

based on just the k groups in common. One can expect $\hat{\sigma}_{\varepsilon_i}^2$ and $\hat{\sigma}_{\varepsilon_j}^2$, being based on many more degrees of freedom, to be subject to much less bias or sampling errors resulting from differences between environments in samples of groups than would $\hat{\sigma}_{g_i}^2$ and $\hat{\sigma}_{g_j}^2$ or conventional estimates of $\sigma_{g_i}^2$ and $\sigma_{g_j}^2$. Indeed, estimates based on more than k groups are likely to be superior in many situations. Equation 3 therefore offers a method that can give convenient and robust correlation estimates while making full use of available information.

Even without missing or unbalanced data Equation 3 can be convenient to use. This is particularly where one wants to explore between-environment correlations for alternative subsets of genetic groups, since genetic parameters are meaningful only in relation to specified populations. This would, however, depend strongly on $\sigma_{\varepsilon_i}^2$ and $\sigma_{\varepsilon_j}^2$ being constant among subsets.

Equation 3 also has the advantage of requiring exchange of the minimum necessary information between organisations involved in collaborative studies of the genetic correlations.

There will be some situations where using Equation 3 may not be ideal, not that alternative approaches would necessarily be better. Obvious difficulties could arise where the presence or absence of groups in different environments reflects differential truncation selection between the environments. Any truncation selection tends to lead to poorer estimates of genetic correlations. A simulation study by VAN VLECK (1986) indicated that the problem is one of reduced precision rather than inherent bias; truncation selection was associated with an increased incidence of r_g estimates outside the bounds $+1$ and -1 , or even imaginary estimates (resulting from $\hat{\sigma}_{g_i}^2$ and/or $\hat{\sigma}_{g_j}^2 < 0$). While VAN VLECK considered only Type A correlation estimates there is every reason to believe that his findings would apply equally to Type B estimates.

In such a situation, though, the use of Equations 1 and 2 would be equally affected, and even the study of interaction by variance component estimates would be subject to bias.

If, within individual environments, different groups are represented by markedly unbalanced numbers of individuals there will also be problems. For Equation 3 single overall values would then not apply to $\sigma_{\varepsilon_i}^2$ and/or $\sigma_{\varepsilon_j}^2$. The problems, however, would not be specific to the use of Equation 3.

If the representation of different groups, however unequal, is in consistent ratios between environments it should then be appropriate to use Equation 2, provided group means are weighted, in calculating the denominators of the equations, according to the numbers of individuals in which the respective groups are represented. With even more troublesome imbalance it would seem appropriate to use analysis of variance with environments as a main effect, and study interaction by the traditional approach of estimating variance components. That, however, might entail accepting that no satisfactory estimates can be obtained of the genetic correlations that reflect the more meaningful aspect of interaction.

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The Estimation of Genetic Parameters for Growth and Stem-Form over 15 Years in a Diallel Cross of Sitka Spruce

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Abstract

Regular measurements of total height from the first to the 15th year after planting were made on families comprising a full diallel cross among 7 parent trees of Sitka spruce (*Picea sitchensis* BONG., CARR.) planted on 2 test sites. Diameter at breast height was measured at intervals after the 8th year and a subjective straightness score was made after 14 years. Although analysis revealed significant proportions of additive variation for height at most assessments, non-additive effects were more highly significant and usually accounted for a greater proportion of variation. In contrast, diameter was under predominantly additive control and straightness appeared to be equally subject to both additive and non-additive effects. The results are discussed with reference to the

current breeding strategy for Sitka spruce in Britain which includes techniques for exploiting the type of genetic control of growth traits suggested by their results.

Key words: *Picea sitchensis*, diallel cross, variance components.

Introduction

Among the forest tree species of commercial importance in Britain, Sitka spruce (*Picea sitchensis* BONG. CARR.) is used in by far the greatest proportion; the species accounts for around 70% of current planting. During the last 20 years, the main breeding effort in this species has concentrated on phenotypic selection and half-sib progeny-testing; over this period more than 3500 selec-

Table 1. — Comparative details of the 2 experimental planting sites.

	Bush	Tywi
Latitude N (°)	55.86	52.24
Longitude E (°)	3.79	3.20
Elevation m	200	420
Rainfall mm	1750	1800
Soil	Brown earth	Deep peat
Vegetation	Commercial grasses	Molinia-predominant sward
Previous land use	Mixed agricultural use	Hill grazing land

tions have been made and 65% of these are represented in forest-stage tests (LEE, 1986).

A study in which individuals from a single population were chosen at random without phenotypic selection and progeny-tested as half-sib families was reported by SAMUEL and JOHNSTONE (1979). From this material, confident estimates of additive genetic variance were obtained. Narrow sense heritabilities were around 25% for annual total height during the first 6 years after planting. However, these studies offered no information on factors other than additive genetic variances.

Information on non-additive patterns of inheritance is nevertheless available from full-sib families of Sitka spruce that resulted from the use of a full diallel mating design among 7 parent trees in an extensive artificial pollination programme carried out in 1968. These families were the subject of detailed investigation in an early glasshouse test reported by SAMUEL et al. (1972). The results reported here follow the growth of this material in two forest progeny-test experiments and provide information on additive, non-additive and reciprocal effects at various assessments during the first 15 years after planting. From this information, inferences are made about the breeding strategy appropriate to Sitka spruce in Britain.

Material and Methods

The parent trees were selected in a small stand of Sitka spruce planted in 1933 in Roseisle Forest, Grampian Region, Scotland and the crosses were made during the spring of 1968. Further details of the source of parents and pollination techniques are given by SAMUEL et al. (1972). At the end of the glasshouse experiment which they reported, half the plants were transferred to a field experiment site at Bush Research nursery, Lothian Region, Scotland. This trial was laid out in 3 randomised complete blocks in which each family was represented by a line plot of 4 trees in each block. The trees were planted in the spring of 1970 at 1.8 m square spacing.

Further seed of the same crosses was sown in 1969 and plants were raised at Alice Holt nursery, Hampshire, England. Standard procedures for raising progeny-test material during the nursery stage (FAULKNER, 1965) were used. In the spring of 1971 these families were planted in Tywi forest, Dyfed, Wales. This trial was laid out in six randomised blocks in which each family was again represented by a 4-tree line-plot in each block. Summarised details of the two planting sites are given in Table 1.

The total height of every tree was measured at the end of each growing season up to the 15th after planting at Bush (omitting years 1, 7 and 8) and up to the 13th year at Tywi. Diameter at breast height (1.3 m) was

measured at Bush at the end of the 13th, 14th and 15th seasons and at Tywi at the end of the 12th, 13th and 15th seasons. An early diameter measurement at a height of 0.5 m above ground had been made at Tywi after 8 seasons. At the beginning of the 9th season an application of PK fertiliser (230 g of 0:20:20 compound fertiliser broadcast around the base of each tree) was given to blocks 1, 3 and 5 only at Tywi as part of an exercise, subsequently abandoned, to study family x fertiliser interaction. A diameter measurement after 11 years was carried out at 0.6 m above ground in the fertilised blocks and 0.5 m in those unfertilised. A subjective score on the scale 1 (= best) to 6 was given to each tree in order to classify it for acceptability of stem straightness and form after 14 seasons at Bush and 13 at Tywi.

The original crosses formed a complete 7×7 diallel set including all selfs. The 7 parents were designated A, C, D, G, H, J and K. All families were represented in sufficient numbers for the full set to proceed to the Bush field test. At Tywi, however, insufficient quantities of seed and survival of plants among those raised in the nursery meant that all families from the C array had to be abandoned. This, in combination with the failure of selfed families from 3 of the parents effectively reduced the experiment at Tywi to a full 6×6 diallel with no selfs.

Statistical Analysis

The main analysis of the data from both experiments has been based on the generalised analysis of variance outlined by GRIFFING (1956). The Bush data accord with his Experimental Method 1 and the Tywi data with his Experimental Method 3. In both methods, three effects are recognised into which the variation among families may be partitioned: general combining ability (gca), specific combining ability (sca) and reciprocal effects. These correspond respectively to the a, b and the sum of the c and d items in HAYMAN'S (1954) analysis previously used by SAMUEL et al. (1972) in their report of the early test of the same material. Omission of the data from selfed families and those in the C array at Bush enabled the experiments to be combined in a joint analysis across both test sites.

Results

This report covers the results and statistical analysis of more than 50 field assessments the aim of which has been to establish trends with time in the values of important genetic variances which relate to the breeding strategy adopted for Sitka spruce in Britain. It has thus been necessary to condense the presentation of the results severely from the form of tables of family means arranged in a diallel pattern together with row, column

and array means (as in Table 2) and their associated analyses of variance (as in Table 3). Such results are given as examples only for height at the end of the 6th season at Bush. This assessment is fairly typical of most assessments, illustrates some of the variation which will be subject of later analyses, and represents the stage in routine half-sib progeny-tests at which initial selections are made in the main breeding programme for Sitka spruce. Differences among overall means in table 2 reflect differences in gca among the parents. Sca effects can be observed by comparing reciprocal means in the body of the table with means of the two contributing parents among the overall means. This comparison reveals both positive (for example H and J) and negative (for example A and D) deviations from expected heights.

Table 2. — Diallel table of family means for height after 6 seasons at Bush.

		Male parents							Female mean
		A	C	D	G	H	J	K	
Female parents	A	1.149	2.064	1.574	1.949	1.897	2.172	1.428	1.748
	C	1.992	1.413	1.738	1.683	1.802	1.890	1.883	1.771
	D	1.494	1.598	1.277	1.583	1.776	1.738	1.624	1.584
	G	1.914	1.767	1.775	1.151	1.923	1.658	1.928	1.731
	H	1.970	1.778	1.796	1.678	1.209	1.863	2.386	1.811
	J	1.778	1.888	1.605	1.833	2.156	1.999	2.109	1.910
	K	1.650	1.842	1.590	2.033	1.753	1.923	1.399	1.742
Male mean		1.707	1.764	1.622	1.701	1.788	1.892	1.823	1.757
Overall mean		1.727	1.768	1.603	1.716	1.800	1.901	1.782	

Table 3 — Analysis of variance for height after 6 seasons at Bush.

Source	Sum of squares	DF	Mean square	F	VC
General combining ability	2.0778	6	0.3463	1.13 ns	0.000289
Specific combining ability	6.4558	21	0.3074	4.62 ***	0.013569
Reciprocal effects	1.3958	21	0.0665	1.55 ns	0.001061
Blocks	0.1183	2	0.0591		
Between plot error	4.1229	96	0.0429	1.07 ns	0.000783
Within plot error	16.8317	421	0.0400		0.0400

Tests of significance: 1 on 2; 2, 3 on 4; 4 on 5; *** = p 0.001; ns = non-significant; VC = estimated variance component.

Table 4. — Summarised results of analysis of variance of Bush data.

Assessment	Mean	σ_p^2	σ_h^2	Significance	σ_g^2	Variance component	σ_e^2
				g s r	σ_g^2	σ_s^2 or σ_r^2	σ_e^2
Ht 02	0.66	0.006	3.8	ns ***	1.7	26.5	9.4
Ht 03	0.87	0.011	3.8	ns ***		28.0	5.9
Ht 04	1.16	0.024	3.2	ns ***		38.9	4.6
Ht 05	1.46	0.041	3.7	ns ***	0.6	27.0	2.4
Ht 06	1.76	0.056	3.7	ns ***	0.5	24.4	1.9
Ht 09	3.28	0.250	3.8	ns *** *		38.1	2.7
Ht 10	4.15	0.320	3.6	ns *** *		39.4	2.2
Ht 11	4.89	0.360	3.6	ns *** *		36.2	2.3
Ht 12	5.67	0.428	3.7	ns *** *		45.3	1.8
Ht 13	6.33	0.491	3.7	ns *** *		42.9	2.1
Ht 14	7.02	0.564	3.6	ns *** *		52.0	1.8
Ht 15	7.82	0.602	3.6	ns *** *		55.2	1.2
Dm 13	10.18	1.758	3.6	ns ***		41.9	58.1
Dm 14	11.16	2.195	3.6	ns ***		45.8	54.2
Dm 15	11.80	2.470	3.6	ns ***		47.1	52.8
St 14	2.12	0.303	3.6	ns ***	1.7	12.2	86.1

Significance levels used in Tables 4, 6 and 7:

ns = non-significant;

= p < 0.10;

* = p < 0.05;

** = p < 0.01;

*** = p < 0.001.

Assessment abbreviations used in Tables 4, 6 and 7:

Ht = height in metres;

Dm = Diameter at breast height in centimetres;

St = straightness score on scale 1 (= best) to 6.

Reciprocal differences may be observed by comparing row and column means for the same parent or by examining specific reciprocal families of the same cross in the body of the table; these two levels of reciprocal difference are not separated in the main analysis. The results of an analysis of variance of these data are given in table 3 in which tests of significance and estimates of appropriate variance components are shown. These are discussed in more detail below, together with the data from other assessments.

Table 4 summarises the results of analyses of the data from each assessment made at Bush. In the table the first column denotes the assessment in coded form in which the abbreviations for height in metres (Ht), diameter in centimetres (Dm) and stem straightness score on the scale 1 (= best) to 6 (St) are followed by two digits identifying the age from planting. For each assessment the following items are given in the table: -

- the overall mean (mean);
- the estimated total phenotypic variance (σ_p^2);
- the harmonic mean of the number of trees per plot (M_h);
- a summary of the significance of the gca, sca, and reciprocal items (g, s and r respectively);
- estimates of variance components for these and error effects, the components denoted as follows: —

σ_g^2 gca

σ_s^2 sca

σ_r^2 reciprocal effects

σ_{fb}^2 between plot residual effects

σ_e^2 within plot residual effects.

The variance component estimates are expressed as a percentage of the total phenotypic variance which is calculated as the sum of all the above components. Components are estimated if non-negative whether significant or not and the harmonic mean of the number of measured trees per plot at each assessment has been used in their estimation instead of the number of trees planted.

Perhaps the most prominent feature of these results is the complete lack of significance of gca effects at any assessment coupled with consistent highly significant sca effects (p < 0.001) at all assessments. Reciprocal effects assume little importance with significance (p < 0.05) for height in years 9 to 14 only. Where estimable, the gca variance component accounts for less than 2% of the total phenotypic variance whilst the sca component accounts for between a quarter and a half at all assessments.

Throughout the life of the experiment, selfed families have contrasted strongly in growth with those from outcrosses. This is clearly shown in table 5 in which overall means of selfs are compared with those of crosses at each assessment. This type of inbreeding depression is to be expected in a naturally outcrossing species such as Sitka spruce. The contrast highlighted in table 5 contributes to the sca variation; in fact this comparison is extracted as item bl in HAYMAN'S (1954) analysis. It is relevant therefore to consider the set of data from which those from selfed families have been omitted. This reduced set is a 7 x 7 full diallel without selfs and the results of an appropriate analysis of variance are summarised in table 6 which has exactly the same format as table 4.

The most general effects of the removal of selfs are the higher overall means and lower phenotypic variances of table 6 compared with table 4. For height, gca effects now reach significance in five assessments at p < 0.05 and a

Table 5. — Comparison of overall means for selfed families with families from outcrosses at Bush.

Assessment	Self	Outcross	Self/outcross %
Ht 02	52.90	68.10	77.7
Ht 03	68.80	90.40	76.1
Ht 04	84.00	121.60	69.1
Ht 05	109.90	152.30	72.2
Ht 06	1.37	1.82	75.3
Ht 09	2.17	3.46	62.7
Ht 10	2.86	4.36	65.6
Ht 11	3.53	5.11	69.1
Ht 12	3.99	5.95	67.1
Ht 13	4.65	6.62	70.2
Ht 14	4.96	7.36	67.4
Ht 15	5.59	8.19	68.3
Dm 13	6.85	10.73	63.8
Dm 14	7.26	11.81	61.5
Dm 15	7.58	12.50	60.6
St 14	2.01	2.79	72.0

further 2 assessments at $p < 0.10$. The sca effect remains highly significant in all height assessments but the reciprocal effects are more often significant from the 10th year onwards. In contrast, only gca effects are significant for diameter at each assessment. These tests indicate that for height some additive control is present but that non-additive effects predominate, whereas for diameter, additive control only operates. A significant but low level of additive control appears to operate for straightness score.

These observations are reflected in the estimated variance components in table 6. Sca variance accounts for around twice as much variation as gca at most height assessments with reciprocal variance accounting for a similar amount to gca. For diameter and straightness, sca and reciprocal variances account for much smaller proportions than gca. The results of the analysis of the data from Tywi are presented in the same way in table 7. Comparison of the overall means in this table with those at Bush (table 6) shows that both experiments had similar rates of growth up to the 6th year, after which the potential for faster growth at Bush became evident. The difference in height was about one metre by the 10th year and over 1.5 metres by the time of the final common height assessment at 13 years when there was a difference in diameter of over 3 centimetres. Phenotypic variances are in general lower at Tywi. Among the significance tests, a similar pattern to that at Bush emerges; for height, sca effects are more highly and consistently significant than gca effects and significant reciprocal effects do not figure prominently. For diameter, significant gca effects predominate, although sca effects are significant at the early 8th year assessment. No effect is significant for straightness score.

Table 6. — Summarised results of analysis of variance of Bush data omitting selfed-families.

Assessment	Mean	σ_p^2	n_h	Significance	σ_g^2	σ_s^2	σ_r^2	Variance component	%
								σ_g^2	σ_s^2
Ht 02	0.68	0.005	3.9	*	5.1	8.8	0.1	10.5	75.5
Ht 03	0.90	0.009	3.9	**	1.5	9.5		9.4	79.6
Ht 04	1.22	0.015	3.2	*	4.2	7.3	3.3		85.2
Ht 05	1.52	0.032	3.8	**	3.0	8.4		3.3	85.3
Ht 06	1.82	0.045	3.8	#	2.9	7.4	2.3	4.3	83.1
Ht 09	3.46	0.177	3.9	#	3.9	9.5	3.1	13.9	69.6
Ht 10	4.36	0.205	3.7	*	4.3	5.0	3.6		87.1
Ht 11	5.11	0.231	3.7	*	3.2	5.1	4.2		87.5
Ht 12	5.95	0.235	3.8	**	2.2	7.6	3.0	10.1	77.1
Ht 13	6.62	0.285	3.7	***	1.8	9.7	4.5		84.0
Ht 14	7.36	0.251	3.7	**	1.7	6.5	4.3	0.4	87.1
Ht 15	8.19	0.230	3.7	*	3.3	2.0	4.0	7.5	83.2
Dm 13	10.73	0.994	3.7	**	4.8	2.4		0.4	92.4
Dm 14	11.81	1.148	3.7	**	5.6	0.1		2.8	91.5
Dm 15	12.41	1.286	3.8	**	4.8	0.1		5.4	89.7
St 14	2.01	0.261	3.7	*	3.3	1.5	0.3		94.9

Table 7. — Summarised results of analysis of variance of Tywi data.

Assessment	Mean	σ_p^2	n_h	Significance	σ_g^2	σ_s^2	Variance component	%
							σ_g^2	σ_s^2
Ht 01	0.49	0.002	4.0	**	14.3	5.9	6.0	73.8
Ht 02	0.67	0.004	4.0	**	11.1	3.7	3.1	82.1
Ht 03	0.87	0.008	4.0	*	7.9	5.8	0.3	84.1
Ht 04	1.23	0.015	3.7	*	9.7	6.0	0.2	83.5
Ht 05	1.47	0.018	3.9	*	11.1	7.0		3.3
Ht 06	1.82	0.027	3.7	**	12.0	5.3		1.9
Ht 07	2.15	0.038	3.7	*	8.6	7.1		0.5
Ht 08	2.47	0.048	3.7	*	6.4	7.9	0.2	2.5
Ht 09	2.95	0.064	3.6	*	5.2	5.5	0.2	4.6
Ht 10	3.34	0.065	3.6	#	4.0	5.2	0.3	4.1
Ht 11	3.80	0.098	3.6	***	2.4	4.6	0.4	2.8
Ht 12	4.40	0.104	3.6	***	1.5	6.2	1.0	3.9
Ht 13	4.78	0.118	3.6	***	0.7	5.7	0.7	3.0
Dm 08	5.29	0.176	3.6	**	6.5	2.0		91.5
Dm 11	7.93	0.425	3.6	*	2.3	0.5		2.1
Dm 12	6.99	0.437	3.6	*	2.7	1.4		95.9
Dm 13	7.56	0.472	3.6	#	2.1	1.5		95.9
Dm 15	9.16	0.629	3.6		2.2	1.8		96.0
St 13	2.28	0.382	3.6		2.2	4.1	0.6	3.5

When the percentage contributions of each variance component are considered, there is a reversal of the situation for height at Bush; often gca accounting for more variation than sca. For diameter the relative proportions are similar to those found at Bush. Another feature of the height results at Tywi is a clear falling trend in the contribution of gca from 14.3% at year one to a negligible 0.7% at year 13.

Combined Analysis Across Sites

Ten height assessments and two diameter assessments were made at the same age in both experiments and were therefore available for a combined analysis across sites. In addition, though the stem straightness assessments were made after 13 years at Bush and after 14 years at Tywi, it seemed reasonable to combine these assessments for an analysis across sites. Such an analysis not only gives tests of significance for the difference between sites and for the main genetic effects across sites but it also provides tests for the interaction of the latter with sites. The data set from Bush was made compatible with that from Tywi by the omission of the data from all families of parent C and all selfed families as a prerequisite of the combined analyses.

For height from nine years onwards there are highly significant differences between sites; these are a reflection of the comparisons of overall means already noted in tables 6 and 7. The results of these combined analyses are presented in table 8 as rounded mean squares. The effects of sites and blocks within sites which are of less interest than the genetic effects have been omitted from the table. For each assessment, a comparison of the mean squares for interactions between genetic effects and blocks within sites with the within-plot mean square indicates that these are fairly homogeneous. However, for the majority of assessments there is a marked contrast between these mean squares and those for the interaction of genetic effects with sites. When the latter are tested against their respective interactions with blocks a large number of them (printed in italics) reach significance at $p < 0.05$. For most assessments, the size of these interactions with sites masks the significance of tests of main genetic effects. In only a few instances (again indicated by italics) do main effects reach significance overall at $p < 0.05$. Only for height at five years and for stem straightness are main effects significant overall without the presence of significant interactions with site.

These analyses confirm the differential expression of genetic effects already noted at the two sites and indicate that more appropriate conclusions must be drawn within

Table 8. — Mean squares from analyses of variance combined across sites.

Item	df	Height										Diameter		Straightness score
		02	03	04	05	06	09	10	11	12	13	13	15	13/14
GCA	5	1032	1533	3743	6516	905	1701	1230	1088	1517	848	5018	7836	3166
SCA	9	197	532	705	1586	185	600	368	437	747	991	1568	1452	751
Reciprocal	15	79	97	214	273	51	128	196	240	311	341	547	637	498
GCA x sites	5	276	365	308	196	66	577	584	664	489	917	6121	6453	361
SCA x sites	9	132	180	273	329	33	260	295	347	344	620	289	427	672
Reciprocal x sites	15	82	113	176	250	56	200	310	350	358	457	476	596	233
GCA x blocks	35	31	80	122	188	21	80	116	131	202	147	524	690	300
SCA x blocks	63	29	76	131	204	34	80	86	113	167	152	572	749	362
Reciprocal x blocks	105	33	84	120	237	33	96	118	122	141	137	617	919	349
Within plots	743—808	32	72	133	199	38	84	105	134	126	166	642	815	313

each site. Such an analysis of the Bush data set, reduced as indicated above, was found to give results very similar to those of the 7 x 7 analysis already presented in table 6.

Discussion

One of the important features of these experiments is that they present the progeny of some of the earliest successful controlled crosses carried out in Sitka spruce in Britain. Furthermore, this complete set of diallel families was among the first to be made in a forest tree species. As pointed out by SAMUEL et al. (1972), when the early growth of this material was reported, there are some shortcomings in the constitution of the set of parents since they were primarily selected on the basis of fecundity and cannot be considered typical of superior phenotypes used in the breeding programme for this species. For the estimates of genetic parameters which the diallel mating design affords, however, it is necessary to consider the extent to which the parents could be taken as a general sample of Sitka spruce phenotypes. The fact that they were not the subject of high selection intensity for vigour supports this view but, in common with much Sitka spruce in Britain of the same age or older, the seed origin of the parents is unknown. It is fairly likely that the plants were from seed which came from the Queen Charlotte islands (the most important and appropriate general source of Sitka spruce seed for British forestry), but there was evidence from extensive analysis of growth patterns in early-tests that at least one of the parents could derive from more southerly latitudes (SAMUEL, unpublished). These are all factors which point to a need for caution in interpreting the results of the analyses reported here in a too wide or definitive context.

Nevertheless, there is a number of clear conclusions to emerge from the analysis of this exhaustive series of measurements. It is obvious that selfed families in the context of an outbreeding species such as Sitka spruce have no serious contribution to make to the evaluation of genetic parameters. When the rather confusing effects of selfs are removed, both additive and non-additive effects have been detected in most analyses. For height and stem straightness, both effects were normally detectable whereas for diameter, additive effects predominated, non-additive effects being often negligible.

In general the proportions of additive variance, despite undeniable fluctuation from year to year, are slightly lower than those found in the population study designed

to estimate these effects (SAMUEL and JOHNSTONE, 1979) in which additive variance accounted for 6% to 7% of the phenotypic variance for height from planting to 11 years and 3% to 4% for diameter over the period 12 to 14 years (SAMUEL, unpublished).

There are, however, clear differences between the relative proportions of additive and non-additive components at the two sites. These are demonstrated in table 9 in which the ratio of additive to non-additive variance is presented for all assessments. These figures have been derived directly from table 6 and 7 since the variance components for gca and sca estimate one quarter of the additive and one quarter of the non-additive variance respectively. (BECKER, 1975). For height, although there are marked contrasts between the two sites, notably during the first six years, there is reasonable agreement in the results over the period from 10 years to 13 years. During the early period, the results are characterised by the high proportions of gca at Tywi. For diameter, the situation is confused by the very large ratios in years 14 and 15 at Bush caused by the very small and non-significant amounts of sca which were nevertheless estimated. If these are disregarded, there is broad agreement among the remaining assessments with higher ratios for

Table 9. — Additive:non-additive variance ratios at each assessment at Bush and Tywi.

Assessment	Bush	Tywi
Ht 01	—	2.42
Ht 02	0.58	3.00
Ht 03	0.16	1.36
Ht 04	0.58	1.62
Ht 05	0.36	1.59
Ht 06	0.39	2.26
Ht 07	—	1.21
Ht 08	—	0.81
Ht 09	0.41	0.95
Ht 10	0.86	0.77
Ht 11	0.63	0.52
Ht 12	0.29	0.24
Ht 13	0.19	0.12
Ht 14	0.26	—
Ht 15	1.57	—
Dm 08	—	3.25
Dm 11	—	4.60
Dm 12	—	1.93
Dm 13	2.00	1.40
Dm 14	56.00	—
Dm 15	48.00	1.22
St 13	—	0.54
St 14	2.20	—

diameter measured at 8 and 11 years. There is reasonable consistency for stem straightness.

Reciprocal effects reach significance in a number of later height assessments at Bush and are estimable at most height assessments. They normally account for smaller proportions of phenotypic variance than the other genetic effects and close examination of the data reveals no consistency when comparing the performance of male and female parentage at either the array of individual cross level.

It is reasonable to conclude in general that height and stem straightness are under stronger genetic control than diameter and that again for height and straightness there is at least as much non-additive as additive variation present. Non-additive variation has little effect on the expression of diameter.

These results have implications for the strategies adopted in the improvement of Sitka spruce in Britain. Reliable data on the amount of additive variance have already indicated the likely achievements from programmes of plus-tree selection combined with clonal orchards. It is now clear that further substantial gains can be anticipated from the use of breeding techniques that specifically exploit non-additive as well as additive variation. These include such methods as the use of biclonal orchards composed of parents with proven specific combining ability or, more importantly, the mass propagation by vegetative means of any good material derived from the exploitation of non-additive variation. Perhaps the most practical among the latter is the propagation of seedling material derived from bulked mixtures of full-sib families proven for sca; the techniques for this are already established (MASON, 1986) and plant material has been raised in commercial quantities from mixtures of proven half-sib families in Britain.

Whilst the results from the experiments reported here point strongly to the use of both additive and non-additive variation in the improvement of Sitka spruce, it would be unwise to attempt to derive anything but broad estimates of genetic gains on the basis of this work. Furthermore, the presence of non-additive variation for height may point to the need for more detailed investigation on this subject. BARNES *et al* (1987), for example, found evidence among full-sib families of *Pinus patula* SCHIEDE and DEPPE of a single gene with possible overdominance controlling diameter growth. In the present study there is also a considerable measure of disagree-

ment between the two sites used and there are some clear trends in the estimates of variance components with time. In particular the fall in the proportion of the total phenotypic variance attributable to gca has also been noted by FRANKLIN (1979) in a number of species, although the present data only encompass the earlier part of the age range he considered. This could also be a consequence of the very small plot size used and the low number of plants per family, notably at Bush. At the later assessments, interaction between adjacent plots could be having a serious influence. A set of crosses comprising an 8 x 8 diallel among parents drawn at random from those contributing to the half-sib population study previously referred to (SAMUEL and JOHNSTONE, 1979) is now complete and should provide sufficient material for progeny testing in larger plots with greater replication on more sites. The results of these further tests should provide more detailed substantiation of those basic conclusions established from the work reported here.

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Giemsa C-Banding in *Fagus sylvatica* L., *Betula pendula* Roth and *Populus tremula* L.

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Abstract

A detailed karyotypic study by Giemsa C-banding has been done in *Fagus sylvatica* L., *Betula pendula* Roth,