	246.2	6.25	20.18	175.0	2.84
Dominants	245.9	6.15	20.98	166.8	2.87
Codominant	247.5	6.20	21.03	170.9	2.80
Subdominant	242.6	6.11	20.77	167.4	2.86
σ^2_f	239.7 (4.5)	0.0221 (1.4)	0.919 (2.2)	68.34 (4.1)	0.047 (2.3)
σ^2_t	5075.0	1.5900	40.660	1609.10	1.995
$\bar{h}^2$	0.180	0.055	0.088	0.163	0.092

Figures in parenthesis are σ^2_f expressed as a percentage of the total variance.

Table 4. — Analysis of variance of height in the nursery and during the first six years at forest sites.

Item	Nursery df	Nursery MS	Forest (MS) df	Year 1	2	3	4	5	6
Families	114	23.9 NS	115	42.2 ***	98.9 ***	196.6 ***	464.9 ***	879.8 ***	1425.1 ***
Sites	1	239.7 NS	2	659.8 *	15541.3 *	21007.5 ***	2877.0 NS	5289.5 NS	34426.5 NS
Families × sites	114	10.8 ***	330	10.4 ***	31.4 ***	71.7 ***	153.4 **	215.8 NS	352.6 NS
Blocks within sites	2	293.9 ***	6	121.0 ***	878.2 ***	2471.3 ***	5467.7 ***	9449.4 ***	13917.9 ***
Families × blocks within sites (plots)	228	13.5 ***	690	6.2 ***	21.1 ***	47.9 ***	116.7 ***	190.2 ***	311.3 ***
Trees within plots	[1]	1.0	[1]	1.9	8.0	12.5	28.0	47.6	65.3

[1]) df tabulated in *table 2*.
NS not significant.
* significant at < 5% level.
** significant at < 1% level.
*** significant at <0.1% level.

classes from which the parent trees derived, however, no differences among dominance class means were found. This information is summarized in *Table 3* from which it is clear that the group of families with the greatest expression for any character does not consistently derive from the plus tree or dominant class.

Table 3 also gives the estimated variance components among families and among plants within families together with an estimate of narrow-sense heritability for each character. The component between families consistently accounts for only a small percentage of the total variance and thus estimates of heritability are not high.

2. *Forest progeny tests*

i. *General analysis of variance*

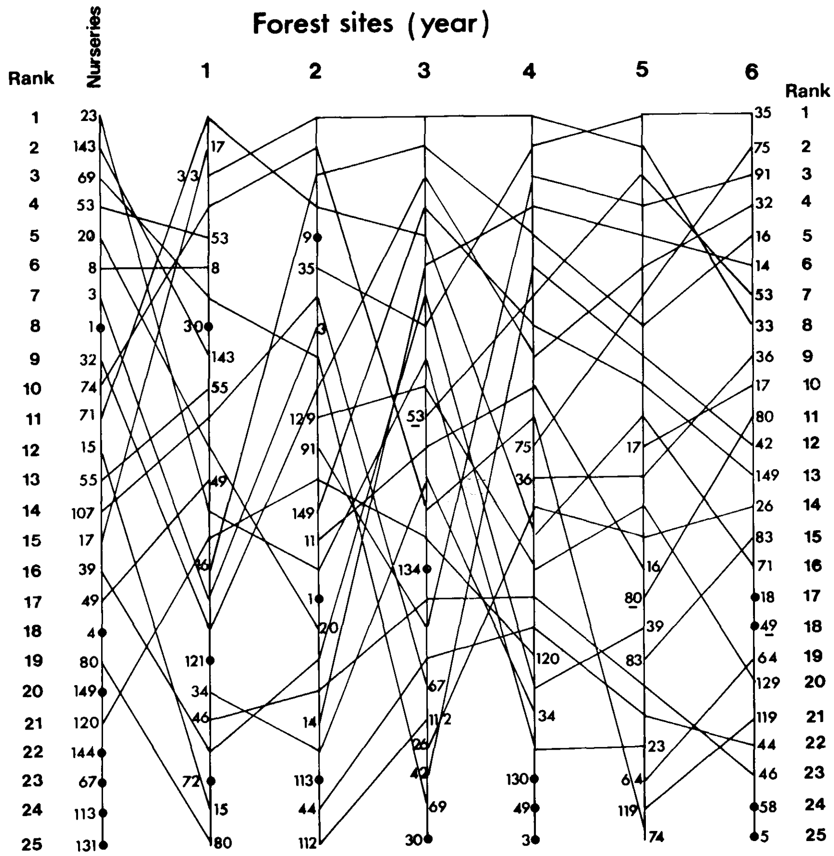
The height measurements from the two nurseries and from each year at the three forest sites were combined and an analysis of variance of the form described in *Table 2* was applied. The results of this are tabulated in *Table 4*. Most of the items are highly significant with the exception of those for sites and the families × sites interaction. The differences between sites fail to reach significance in the nursery assessment and from the 4th year onwards in the forest tests. In fact at the sixth year mean growth on the best site (Gargrogo) was 1.90 metres with that on the poorest site (Tywi) only 0.19 metres lower. The families × site interaction is also non-significant in the nursery assessment and from the 5th year in the forest test indicating little differential ranking of families at the different sites. The similar performance of families in the two nurseries reflects the comparable refinement of techniques used at each nursery in raising experimental plants. At the forest stage these findings are chiefly a reflection of the sites themselves which, as stated before, fall close to the average conditions in which Sitka spruce is grown in Britain. They also confirm other work reported by Johnstone and Samuel (1978) which considered the potential of these sites among a number of more extreme ones by comparing the performance of a wide variety of selected material of this species.

The chief importance of these analyses of variance is to show the significance of the variance components in the random model assumed. Estimates of these and their associated genetic parameters are given later.

ii. *Relative performance of individual families and dominance classes*

A detailed presentation of the performance and ranking of the families at each assessment would be largely irrelevant to this study since the parents are unselected and therefore of no individual importance in the breeding programme for Sitka spruce. At the six year assessment, family performance ranged from 2.17 m to 1.50 m around the mean height of 1.90 m previously noted. In addition to providing estimates of variance, however, these progeny tests can provide information on the consequences of making selections at different ages by considering the rankings of individual families at each assessment. Overall family means across the two nursery and three forest sites are compared in *Figure 1* which is a diagrammatic representation of the changes in rank among the tallest 25 families (an arbitrarily selected number) during the six seasons.

From the figure it is clear that many families appearing tallest in the nursery and the first year in the forest tests do not subsequently rank among the tallest 25 and that few of those which do re-appear persist through to the sixth year. Many changes in rank then occur between the second and third year and a number are then reversed between the third and fourth year. The effect of this is an



67 • Single occurrence in that assessment

49 Recurrence in a later season

Figure 1. — Changes in rank among the tallest 25 families from the nursery through the six annual forest stage assessments.

impression of family performance at these early assessments, and notably so at the third year, which may bear little relationship to performance in later seasons. From the fourth season onwards, family rankings are more steadily maintained.

These trends are summarized in *Table 5* in which the numbers of families recurring in later seasons out of the original tallest 25 families in any one season are recorded. Close study of the table shows that persistent occurrence in later seasons improves in the later assessments. Reading *Table 5* horizontally, therefore, from the 25 tallest families in the nursery only 18 appear in year 1 in the forest, 10 in year 2 and so on, whereas from the 25 in year 4, 20 appear in year 5 and 16 in year 6. Alternatively, reading *Table 5* vertically it becomes clear that of the 25 tallest

Table 5. — Numbers of families among the tallest 25 in any one year and their recurrence in subsequent years.

	Recurring in year: N	1	2	3	4	5	6
N	25	18	10	8	6	5	2
1		25	14	12	10	8	5
Present in year 2			25	20	17	15	11
Present in year 3				25	20	18	14
Present in year 4					25	20	16
5						25	21
6							25

N = nursery

Table 6. — Representation of parents in the four dominance classes by the 25 tallest families in each year (Per cent).

	Year: N	1	2	3	4	5	6	Parents
Plus trees	8	12	8	8	12	8	8	4
Dominants	36	40	28	32	36	40	52	34
Codominants	36	32	44	48	40	40	36	40
Subdominants	20	16	20	12	12	12	4	23

N = nursery

families in year 6, 21 were also among the tallest 25 in year 5, 16 in year 4 and so on down to 5 families which held ranks among the top 25 over all the 6 seasons and only 2 families from the nursery stage onwards.

In addition to providing the type of information on changes of rank discussed above, consideration of the top ranking families can also throw light on the process of phenotypic selection. In *Table 6* the tallest 25 families in each year have been classified according to the dominance class of their parents and the numbers of families from parents of each dominance class are presented for each year as percentages — in order to compare them with the percentages of the 116 parents in the different dominance classes.

It is clear that in the nursery and the first two years in the forest the lowest three classes are represented in pro-

Table 7. — Estimates of variance components for the height assessment in the nursery and during the first six years at the forest sites.

	Nursery	Forest					
		Year 1	2	3	4	5	6
Families	0.097	0.176	0.360	0.505	1.660	3.547	5.515
Sites	—	0.077	2.020	1.936	—	—	—
Families × sites	—	0.069	0.166	0.289	0.588	—	—
Blocks within sites	0.072	0.049	0.355	0.760	2.218	3.838	5.428
Families × blocks within site	0.368	0.214	0.626	1.287	4.264	6.854	11.385
Trees within plots	1.031	1.923	8.018	12.481	28.043	47.645	65.325
Narrow-sense heritability	0.317	0.296	0.157	0.139	0.193	0.244	0.268

Components with no value given are for items with non-significant mean squares.

portions which are similar to the parents as a whole and that thereafter the proportion of sub-dominants falls. Only in the sixth year is there a preponderance of families from parents in the top two classes. When the plus trees alone are considered, out of 5 occurring in the 116 parents, only three are represented among the tallest 25 families in all years and only one of these consistently emerges among the tallest 10 families. Again these findings point to the need for caution in the early interpretation of progeny tests but, in addition, they place in debate the practice and achievement of phenotypic selection based on relative size. In a traditional programme, trees would be selected on the basis of phenotype from the plus trees and dominant classes. Not only do many families from parents in these fail to rank among the tallest, but equally importantly a large proportion of the tallest families come from parents in the lower dominance classes, some even from the sub-dominant or slowest-growing members of the original forest stand.

iii. *Estimates of variance components and heritabilities*

Variance components calculated by the methods outlined previously are tabulated in *Table 7*.

The larger components are due to trees within plots and to plots themselves, the component between families being of the same order as that for blocks. Components for sites and families × sites have not been estimated when the mean squares for these items have been non-significant at the 5 per cent probability level. An estimate of narrow-sense heritability for each assessment is given in the last line of *Table 7*. A high value is obtained for nursery height and height in year 1 in the forest; the estimates fall in years 2 and 3 and then rise through to year 6. This trend can be compared with the pattern which emerged from *Table 6*. In the most recent forest assessments, heritability is found to be high in those years when families from parents among the best phenotypic groups predominate among the tallest, but higher values are also obtained from the nursery and first-year forest assessments. This could be associated with a juvenile phase of growth in which the effects of seed size are perhaps important.

Discussion

Good estimates of genetic parameters form an important basis for meaningful breeding work. This study has centred on a population which is representative of the majority of Sitka spruce grown in Britain and it is from such populations that selected material has entered the breeding programme for this species. The initial progeny tests reported here are based on families grown from open-pollinated seed of 116 out of an original sample of 150 trees randomly distributed throughout all phenotypes in the parent population. The progeny tests have been planted on three sites which typify the locations on which Sitka spruce is commonly planted.

The glasshouse test, nursery test and annual height assessments in the forest experiments have provided the chance of close scrutiny of the ranking of families for vigour over this initial period of growth. A correlation between assessments which diminishes as the time between the assessments increases was noted by Johnstone (1973) who considered height at the traditional 1, 3, 6 and 10 year assessments in a Scots pine progeny test. The results from the annual height measurements made in this study have indicated that juvenile assessments do not necessarily provide information on family performance which bears a close correspondence to performance in later years and that it is only from the fourth year onwards that extreme changes in rank become less evident. Thus although selection on the basis of early progeny-test information is one means of advancing progress in breeding work, these results indicate that it cannot proceed with any confidence until after 4—6 years; this finding is in general agreement with those of Nanson and Baradat (1976).

Selection for height on the basis of the glasshouse as opposed to the early forest test performance of families would be equally uncertain. Of the families common to both glasshouse and forest experiments, only nine ranked among both the top 25 for glasshouse height and the families occurring in the top 25 from the fourth year onwards in the forest. Likewise only nine of the tallest families raised in the glasshouse appear among leading families in the nursery. In addition, the variance components between families account for no more than 4.5% of the total variance for all the characters measured in the glasshouse and the associated estimates of heritability are much lower than these estimates in the nursery and forest. Clearly therefore there is little evidence to emerge from the record of early performance under the intensive conditions used in this study which would justify confident selection from the glasshouse test.

The family performance results cast great doubt, furthermore, on the achievement to be gained from a system of phenotypic forest selection. Traditionally, breeding programmes rely heavily on the screening of plantations for outstandingly vigorous phenotypes or plus-trees. Of six such trees included among the parents in this study, only two appeared among the top 25 families in the glasshouse. The families of five were present in all progeny tests but only two of these appeared in the top 25 in the nursery and only three appeared similarly in any of the six forest-stage assessments, only one of these ranking consistently among the top families at all assessments.

The mean of the families deriving from the five plus trees is 4.1% higher than the mean of all families for sixth year height but the mean of the five tallest families at the same assessment is 14.2% higher than the overall mean. This highlights two alternative methods of screening for basic breeding material. On the one hand the present study has identified parents, from throughout the range of vigour found in the population, the best of which have yielded open-pollinated families with a 10% greater height than the mean height of the families of plus-trees. In addition, the trees were all flowering heavily so that an open-pollinated test could be made immediately after selection. This can only contrast with the plus trees which yielded on average less vigorous families and which are not always found to be flowering at the time of selection, thus delaying the process of open-pollinated testing until perhaps flowering of grafted material in a clone bank is in progress.

These facts were suspected from the results of an earlier study in Scots pine and when the results of the earlier assessments of this study became available a new system of screening for potential breeding material was adopted for Sitka spruce. Under this scheme, populations of known origin or interest are screened for trees which are of good form and flowering reasonably well but without placing a heavy emphasis on vigour. Not only does this enable the immediate progeny testing of new selections, but it is possible to estimate selection intensities more meaningfully than in previous plus-tree selection work and so to predict gains from various schemes of further improvement. In addition unit costs for mother tree selection are vastly lower.

However, the maximization of selection differential is important when considering the estimates of heritability which have been obtained in this study. Whilst these are notably higher in the nursery and first year in the forest and lower during the second and third year in which notable changes in family rank take place, they approximate to 0.25 in the more reliable fifth and sixth years. Thus gain from individual tree selection would not be high. Various simple schemes of selection using variance component estimates derived from the sixth year height and formulae given by SHELBOURNE (1969) can be considered. Simple mass selection, that is, collecting seed from the best 5%, say, of the parent phenotypes would give an expected gain of 1.4%. This would be doubled (2.8%) if the parents were isolated in a seed stand or untested clonal orchard. With progeny testing and subsequent retention of 50% of the clones in such an orchard, gain would be increased to 4.3%. None of these gains is particularly high and the heritability estimates obtained would suggest that selection procedures which exploit non-additive variation would give greater rewards. More important information from the continued annual assessment of these tests, which will monitor any further trend in heritability and family ranks, together with estimates of non-additive genetic variances which will result from progeny tests of material from controlled crosses among the parent trees, will clarify these facts and influence future breeding strategy.

Acknowledgements

The experimental programme was initiated by Mr. R. FAULKNER and the selection of parent trees and progeny testing of the material were undertaken by Dr. A. M. FLETCHER. The authors wish to thank many members of staff of the British Forestry Commission Research and Development Division for technical assistance and for work on statistical analysis.

Literature Cited

FAIRBAIRN, W. A.: Climatic zonation in the British Isles. Forestry 41: 117—130 (1968). — FAULKNER, R.: Procedures used for progeny testing in Britain with special reference to nursery practice. For. Rec. For. Commn. London. 60 (1967). — JOHNSTONE, R. C. B.: An approach to selection for second phase clonal seed orchards. Paper for International Symposium on genetics of Scots pine, 1973. Warsaw: Polish Academy of Sciences (1973). — JOHNSTONE R. C. B. and SAMUEL, C. J. A.: The interaction between genotype and site. Its influence on tree selection programmes in Britain. Res. Div. Pap. For. Commn. Lond. 122 (1978). — NANSON, A. and BARADAT, P. H.: Juvenile — mature relationships. Proc. Joint IUFRO, Meeting on Advanced Generation Breeding, Bordeaux (1976). — SHELBOURNE, C. J. A.: Tree breeding methods. New Zealand Forest Service. Technical Paper No. 55 (1969). — SNEDECOR, G. W. and COCHRAN, W. G.: Statistical Methods. 6th Edition Iowa State University Press, Ames, Iowa (1967).