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A Diallel Cross in Sitka Spruce
Assessment of First Year Characters in an Early Glasshouse Test

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Summary. The successful pollination of a complete diallel cross among six Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees is described, together with the assessment of a range of characters in the first growing-season of an early progeny-test in a glasshouse. Those characters chiefly concerned with tree form were found to be inherited in a predominantly additive fashion, whilst those characters reflecting various aspects of tree vigour were found to be under additive, dominance and maternal control. The results are discussed in the light of selection criteria and current techniques in Sitka spruce breeding.

Introduction

Over the last two decades the diallel cross has been exploited by many quantitative geneticists and plant breeders. A number of types of analysis have been developed and have provided considerable evidence on the genetic control of various characters in a number of species.

As Libby *et al.* (1969) point out, however, these techniques have not been used to any extent on tree species; the reasons for this are essentially practical. In the *Pinaceae*, the family in which most of the commercially important conifers in Britain occur, the flowers are monoecious. The males usually occur in the lower and the females in the upper parts of the crown. Although some overlapping does occur, the bulk of the pollen of an individual tree is usually shed before the female flowers are receptive. Consequently the pollen has to be collected and stored if self-pollinations or certain specific crosses are to be made. Between-tree variations in the periods of pollen shedding and female flower receptivity may be as much as three to four weeks within a population. The female flowers are only receptive for a few days, and regular inspections at short intervals are necessary to ensure that pollinations are made at the correct time. In addition, for experimental purposes, more than thirty pollinations are usually made for each cross to be certain of obtaining sufficient seed for subsequent progeny tests. When these aspects are considered, together with the fact that female flowers usually occur at a height above the ground which often necessitates climbing, the difficulties of the tree breeders are readily apparent.

A previous attempt (Matthews *et al.* 1960) at a full diallel cross between a number of selected European larch (*Larix decidua* Miller) and Japanese larch (*Larix kaempferi* (Lambert) Carr.) trees failed due to the low seed production from some crosses.

This paper describes the successful pollination and first-year assessment of a complete diallel cross in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Pollinations were completed on seven parent trees but, for reasons to be given, this was restricted to a 6×6 diallel for analytical purposes.

Some attention has recently been focused on the use of early-testing procedures under controlled environmental conditions in the assessment of forest tree progeny (Schmidt 1957, Nanson 1968, Herbert 1971). In the light of this, the use of a glasshouse for raising progeny in the first growing-season and their assessment from measurements of a number of young plant characters will be described.

Material and Methods

Crossing Programme

Parents. In 1933, a small stand (approximately 0.4 ha) of Sitka spruce was planted in Roseisle Forest, Morayshire, Scotland, on a site now predominantly surrounded by Scots pine (*Pinus sylvestris* L.). Abundant flowering was noted in 1964 and observations were subsequently made on flowering over the next few years. In 1968, fairly heavy flowering was observed again and it was decided to use certain trees as parents for a diallel cross. Seven parent trees were selected and labelled A, C, D, G, H, J, K. Selection aimed to include a wide range of phenotype variation for as many characters as possible, such as vigour, branch size, branch angle, colour of foliage.

Details of the seven trees are summarized in Table 1.

Pollination. Over 210 female flowers were isolated on each tree to provide at least thirty flowers for each cross.

Five stages are recognised in the development of female flowers in this species: —

Stage 0 — Resting, winter stage; flowers completely enclosed in the bud scales.

Stage 1 — Flower starting to elongate and becoming very pointed; no rupture of the bud scales (flower non-receptive).

Stage II — Flower elongating, bud scales ruptured but possibly a cap of scales retained at the top of the flower (flower possible receptive).

Stage III — Flower at intermediate elongated stage and cone scales fully open, position approaching horizontal (flower receptive).

Table 1. *Summarized details of the parent trees*

	Parent			Trees			
	A	C	D	G	H	J	K
Total Height (m)	13.72	13.41	13.41	14.33	15.54	13.41	13.11
Girth at 1.3 m above ground (cm)	89	76	91	114	102	89	86
No. of branches per whorl	6	4	6	7	4	5	3
Branch length (cm)	227	189	220	269	185	243	257
Branch angle (degrees)	120	150	110	100	160	120	110
Stem straightness	Very straight	Fairly straight 1 bend	Crooked 4 bends	Crooked	Some persistent bends	Fairly straight	Straight
Stem taper	Rapid	Slow	Rapid	Moderate	Slow	Moderate	Slow
Foliage colour	Blue-green	Green-blue	Green-blue	Green-blue	Green	Blue-green	Deep blue Glaucous
Other features	No internodal branching		Internodal branching		Damaged leading shoot	Moderate internodal branching	Sharp needles many internodal branches

Stage IV – Cone scales closing and flower becoming slightly woody, further elongation will take place soon (flower non-receptive).

Isolations of individual flowers were started when they reached Stage 1. 43 cm × 23 cm non-woven 'Terylene' fabric bags fitted with a transparent PVC observation window were used for isolating the female flowers. After placing the bags over the developing flower buds the open end was sealed around the base of the flower-bearing shoot using a plug of non-absorbent cotton wool and a wire within paper twist tie. Flowers with slightly fractured bud scales were removed before completing the isolation. Isolation work commenced with trees A, C, D and G on May 2nd; all the isolations were completed on 6th May.

Pollen required from each of the same seven trees was extracted before it was naturally shed by removing the male flowers and placing them under gentle heat from an infra-red lamp for a period of up to 48 hours. Pollen extraction and cleaning (by sieving) started on 1st May and was completed by 19th May. Pollen from each tree was handled separately throughout the period to avoid cross contamination.

Regular inspections of flower development were made on all the trees and artificial pollinations were made at Stage III. This stage is short in duration and is the period of optimal female flower receptivity. Pollination began with tree H on 13th May and finished with tree K on 22nd May. All pollinations were carried out between 10 a. m. and 6 p. m. since it had been observed that the flower bracts tended to close together during cool periods and in the early evening. Removal of the isolation bags took place on 28th May after all other pollen on the experimental and neighbouring trees had been naturally shed. The number of healthy and undamaged flowers was recorded for each isolation. An assessment of cone ripening was made at the end of August and collection of the controlled pollinated cones, together with cones derived from wind pollinated flowers were made from each tree during September. Summarized details of the complete crossing programme are given in Table 2.

Table 2. *Summarized details of Pollination Programme (Days after 1. 5. 68)*

	Parent			Trees			
	A	C	D	G	H	J	K
Isolation	2	2	2	2–3	6	6	3–4
Pollination	16	14	14	14	13	14	17–22
Liberation	28	28	28	28	28	28	28
Natural pollen shed commenced	15	13	14	13	12	14	18

Assessment Phase

Glasshouse. Individual seeds from several randomly chosen crosses were weighed; these all showed a high degree of uniformity and on this evidence it was decided that weighing individual seed was unnecessary. Instead 100 seeds were chosen at random from each of the forty-nine crosses and separately sown in individual poly-vinyl-chloride seed trays on a medium of John Innes seedling compost; sowings were made in mid-February 1969. After sowing and watering, the trays were covered with glass to reduce moisture loss and then placed in a cold store at a temperature of 2 °C for three weeks in order to break the dormancy of the seeds and to promote more uniform germination of the seed.

All operations after the pre-chilling treatment were carried out in the same glasshouse using the procedures and equipment described by Herbert (1971). Prior to germination, the seed trays were plunged into a peat/sand mixture which was maintained at a temperature of 21 °C with a minimum air temperature of 7 °C. Germination began after 13 days. Following germination, the minimum air temperature was raised to 15 °C and supplementary lighting was given to provide a 15-hour daylength

When the seedlings were six-weeks-old, forty-eight from each family were pricked out into peat pots and placed in standard seed trays on the plunge-bed, maintaining the same minimum soil and air temperatures and daylength. Artificial lighting was discontinued after the natural daylength reached fifteen hours. Crosses C × C and C × J failed to provide the necessary forty-eight plants.

Nine weeks later in early-July, the plants were potted-up into 130 mm clay pots for the final assessment phase; at this stage they fully occupied the entire glasshouse. From mid-August onwards plants in half the glasshouse area were given artificial lighting to extend the daylength to fifteen hours. Black polythene curtains were used to screen this area from the remainder of the glasshouse. Space-heating in the whole glasshouse maintained a minimum air temperature of 15 °C. In early October the artificial lighting was discontinued and the minimum air temperature was initially allowed to fall to 5 °C and by the end of October to 2 °C, at this time shoot growth had ceased.

Design and layout. The glasshouse experiment consisted of 56 families, 49 derived from the complete diallel cross on the seven parents, and 7 derived from open-pollinated material from the same seven trees.

Five-plant line-plots were used throughout; these were laid out in 8 replicates in a randomised block design; two blocks occupied each of the four sub-sections of the glasshouse. Blocks I—IV received the artificial lighting; spaces were not left between plots but two access paths, each 30 cm wide, split each block; a 30 cm wide path surrounded each block to provide access and to minimise possible shelter or other side effects of the glasshouse walls. There was no surround or buffer of potted plants. Because the crosses C × C and C × J failed to provide forty (5 × 8) seedlings it was necessary to use filler plots for these families in five of the replicates. These fillers were composed of a mixture of surplus plants from other families.

Characters measured. The first-year assessments were made at the end of November six weeks after shoot growth had ceased. The following eight characters were measured.

i. and ii. Tip and Extreme variation — measures of stem straightness. Respectively the deviations of the apex of the main stem, and the point of maximum deviation of the main stem, from a vertical line through the root collar of the plant. Measured in 1 cm classes.

iii. Number of dormant buds. The total number of buds on the whole plant (excluding terminal buds).

iv. Branch angle. The angle between the longest branch and its opposite branch. Measured in 5 degree classes.

v. Height. The distance between the highest living point on the plant and the top of the pot. Measured in cm.

vi. Branch number. The total number of branches was recorded, a branch being designated for any observable elongation of any bud.

vii. Branch length. The length of the longest branch. Measured in cm.

viii. Dry weight. The total mass of the plant, i. e. roots, shoots and needles, dried to a constant weight and measured in grammes. As such an assessment was destructive and most of the material was required for second year studies, only one plant from each plot was sampled; this plant was chosen at random from each five-plant plot.

The eight characters were considered in two groups, namely, those concerned with tree form (tip and extreme variation, dormant bud number and branch angle), and those related to the vigour of the tree (height, dry weight, branch number and branch length). For analytical purposes the characters have been considered in this way.

Analysis. In addition to the poor germination of crosses C × C and C × J previously referred to, several other families involving parent C had such a poor survival that the full data was unsuitable for analysis. All the progenies based on this parent together with the open-pollinated material were omitted and the analysis was carried out on the remaining 36 families which constituted a full 6 × 6 diallel crossing pattern using parents A, D, G, H, J and K.

Although the data were amenable to a number of forms of diallel analysis it was decided to restrict it to the analysis of variance proposed by Hayman (1954a) and the method of Jinks (1954) and Hayman (1954b). This analysis of variance involves the partitioning of the variation between families into four genetic components. Using Hayman's (1954a) terminology these are; an *a* item, measuring any additive genetic differences between parents; a *b* item detecting the presence of additional dominance effects among reciprocal sums; a *c* item indicating any maternal or paternal contribution from certain parents and a *d* item measuring the extent of any specific differences between individual reciprocal crosses. The *a* and *b* items can be equated with the terms 'general combining ability' and 'specific combining ability' respectively. Furthermore the *b* item can be considered in three parts; b_1 due to any overall dominance difference between the progeny and parental means; b_2 due to interactions between specific arrays and often attributed to asymetrical gene distributions; b_3 due to individual cross interactions. In the absence of any b_2 effect, b_1 and b_3 together provide a test equivalent to the overall *b* item.

Since the lighting regimes were not randomised within blocks, they cannot be considered as independent treatments in the overall design, rather the full analysis may be considered as a combination of two separate analyses, one within each lighting regime. Thus the variation is partitioned as follows: —

Item	d. f.
(i) Genetic components (*a*, *b*, *c*, *d*, items) (G)	35
(ii) Effect of lights (L)	1
(iii) G × L	35
(iv) Within lights; Blocks (B)	6
(v) G × B	210
(vi) Within-plot error	1152

In this breakdown, the genetic components (i) are calculated on the basis of overall means and are tested against their interactions with lighting effects (iii); they indicate any overall trends in the genetic control of variation as outlined above. There is no strictly valid test for the effect of lights (ii) but this can be tested against the blocks item (iv). The genetic components × lights interaction (iii) can be tested against the components × blocks item (v); this indicates any differential expression of genetic control under the two lighting regimes. The blocks (iv) and components × blocks (v) items are tested against the within-plot error (vi).

Further analysis of these data centred on one particular aspect of the methods of Jinks (1954) and Hayman (1954b), namely the relationship between the variance of an array (*Vr*) and the covariance, in the same array, between the crosses and their non-common parental selfs (*Wr*). This is achieved by the regression of *Wr* on *Vr* for each array, the points falling on a straight line of unit slope through the origin in the presence of full dominance. Those parents with the greatest number of dominant genes are expected to have the lowest *Wr* and *Vr* values, and *vice versa*. Thus from the positions of the points for each array on such a graph and the slope and position of the fitted regression line through them, it is possible to make a number of inferences about the parents, particularly in terms of dominance relations.

Table 3. *Overall family means for 3 form characters*

(a) Tip variation cm

		Male parents A	D	G	H	J	K	Mean
Female parents	A	3.90	3.45	3.38	7.45	5.38	5.28	4.80
	D	4.10	2.53	3.70	5.45	3.78	3.85	3.90
	G	3.78	3.48	2.55	5.70	3.50	3.68	3.78
	H	6.00	4.10	5.30	7.15	6.60	7.08	6.04
	J	4.30	3.53	4.35	6.65	3.95	4.70	4.58
	K	4.35	3.78	3.85	5.45	4.05	3.78	4.21
	Mean	4.40	3.48	3.85	6.31	4.54	4.73	4.55

(b) Dormant bud number

		Male parents A	D	G	H	J	K	Mean
Female parents	A	2.38	2.05	2.30	3.33	1.88	1.83	2.29
	D	2.18	2.20	2.55	3.63	2.35	1.90	2.47
	G	2.58	2.08	2.93	4.35	2.53	2.03	2.75
	H	3.33	4.18	4.38	6.55	4.35	3.10	4.31
	J	1.93	2.15	2.90	4.73	2.23	1.83	2.63
	K	1.63	1.83	2.23	3.43	1.80	1.85	2.13
	Mean	2.33	2.41	2.88	4.33	2.52	2.09	2.76

(c) Branch angle. 5 degree classes

		Male parents A	D	G	H	J	K	Mean
Female parents	A	130.50	133.25	124.50	134.38	127.25	131.63	130.25
	D	136.38	127.50	125.88	135.13	127.00	128.75	130.10
	G	122.75	127.50	111.75	128.13	114.88	121.13	121.02
	H	129.38	131.75	116.08	125.50	117.00	123.50	123.87
	J	125.50	131.25	119.25	124.50	117.25	123.75	123.58
	K	123.75	128.38	118.25	128.13	127.25	124.50	125.04
	Mean	128.04	129.94	119.28	129.29	121.77	125.54	125.64

Results

Form Characters

The data for extreme stem variation were subjected to the same analysis as all other characters but were found to be virtually identical to tip variation at all stages. Thus only the latter has been considered for the purposes of this presentation. The overall family means for tip variation, number of dormant buds and branch angle are presented in Tables 3 a—c.

For tip variation and dormant bud number, parent H is outstanding in comparison with the other parents. This pattern, reflected particularly among the parental selfs, is also prominent among the array means. For branch angle, differences between the parents are less distinct, H in particular occupying an intermediate position among both selfs and array means.

These data have been analysed by the methods of Hayman (1954a) in the manner outlined above (Table 4). It is evident that most of the variation can be accounted for in terms of additive differences between the parents since a significant *a* item predominates among the main effects for all three characters. The significant *c* item for tip variation can be traced to differences between reciprocal array sums in Table 3 a while the b_1 effect, which is present for branch angle, is a reflection of a higher mean expression among F_1 crosses than among parental selfs for that character (Table 3 c). Among interaction effects, all those of *b* items with lighting regime are significant for tip variation. If the same analysis is considered separately within each of the lighting regimes, significant dominance effects are present in both instances, attributable to the b_1 item under lights and the b_3 item in the absence of lights.

Although the analysis reveals a strong similarity between these three form characters in terms of chiefly additive control of genetic differences, some dominance effects have been recognised and the use of the *Wr/Vr* graph may assist in the interpretation. The appropriate graphs are shown in Figure 1 and are based on overall reciprocal means. It can be seen for each character that there is a small scatter of points about a line approaching unit slope. In the complete absence of dominance, the points would all lie close to the point $Wr = 2\,Vr$ but since a significant linear regression can be fitted through the points on each graph the presence of dominance is indicated.

Table 4. *Analysis of variance of the diallel tables of form characters*

Item	d. f.	Tip variation M. S.	Dormant Bud No.	Branch angle M. S.
a	5	376.85***	308.23***	6853.00***
b_1	1	95.68	19.43	2275.88*
b_2	5	1.43	5.93	282.40
b_3	9	10.92	5.40	278.30
b	15	13.42	6.51	412.83
c	5	16.51*	0.83	981.34
d	10	12.98	1.85	304.61
Lights	1	113.35	110.00	4061.00
La	5	3.06	3.13	65.20
Lb_1	1	59.77*	0.06	88.44
Lb_2	5	14.69**	2.22	469.76
Lb_3	9	14.75*	0.73	250.54
Lb	15	17.73**	1.18	313.48
Lc	5	3.44	1.69	213.06
Ld	10	7.30	2.94	371.43
Within lights				
Blocks	6	44.41**	17.49*	472.23
Ba	30	7.80	3.00	270.46
Bb_1	6	4.42	0.80	420.29
Bb_2	30	3.52	3.66	230.73
Bb_3	54	6.55	1.67	322.34
Bb	90	5.40	2.28	298.14
Bc	30	6.97	1.89	290.33
Bd	60	6.49	1.91	232.72
Within-plot error	1152	5.67	2.05	243.30

In Tables 4 and 5: * $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P = <0.001$.

From the positions of the points on the graphs for tip variation and dormant bud number it is interesting to note that in the former, parent H appears among those parents with the greatest number of dominant genes, whereas in the latter, it contains the greatest number of recessives. However, it is evident from Table 3 that the superiority of parent H is strongly reflected in most crosses for tip variation, but that the high expression of the H 'self' accounts for much of the effect for dormant bud number.

For branch angle, the *Wr/Vr* graph indicates a low level of dominance with H among the recessive parents and D the most dominant. These analyses indicate, therefore, that in addition to predominantly additive control, dominance effects are operative in the inheritance of these characters.

Vigour Characters

Overall means for the vigour characters, height, dry weight, branch number and branch length, are given in Tables 5a—d. In these characters, a lower

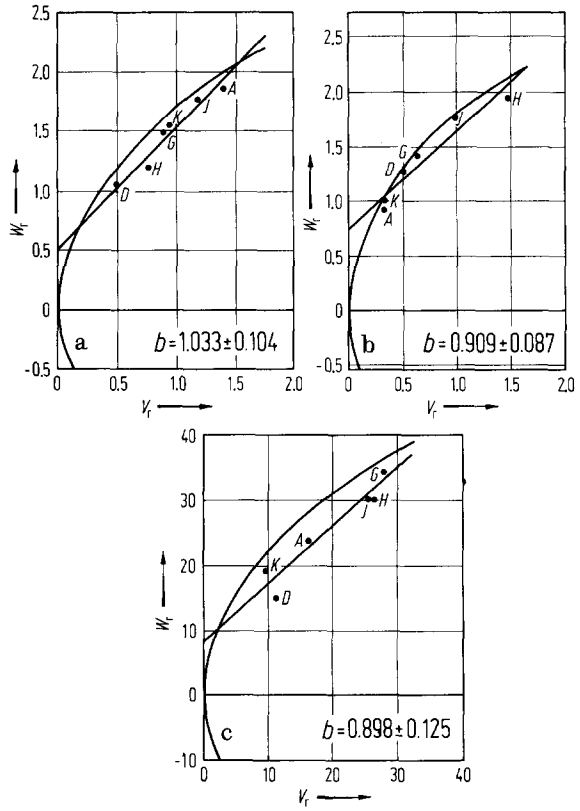

Fig. 1. The regression of array covariance (*Wr*) on array variance (*Vr*) for three form characters, a) tip variation (cm), b) number of dormant buds, c) branch angle (degress)

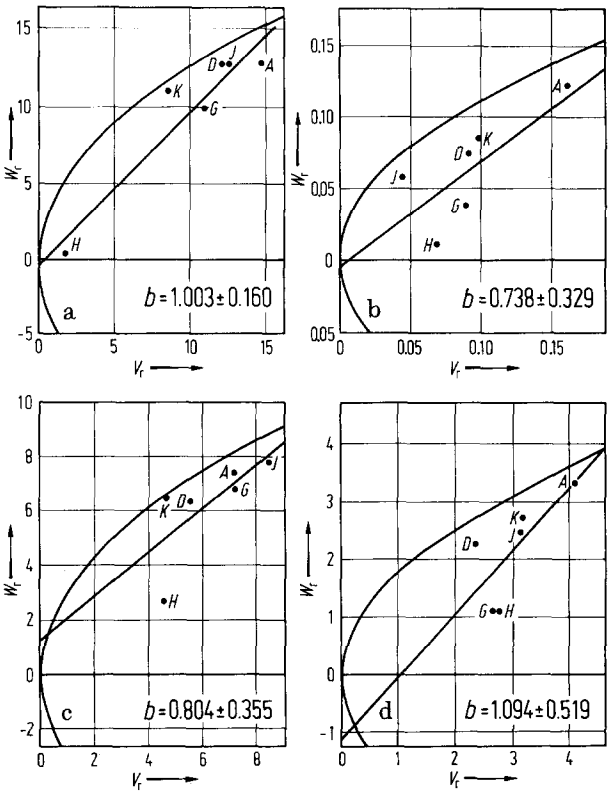

Fig. 2. The regression of array covariance (*Wr*) on array variance (*Vr*) for four vigour characters, a) height (cm), b) dry weight (gm), c) number of branches, d) length of longest branch (cm)

Table 5. *Overall family means for 4 vigour characters*

(a) Height cm

		Male parents A	D	G	H	J	K	Mean
Female parents	A	20.20	23.30	27.50	31.43	25.25	25.13	25.47
	D	23.88	18.25	24.43	29.03	23.78	23.53	23.81
	G	27.35	25.00	21.80	30.65	26.58	24.50	25.98
	H	31.23	29.00	32.23	29.45	31.90	28.95	30.46
	J	22.48	21.45	26.75	31.45	22.65	24.00	24.80
	K	21.28	19.88	22.85	28.20	21.63	19.40	22.20
	Mean	24.40	22.81	25.93	30.03	25.30	24.25	25.45

(b) Dry weight gm

		Male parents A	D	G	H	J	K	Mean
Female parents	A	0.74	1.24	1.94	2.02	1.61	1.50	1.51
	D	1.32	0.82	1.53	1.79	1.35	1.26	1.35
	G	1.51	1.60	1.41	20.3	1.35	1.50	1.57
	H	1.79	1.49	2.44	1.45	1.99	1.59	1.79
	J	1.21	1.01	1.76	1.54	1.37	1.35	1.38
	K	0.98	0.95	1.43	1.78	1.11	0.75	1.17
	Mean	1.26	1.19	1.75	1.77	1.46	1.32	1.46

(c) Branch number

		Male parents A	D	G	H	J	K	Mean
Female parents	A	12.28	15.18	16.78	20.33	16.30	13.63	15.75
	D	14.55	13.00	16.10	19.28	15.65	13.45	15.34
	G	16.98	17.90	14.50	20.75	17.55	13.43	16.85
	H	18.75	18.20	21.13	17.68	21.28	15.50	18.75
	J	14.15	14.20	16.10	20.88	13.85	13.30	15.41
	K	11.78	11.70	12.60	15.38	12.45	8.68	12.10
	Mean	14.75	15.03	16.20	19.05	16.18	13.00	15.70

(d) Branch length cm

		Male parents A	D	G	H	J	K	Mean
Female parents	A	6.85	9.10	12.00	12.15	10.78	10.08	10.16
	D	9.20	7.43	11.18	11.45	10.08	9.93	9.88
	G	12.65	11.43	10.80	14.75	12.58	12.00	12.37
	H	11.98	11.75	16.18	10.90	13.63	12.88	12.88
	J	9.30	8.73	12.45	13.98	9.73	10.75	10.82
	K	8.93	8.58	11.70	12.33	10.03	7.75	9.88
	Mean	9.82	9.50	12.38	12.59	11.13	10.56	11.00

expression among 'selfs' than among the crosses is more evident than in the 'form' characters. A common feature to both, however, is the superiority of crosses involving parent H. Although H is not as outstanding among 'selfs', (as it was found to be with few exceptions, for dormant bud number and tip variation), the highest expressions for all characters are still to be found in those arrays based on H as either male or female parent.

A more complicated picture emerges when these data are subjected to the same analyses as the data for 'form' characters (Table 6). Although additive genetic differences between pa rents continue to account for the greatest part of the variation in all characters, significant dominance effects and, to a lesser extent, maternal effects now also figure prominently. The overall b item, however, is not consistently attributable to any one effect when it is re-partitioned. For height and branch number b_2 and b_3 effects are present; for branch length b_1 and b_2 effects operate; for dry weight none of the items contributed significantly. These facts suggest a complicated picture of dominance interactions which is simplified somewhat if the dominance effects in the separate analyses under each lighting regime are considered. These results are not presented but for all characters the b_1 and b_2 items are significant. In these analyses, the test for b_1 is more sensitive than in the overall analyses due to the greater number of degrees of freedom available for error. All the b_1 items in the overall analyses are found to be significant when tested against d. Thus it seems fair to assume that overall mean dominance effects are important in the inheritance of the vigour characters, indeed this is apparent from the superiority of crosses over selfs in Tables 5a–d. Nevertheless, other dominance interactions at different levels do contribute significantly.

Closer investigation of Tables 5a–d reveals that the significant c item involves certain consistent differences between reciprocal array means. For all characters, A and D have a greater expression as female parents while J and K have a greater expression as male parents, G and H showing no consistent pattern. Few of the interactions with lighting regimes, or with blocks, are significant although differences between blocks appear to reach a higher level of significance among the vigour characters than among the form characters previously considered.

It should be emphasised that the absence of a within-plot error item for dry weight is because the measurements had to be restricted to a single plant from each plot.

The *Wr/Vr* graphs for these characters are presented in Figures 2a—d. Although the presence of dominance is indicated, only the line for height is significant and it is clear that the deviations of the points about the regression lines are often quite large for the other characters. The point for the array involving parent H is found to deviate from the line considerably and, furthermore, is often far removed from the other arrays in position on the graph. Generally, A, D, J and, to a lesser extent, K lie close to the regression line with high values of *Wr* and *Vr* in comparison with H and G which often fall below the line. A classical interpretation of these graphs would suggest a complicated picture of gene interaction but it is nevertheless very pertinent to bear in mind the heterozygous nature of this material which could contribute to this.

It has become clear that a large amount of the observed variation among all these characters can be attributed to the superiority of parent H at both the array and specific cross level. Considering the latter in more detail, it is evident from Tables 5a—d that H×G, and H×J and their reciprocals are among the highest performers for any of the vigour characters. From the aspects of vigour under consideration therefore, parents H, G and J stand out as distinctly superior in terms of both general and specific combining ability.

So far it has been found that similar patterns of inheritance exist among the characters within each of the groups for 'form' and 'vigour'. For the vigour characters, this is reflected when pair correlations are made between them. The appropriate correlation coefficients, presented in Table 7, are based on family means and are all highly significant ($P = < 0.001$), the lowest accounting for 64 per cent of the variation present. Thus the chosen characters obviously reflect various aspects of overall vigour in the progenies. Understandably this situation does not arise among the 'form' characters since they are concerned with unrelated aspects of growth habit.

Table 6. *Analysis of variance of the diallel tables of vigour characters*

Item	d. f.	Height M. S.	Dry Weight M. S.	Branch No. M. S.	Branch length M. S.
a	5	3386.55***	111.99***	2049.76***	793.13***
b_1	1	3516.81	195.08	1617.86	1257.51*
b_2	5	140.06*	16.46	93.73*	61.71**
b_3	9	43.68*	1.26	40.347**	10.94
b	15	310.35***	19.25**	163.38***	110.96***
c	5	162.16*	15.72**	72.01***	21.64**
d	10	26.15	6.81	12.67	10.87
Lights	1	71.10	3.81	101.90	42.37*
La	5	62.20	4.44	48.90	9.29
Lb_1	1	150.22*	8.07	31.10	4.56
Lb_2	5	16.33	4.25	17.67	5.42
Lb_3	9	10.00	3.80	10.68	6.64
Lb	15	21.46	4.24	14.37	6.10
Lc	5	22.43	0.91	7.15	2.39
Ld	10	49.26*	4.41	12.91	10.09*
Within Lights					
Blocks	6	179.52**	5.96	93.50***	23.99*
Ba	30	28.11**	4.47	16.79	7.85
Bb_1	6	20.51	4.47	5.88	2.66
Bb_2	30	12.28	3.87	8.79	4.82
Bb_3	54	18.31	2.68	12.38	3.74
Bb	90	16.44	3.20	10.75	3.78
Bc	30	25.28*	3.24	11.35	3.43
Bd	60	22.25*	4.25	8.17	4.76
Within-plot error	1152	13.854		7.64	4.53

Table 7. *Pair correlations between four vigour characters based on family means*

Dry weight	0.875		
Branch number	0.904	0.824	
Branch length	0.869	0.891	0.799
	Height	Dry Weight	Branch Number

All significant $P = <0.001$

Discussion

When selecting breeding material the breeder of temperate tree species usually has to take into account quite a number of criteria, many of which can be fairly readily assessed. Primarily, attention must be paid to volume production which is associated with several characters related to tree vigour, the most important of which are recognised as height and stem girth, together with branching habit and number and size of branches. Other attributes which are not dealt with in this paper govern the quality of the timber. Tree form is a term used traditionally to describe stem straightness but other important morphological features such as the size of branch and the angle of branching affect the timber quality by influencing the size of knots and the volume of knotwood. The characters measured in this experiment attempt to relate some of these criteria to very young seedling material and many are identical to

measurements commonly made on mature trees. Tip and extreme variation were, however, an attempt to quantify stem straightness more rigorously than subjective scoring which are normally used in adult tree assessments. Stem diameters at the root collar were measured in mm classes; variation between individual trees was found to be very small and consequently the results are not reported here. One particular advantage of using young material is that whole plant production can be assessed on the basis of dry weight measurements.

Those characters considered to be important for the expression of tree form were shown to be inherited in a comparatively simple additive manner. For the practical tree breeder the situation is not straightforward because although the analyses show that selection on the basis of general combining ability is sufficient to isolate the most suitable parents, it must be remembered that in terms of 'form', it is only the trees which have the lowest 'form' values which are the most desirable for forestry uses. This in no way invalidates the criterion of general combining ability for selection but progenies with the lowest values are less consistent among these 'form' characters than are those with the highest values.

Such inconsistency need not be surprising since although the inheritance of the 'form' characters is similar, there is no reason to assume that they are controlled by the same gene systems. This was very evident from the correlations of family means.

The inheritance of vigour characters was more complicated but more consistent. There were clear signs of inbreeding depression in the selfs. The superiority of the crosses, together with the significant b_1 effect in part of the analysis of variance indicated potential heterosis in the material under study. This is partially confirmed from the family means of crosses which were generally higher than those of wind-pollinated material obtained from each parent in the same year and raised in the same experiment. For the breeder the task of selection is simplified since the progenies of H, G and J, and more specifically the crosses between them, show considerable superiority for all characters. Furthermore, selection for any of the four vigour characters considered in the experiment would have given very similar results in view of the extremely high correlations between all of them.

Other factors may have contributed to the outstanding performance of the progenies from parent H. It is a matter of observation that this tree differs from the other parent trees in showing a number of features generally common to Sitka spruce trees from sources in more southerly parts of its natural range, for example, pale green, soft foliage and greater vigour. Under British conditions plants raised from seed collected at various points through its natural latitudinal range show a cline for vigour which increases from north to south (MacDonald *et al.* 1957). However, in parts of Britain, early autumn frosts frequently seriously damage the current seasons shoots and so limit the rate of development of more southerly sources. Thus it can be postulated that if tree H was derived from a parent tree of a southerly origin, then a longer period of active growth in a single season could be expected among its progeny and particularly in the favourable conditions provided inside the glasshouse used in this experiment. In fact, periodic height measurements during the second growing-season have confirmed that progenies from tree H do continue growth for a longer period in autumn than progenies from other parents. A check on the parent tree itself has shown previous stem damage which is highly suggestive of frost damage at irregular intervals.

Two factors must be borne in mind when considering this work in the broader context of a Sitka spruce breeding programme, if indeed it is acceptable to do so. Firstly that methods of diallel analysis find their basis in the use of fixed sets of inbred lines as parent material. Not only is it improbable that the parent trees used as breeding material are homozygous, but a number of unfamiliar patterns in the Wr/Vr analysis may possibly be attributable to heterozygosity in the parents. Second, it is not possible to assume that the inheritance patterns encountered here will apply to the species in general and additional studies on different material will be needed to confirm the value of the findings. This experiment is believed to be the first of its kind in which a 6×6 diallel cross has been successfully achieved with any species in the genus *Picea* and in which material has been raised using early-test procedures under glasshouse conditions. The parent trees used in this experiment were not outstanding phenotypes from a tree breeding point of view and therefore similar experiments in which highly selected parent trees are used as the basis should yield much needed information on the genetic influences and modes of inheritance of some of the characters important to forestry. Later publications will be based on the second year measurements and the growth rhythms of the material reported on here.

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