Genetic Variation in 38 Provenances of Sitka spruce1)

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1. Materials and Methods

During the 1970 fall, the I.U.F.R.O., Section 22, "Working group on Procurement of Seed for Provenance Research" organized an expedition to collect Sitka spruce cones from British Columbia and Alaska. In most cases, the collections were made from 15 trees in each location.

The locations of the 38 provenances range from 48° 38 to 58° 37 latitude N and from 121° 93 to 134° 58 longitude W. The elevation varies from 0 to 700 meters above sea level. All the provenances originate from British Columbia (Canada) except the provenances 23, 24, 25, 26, 27 and 28 which come from Alaska (U.S.A.). *Figures* 1 *and* 2 show the geographic locations of the provenances studied. See *table* 1 for more details on the origins of the provenances studied.

It was decided to keep the single tree progenies separate so as to be able to compare the two hierarchical levels of

Table 1. — Geographical coordinates of the Sitka spruce I. U. F. R. O. provenances in 1970

No. of the: Provenance	Region	Location	Latitude °hundredth	Longitude °hundredth	Elevation metre	No. of trees
1	I	Vedder	49.12	121.93	30	10
2	I	Squamish River	49.92	123.25	30	15
3	I	Big Qualicum River	49.38	124.62	0	15
4	I	Salmon Bay	50.38	125.95	0	15
5	V	Cranberry River	55.47	128.23	518	15
6	V	Kitwanga	55.17	127.87	671	15
7	V	Usk Ferry	54.63	128.40	137	15
8	V	Shames	54.40	128.95	30	15
9	V	Wedene River	54.13	128.62	167	15
10	V	Kitsumkalum Lake Park	54.72	128.77	137	15
11	V	Derrick Lake	55.68	128.68	244	15
12	V	Dragon Lake	55.35	128.95	259	7
13	V	Zolap Creek	55.15	129.22	15	15
14	V	Fulmar Creek	55.15	128.97	396	15
15	V	Aberdeen Creek	54.20	129.92	0	15
16	—	Pacific Ocean	54.77	128.25	107	—
17	—	Wesach Creek	54.80	128.72	366	—
18	V	Cedarvale	55.02	128.32	243	15
19	V	Kasiks River	54.28	129.42	30	15
20	V	Humpback Creek-Porcher Is	54.03	130.37	304	11
21	V	Inverness	54.20	130.25	15	15
22	—	Hays mtn., Prince Rupert	54.27	130.32	640	15
23	IV	Mosspoint, Annette Island	55.03	131.55	0	15
24	IV	Craig	55.50	133.13	0	15
25	IV	Old Hollis	55.47	132.67	0	15
26	IV	Ward Lake	55.42	131.70	15	15
27	IV	Ohmer Creek	56.58	132.73	7	15
28	IV	Duck Creek	58.37	134.58	30	15
29	I	Allouette River, Haney	49.25	122.60	198	15
30	II	Muir Creek, Sooke	48.38	123.87	0	15
31	II	Port Renfrew	48.58	124.40	7	15
32	II	Tahsis 1	50.08	127.50	30	15
33	II	Tahsis 2	49.83	126.67	3	15
34	II	Holberg	50.62	128.12	30	15
35	III	Moresby Is. Skincuttle Inlet	52.28	131.22	15	8
36	III	Moresby Is. Sewell Inlet	52.87	132.08	15	15
37	III	Moresby Is. Cumshewa Inlet	53.05	132.08	60	15
38	III	Sandspit, Queen Charlotte Is.	53.13	131.80	76	15
39	III	Juskatla, Queen Charlotte Is.	53.50	132.17	91	15
40	III	Masset Inlet	53.92	132.08	0	15
41	V	Blenheim, Sarita	48.90	124.95	213	11
		Total				557

Individual tree samples were not available from provenances 16 and 17.
Provenance 22 had not enough viable seeds, consequently these three collections were not included in this study.

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variation: between populations (= provenances) and between trees (= population variability). Such a study offers the advantages of a provenance test and those of a maternal test enabling, therefore, the comparisons of different nested levels of genetic variability. These comparisons are fundamental if we wish to determine rationally which type of selection is best for the material studied (mass selection or family selection).

This study is thus more comprehensive than the one proposed for an international experiment by Driscoll, 1972.

A randomized complete block design with four replications was used. Each provenance was randomized within each block and within each provenance plot, the single tree progenies were kept separate and randomly placed. The seeds were placed in the cavities of styro-foam blocks. Each progeny, for a given replication, occupied 24 cavities, i.e. a total of 96 seedlings per progeny was aimed at. The four blocks were seeded in 4 days between the 20th of April 1971 and the 2nd of May 1971. The containers were treated according to Matthews, (1971) provisions. In May 1972, the

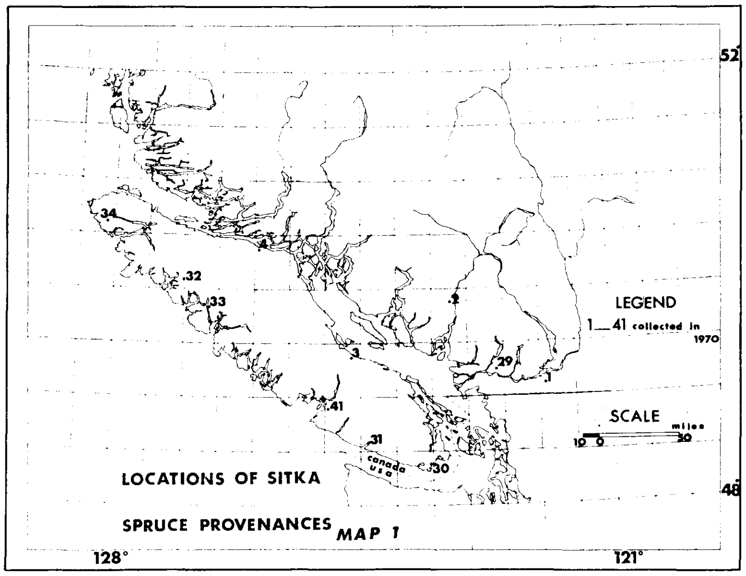

Figure 1. — Location of the provenances in the southern part of the range sampled (British Columbia, Canada).

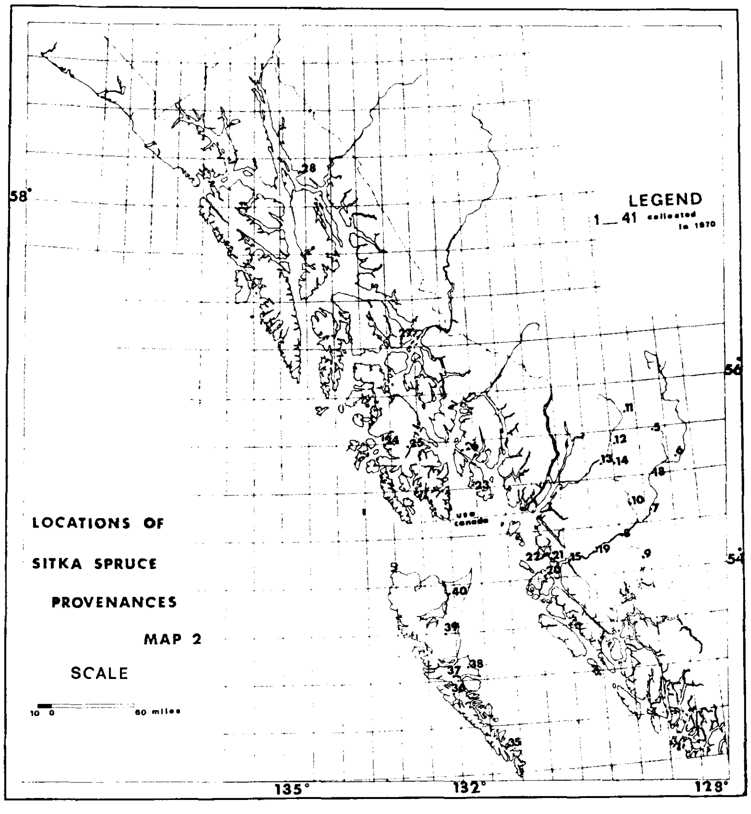

Figure 2. — Location of the provenances in the Northern part of the range sampled (British Columbia, Canada, and Alaska, U.S.A.).

seedlings were transplanted to a spacing of 6" to 6" in plain soil, in the same nursery and treated according to the latest nursery methods in use in British Columbia (Canada). The nursery was located at surrey, near Vancouver (B.C.).

1.1 Measurements made:

Germination rate

The number of cavities with at least one germinant was counted for each progeny and each replication, on the following dates: 3rd, 9th, 15th, 21st, 28th of June, 1971, the 5th, 12 th of July, 1971.

Bud set

Bud setting was determined for each provenance and each block separately at two dates in 1971 and at one date in 1972. The following procedure was used: bud set was observed at different dates during late August and in September until the provenances displayed a variety of stages of bud set. Then an empirical scale of six bud stages was determined by careful examination of the provenance shoot apices. (See Falkenhagen, 1974). For each replication and each provenance, at least 30 seedlings were randomly chosen and classed according to this scale in order to establish a frequency distribution of the six bud stages and to calculate a weighted mean for each provenance and each block, A, B, C or D. No attempt was made to estimate the average bud stage on a progeny basis because of the length of time involved and the irregular and often small number (less than 24) seedlings representing each progeny. Only the apex of the main shoot was considered because lateral branches may be at a stage different from the one of the leading shoot.

Bud set was estimated on September 26th, 1971, on October 2nd, 1971 and on September 8th, 1972. All the blocks were measured in one day to avoid any effect due to a sudden weather change.

Bud burst

Flushing rate was assessed using the same procedure as for bud set on the 3rd of April, 1972. 5 stages were used.

Colour of the needles

Needle colour was estimated on the 13th of September 1972. A similar procedure as for bud set was used for studying this characteristic. Three classes were distinguished:

0 = needles pale green (parsley-like);
1 = glaucous, intermediate;
2 = bluish.

Length of the epicotyl

The length of the epicotyl of the three tallest seedlings, for each progeny and for each replication, was measured to the nearest mm during the winter 1971/72. I tried only to measure a constant upper percentage (±20%) of the seedlings present in a progeny. Therefore, I eliminated the replications which were represented by only a few seedlings. This length is supposed to represent the total height growth after the first growing season, irrespective of the size of the embryo hypocotyl. About 3,000 measurements were made.

Total height

In February, 1973, a random sample of 5 transplanted seedlings was measured for each progeny in each replication so as to estimate the natural variation occurring in a progeny and a provenance. About 10,000 measurements of total height were made to the nearest 1/2 cm.

Survival rate

The seedlings were transplanted with the soil attached to their roots, under optimum conditions, and there was no noticeable mortality at the end of 1972: all the transplants survived the winter 1972/73 as well as the summer 1973.

1.2 Methods used in the analyses:

Multiple correlation and regression analyses

A simple correlation matrix was calculated between the provenance means of the traits assessed and between these characters and latitude, longitude and altitude of the place of origin of the provenances, over all the provenances, ignoring regions. The geographical coordinates were chosen because the climatic data were not sufficient for each place of origin. The traits were plotted against these geographical coordinates in order to check visually the relationships between the provenance means and these variates. A multiple regression equation was calculated between each trait and all or a few selected variables. A backward step-wise program (Draper and Smith, 1966) was used.

Analysis of variance models

For all the traits studied, on a provenance basis, i.e. all the traits except the two growth measurements, univariate analyses of variance were done, using a randomized complete block design model — completely random — (Model II) with four replications. The provenances not represented by four blocks were not included. Only the growth measurements will be analysed here.

For the growth characteristics, two elaborate models were used to take into account the family (single tree progeny) level. As the number of families varied from one provenance to the other, the data were unbalanced for this level and special computing techniques for unbalanced models were used.

Model for maximum epicotyl length

A nested model crossed with the blocks was used so as to get the different interactions corresponding to the different levels of variation.

The statistical model, completely random, is of the form:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_{ik} + (\alpha\beta)_{ij} + (\beta\gamma)_{ik/j} + \varepsilon_{ijkl}$$

The general formulas to obtain the components of variance for this model are presented elsewhere (Falkenhagen, 1976).

The errors of the variance components have been estimated according to Anderson and Bancroft (1952, p. 321), for the most important sources of variation, because the formula used is only strictly valid for balanced data.

Total height after the second growing season was analysed by using a completely nested model with the blocks considered as simple replications, because no interaction was detected using the first model and because the exact formulas for the error of components of variance have been developed for this model.

The model is of the form:

$$Y_{ijkm} = \mu + \alpha_i + \beta_{ij} + \gamma_{ijk} + \varepsilon_{ijkm}$$

The components of variance and their error were obtained by using the formulas given by Mahamunulu (1963).

Forest genecology (Stern, 1964) tells us that the natural populations of a tree species are locally adapted to their environment of origin. It was decided to subdivide the material into 5 ecological regions on the basis of the climatic and physiographic data available and to analyse these 5 regions separately except for the correlation and regression analyses which were performed over all the provenances. Thus, the heterogeneity of the variances is likely to be reduced and safe multiple comparison tests of the means can be performed on reduced sets of provenances generally less than 12, except for region 5 which contains a maximum of 16 provenances. Variance components estimation thus makes more sense on a regional basis.

These regions are defined as:

Region 1 comprises the provenances 1, 2, 3, 4 and 29
Region 2 comprises the provenances 30, 31, 32, 33, 34 and 41.
Region 3 comprises the provenances 35, 36, 37, 38, 39 and 40.
Region 4 comprises the provenances 23, 24, 25, 26, 27 and 28.
Region 5 comprises the provenances 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 18, 19 and 20.

See also *table 1.*

The basis of these ecological regions has been studied extensively in a paper soon to be published (FALKENHAGEN and NASH, 1977).

2. Results

Germination rate

For each provenance, the percentage of cavities with at least one germinant was calculated for each date. The percentages have been plotted against time in number of days, for some selected provenances. The graphs showed that there was no clear geographical pattern of variability in germination curves and no relationships with height growth.

Phenological observations

A correlation matrix *(Table 2)* between all the traits which presented some systematic variation has been calculated and between these traits and the geographical coordinates of the place of origin of the provenances. The means of the provenances have been used to calculate this correlation matrix.

The legend of the matrix is as follows:

LAT = latitude (°, 1/100).
LON = longitude (°, 1/100).
ALT = altitude (feet).
BST 1 = bud set estimated on the 26th of September, 1971.
BST 2 = bud set estimated on the 2nd of October, 1971.
BST 72 = bud set estimated on the 8th of September, 1972.
BBT = bud burst estimated on the 3rd of April, 1972.
EPL = maximum epicotyl length.
HET = mean total height after the second growing season.
HMN = mean minimum total height after the second growing season.
HMX = mean maximum total height after the second growing season.
COL = needle colour estimated in 1972.

Latitude and longitude of the place of origin of the seed lots are positively correlated (r = 0.78). This fact results from the particular physiography of the northern part of the west coast of North America. Therefore, multiple re-

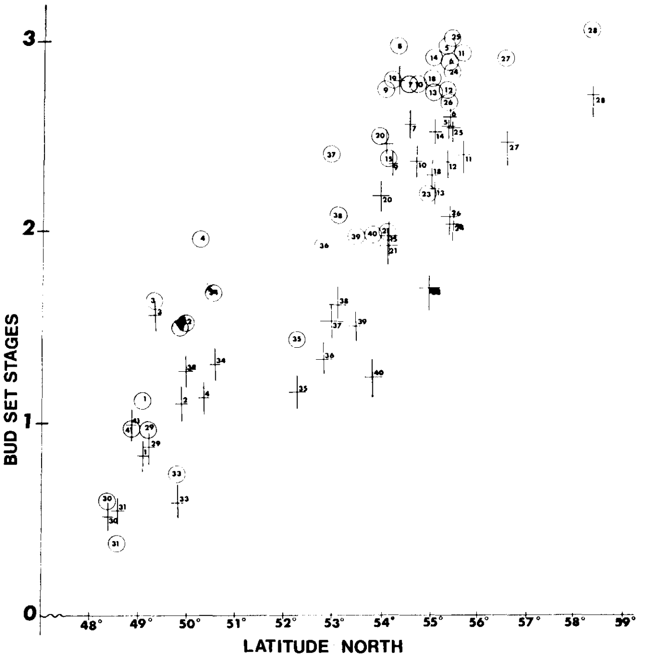

Figure 3. — Relationships between bud set of the Sitka spruce provenances and latitude of place of origin at two dates, in 1971. The numbers 1 to 41 are the provenance numbers. The coefficients of determination were 79% and 83% for bud set estimated on the 26th Sept. 1971 and on the 2nd Oct. 1971 respectively. The crosses indicate the measurements made on the 26th of Sept. 1971, the circles those made on the 2nd of Oct. 1971.

Table 2. — Correlation matrix between the traits and the geographical coordinates of the place of origin.

LAT = latitude (°, hundredth), LON = longitude (°, hundredth), ALT = altitude (feet), BST 1 = bud set estimated on the 26th of September, 1971, BST 2 = bud set estimated on the 2nd of October, 1971, BBT = bud burst estimated on the 3rd of April, 1972, EPL = maximum epicotyl length, BST 72 = bud set estimated on the 8th of September, 1972, HET = mean total height after the second growing season, HMN = mean minimum total height after the second growing season, HMX = mean maximum total height after the second growing season, COL = needle color estimated in 1972.

	LAT	LON	ALT	BST1	BST2	EPL	BBT	BST72	HET	HMN	HMX	COL
LAT	1.0	.										
LON	.78	1.0										
ALT	.26	—.12	1.0	.								
BST1	.89	.53	.39	1.0								
BST2	.92	.63	.32	.96	1.0	.						
EPL	—.71	—.34	—.56	—.74	—.70	1.0						
BBT	—.14	—.51	—.42	.13	.07	—.13	1.0	.				
BST72	.88	.59	.47	.91	.92	—.75	.12	1.0				
HET	—.78	—.49	—.52	—.74	—.74	.91	.04	—.80	1.0	.		
HMN	—.80	—.54	—.49	—.72	—.76	.88	.07	—.81	.98	1.0		
HMX	—.74	—.43	—.53	—.72	—.72	.90	.02	—.77	.98	.95	1.0	.
COL	.64	.72	—.04	.58	.62	—.44	—.37	.61	—.50	—.53	—.48	1.0

$\varrho .05 = .32$, $\varrho .01 = .41$ and $\varrho .001 = .51$ with 36 d.f.

gression techniques or partial correlation coefficients are necessary to dissociate the effects of these two variates.

Bud set 1 and 2 and but set 72 are strongly correlated with latitude (r = 0.89, 0.92 and 0.88). They are also significantly correlated with longitude and altitude but the relationships are somewhat weaker. What is most important is the constancy of all correlations over the years '71 and '72. This would indicate a strict genetic control of bud set, at least in comparison with the differences in the growing conditions of the two years and the two nursery locations.

Fig. 3 shows the relationship between bud set 1 and 2 and latitude. The general relationship is linear.

There is a negative correlation of 0.51 between bud flushing and longitude for fixed latitude and altitude, but not with the other parameters: the more maritime the local climate, the later the provenances flush.

Bud set 1 and 2 may be considered as one trait because of the strong correlation coefficient between them and the other traits. Bud set 72 is strongly correlated with epicotyl length and total height (r = —0.75 or —0.81).

The higher the latitude of the place of origin of the provenances, the earlier these provenances set their bud and the shorter the height of the provenances.

Bud burst is not significantly correlated with bud set or epicotyl length.

Needle colour

Needle colour is positively correlated with latitude, longitude, (r = 0.64, 0.72), with bud set 1, bud set 2 and negatively correlated with epicotyl length or total height *(Table 2)*. Thus, the higher the latitude or longitude, the more bluish the provenances are and the shorter they are.

Growth characteristics

Maximum epicotyl length (EPL)

Table 3 summarizes the results of the different multiple correlation and regression analyses of the growth traits studied. These results are presented in details because they can generate hypotheses concerning the pattern of geographic variation observed and causal relationships between the variables studied. For instance, latitude and altitude of place of origin explain together 65% of the total variation in EPL and 73% in HET.

The analyses of variance, the components of variance and the DUNCAN's tests have been calculated for each ecological region separately. See *tables 4, 5* and *6*.

Table 3. — Results of the multiple correlation and regression analyses of the growth traits studied (For definitions of independent variables, please refer to Table 2)

Dependent variable:	LAT	LON	ALT	BST1	BST2	EPL	BBT	BST72	HET	COL	Coefficient of determination (%)
					Independent variables*)						
EPL (Maximum	×	×	×				×			×	80.0
epicotyl length)	×		×								65.0
	×										50.0
			×	×							74.0
				×							66.0
HET (Mean total	×		×								73.0
height after the	×										61.0
second growing						×	×	×			89.0
season)						×					82.4

*) contribute at least significantly (P = 0.05) in explaining the variation of the dependent variable.

Table 4. — Summary of the analyses of variance and DUNCAN's Multiple range test of epicotyl length, on a region basis

Analyses of variance	Region 1		Region 2		Region 3		Region 4		Region 5	
Sources of variation	D.F	F	D.F	F	D.F	F	D.F	F	D.F	F
Blocks	3	NS	3	NS	3	NS	3	NS	3	***
Provenances	3	NS	3	*	4	***	3	NS	13	***
Trees in prov	41	***	17	***	24	***	18	***	83	***
Prov. X block	9	NS	9	NS	12	NS	9	NS	39	NS
Trees in prov X block	123	NS	51	NS	72	NS	54	NS	249	NS
Error	360		168		232		176		776	
Total : —	539		251		348		263		1163	

DUNCAN's tests ($\alpha = 0.05$)
Region 1 = provenances 2, 3, 4, 29
No significant differences between provenances, thus no DUNCAN's test.

Region 2 = provenances 30, 32, 34, 41

Prov. No.	30	41	34	32	
EPL	90.5	78.8	78.5	78.5	mm

Region 3 = provenances 35, 36, 37, 39, 40

Prov. No.	37	40	35	39	36	
EPL	92.0	86.8	83.6	70.8	70.5	mm

Region 4 = provenances 24, 25, 26, 27
No significant differences; thus no DUNCAN's test, for the provenance effect.

Region 5 = provenances 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 18, 19, 21

Prov. No.	15	21	10	8	7	13	14	9	12	19	5	6	11	18	
EPL	81.0	78.8	75.0	72.6	72.0	66.4	65.6	65.5	62.7	61.9	60.4	59.4	58.6	57.0	mm

Table 5. — Variance components of some important sources of variation and their standard error for maximum epicotyl length

Number of the Region	Sources of the Effect		
	Provenances	Trees	Error
1	4.0 ± 5.5	30.0 ± 8.5	86.9 ± 6.4
2	23.2 ± 21.8	31.1 ± 13.9	102.8 ± 11.2
3	95.0 ± 29.6	23.8 ± 10.0	100.0 ± 9.2
4	8.7 ± 13.4	49.9 ± 18.8	70.0 ± 7.4
5	63.0 ± 25.5	38.2 ± 6.9	66.0 ± 3.3

Table 6. — Components of variance for maximum epicotyl length expressed as percentage of their sums, for each separate region

Sources of variation	Regions				
	1	2	3	4	5
Blocks	0.6	1.6	2.2	2.2	2.4
Provenances	3.0	12.9	39.0	5.9	35.6
Tree within provenance	22.5	17.3	9.8	34.0	21.6
Prov. × Block	3.0	4.9	2.8	1.0	0.8
Tree within provenance × Block	5.6	5.9	5.1	9.1	2.2
Residual error	65.2	57.3	41.1	47.7	37.3

Total height after the second growing season (HET)

HET was measured in 1973 on the basis of a random sample of five seedlings per replication and per progeny. In order to study the relationships between HET and EPL, the average maximum height (HMX) and the average minimum height (HMN), for each provenance, have been calculated by taking the greatest and the smallest seedling of each progeny and summing over all the replications and progenies for each provenance.

The correlation matrix (*Table 2*) shows that the correlations between HMX, HMN, EPL and HET are highly significant (r = 0.88; 0.90; 0.91, etc.) Consequently, the conclusions concerning EPL should be equally valuable for HET, as far as the correlations analyses are concerned.

Table 3 summarizes the multiple correlation and regression analyses performed.

The plotting of HET on latitude shows that the general relationship is linear (see *fig. 4*). However, when the place of origin of the provenances is taken into account, some regions appear. The provenances of Vancouver Island can be separated into two sub-groups: the west coast and the east coast groups of the Island. On this Island, HET sharply decreases with increasing latitude. Altitude cannot be responsible for this behaviour, because the altitude of the provenances remains fairly constant.

The provenances of the Queen Charlotte Islands seem to behave differently from the other groups of provenances: HET increases with latitude. Altitude cannot be the factor responsible for this odd behaviour.

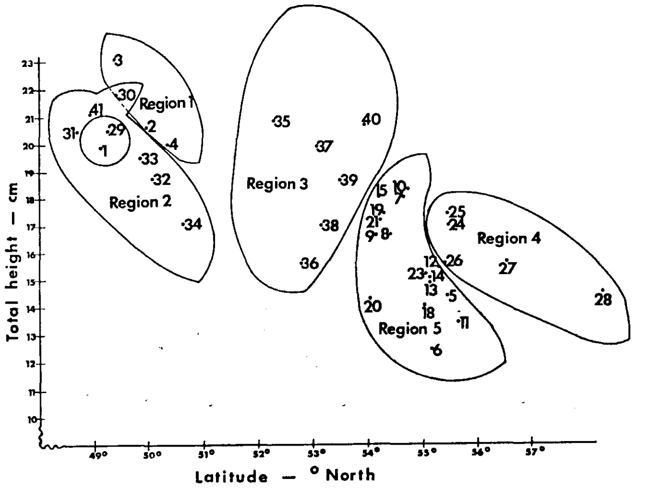

Figure 4. — Relationship between total height after the second growing season and latitude of place of origin of the provenances.

Table 7. — Summary of the analyses of variance and Duncan's multiple range test for total height on a region basis

Analyses of variance Sources of variation	Region 1 D.F.	Region 1 F.	Region 2 D.F.	Region 2 F.	Region 3 D.F.	Region 3 F.	Region 4 D.F.	Region 4 F.	Region 5 D.F.	Region 5 F.
Provenances	3	***	3	***	3	***	4	*	11	***
Trees in prov.	43	NS	30	NS	48	NS	45	NS	118	NS
Rep. in tree in prov	94	***	68	***	104	***	100	***	260	***
Error	564		408		624		600		1560	
Total:—	704		509		779		749		1949	

Duncan's test: ($\alpha = 0.05$)

Region 1 = provenances 2, 3, 4 and 29

Prov. No.	4	2	29	3	
HET	203.3	206.3	212.5	234.4	mm

Region 2 = provenances 30, 32, 34, 41

Prov. No.	30	41	32	34	
HET	220.7	215.5	198.9	164.6	mm

Region 3 = provenances 36, 37, 39, 40

Prov. No.	40	37	39	36	
HET	205.7	200.1	187.2	158.5	mm

Region 4 = provenances 23, 24, 25, 26, 28

Prov. No.	25	24	23	28	26
HET	168.7	168.6	152.0	147.4	144.5

Region 5 = provenances 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 18, 19

Prov. No	15	10	7	19	8	9	5	14	13	11	18	6	
HET	188.5	183.1	181.9	180.0	171.5	170.2	150.7	150.7	142.0	133.8	131.9	128.2	mm

Table 8. — Second year height variance components and standard error

Region	Absolute values Provenances	Trees within provenance	Repetitions	Residual variances	Percentages of their respective sums Provenances	Trees within prov.	Repetitions	Residual variances
1	224.6 ± 218.0	57.7 ± 86.5	375.4 ± 130.9	2.494.0 ± 148.5	7.1	1.8	11.9	79.1
2	639.1 ± 587.9	56.5 ± 110.2	564.6 ± 164.4	1.907.7 ± 133.6	20.2	1.8	17.8	60.2
3	370.2 ± 105.2	—29.4 ± 117.3	1.020.6 ± 207.7	2.324.4 ± 131.6	9.9	0.8	27.2	62.1
4	91.6 ± 96.0	77.0 ± 97.4	550.9 ± 141.8	2.177.8 ± 125.7	3.2	2.6	19.0	75.2
5	430.0 ± 204.6	72.2 ± 63.8	673.2 ± 94.6	1.967.3 ± 70.4	13.7	2.3	21.4	62.6

The narrow sense heritability and its standard error, on an individual basis, has also been estimated (Becker, 1967) and varied from 0 for Region 3 to 0,11 for Region 4. These estimates had large standard errors and are not considered reliable.

The Alaska and the Skeena River watershed provenances do not form two very distinct groups, but some divergences are noticeable. HET again decreases sharply with latitude. Within the region 5, two subsets seem to appear: a low elevation, coastal group consisting of the provenances 7, 8, 9, 10, 15, 19 and 21 and a group consisting of the remaining provenances with the exception of provenance 20 that can be perhaps explained by its elevation (300 m.).

The analyses of variance, the components of variance and their standard error, and the Duncan's tests of the means of the provenances have been calculated for each region separately. See *tables 7 and 8* for a summary of these analyses.

In this case, only the provenances represented by at least five families and the families with three replications were considered.

3. Discussion

Bud burst and bud set rates are important adaptive traits as they determine the co-adaptation of the vegetation period of the tree to the periodic variation of the climatic components of the environment where the tree thrives. This co-adaptation is particularly important for the species growing in the temperature regions where important cyclic variation in day length, temperature regime or rainfall may exist.

Bud set is linked with the cessation of the elongation of the stem, but it is also related to the adaptation to the cold season and the onset of dormancy which generally accompanies it, in temperate tree species.

Bud set and bud flushing have been particularly studied in Europe, for different tree species, in connection with height growth, and late and early frost damage (see Schober, 1962, for Sitka spruce). In a maritime, irregular climate as in the natural range of Sitka spruce, these traits could be of paramount importance, especially if this maritime climate is superimposed on a wild mountainous topography with abrupt changes in aspect, altitude, rainy windward and drier leeslopes or frost pockets due te temperature inversion.

The methodology of the study of bud set or bud burst is thus particularly important if precise comparisons are needed.

Schober (1962) studied the late frost and winter frost damage variability of ten Sitka spruce provenances. Flushing rate was assessed every 3—4 days using an empirical scale of four bud stages. The graph representing the development of the terminal bud takes the shape of a sigmoid. Bud set also takes a sigmoidal form.

Several methods can be used to assess bud set and bud burst. One can estimate the percentage of buds at a given stage of development every two or three days and draw a curve expressing the evolution of the percentage with time, or count the number of days until some type of bud appears. This latter method was used by Burley (1966 a). These procedures may be long and tedious, depending on the size of the material and also imprecise because of the lack of clear definition of the type of bud considered or the small number of trees assessed: Burley (1966 a) assessed two seedlings per treatment. Another method, used in this study, consists of taking into account the continuity of the bud formation process, in distinguishing different stages and in establishing, for each population, the frequency distribution of the stages and in calculating the average bud stages. The relationship between the two methods are shown in *fig. 5*, for an idealized example of three provenances. The method used in this study estimates the average bud set of a given provenance at a given date. It is a one-day estimation; therefore, the differences expressed by the provenances vary with the date chosen for the estimation. The differences estimated are indicated along the vertical line in *fig. 5*. The differences in days given by Burley's method are indicated by the arrows corresponding to the horizontal line. Before bud set starts, all the provenances are growing and the differences in bud setting, between them, are equal to zero; when all the provenances are resting, again, the differences in bud set are equal to zero, consequently, there must be some date where, on the average, the differences are maximum and consequently, the genetic variance maximum (Falkenhagen, 1968).

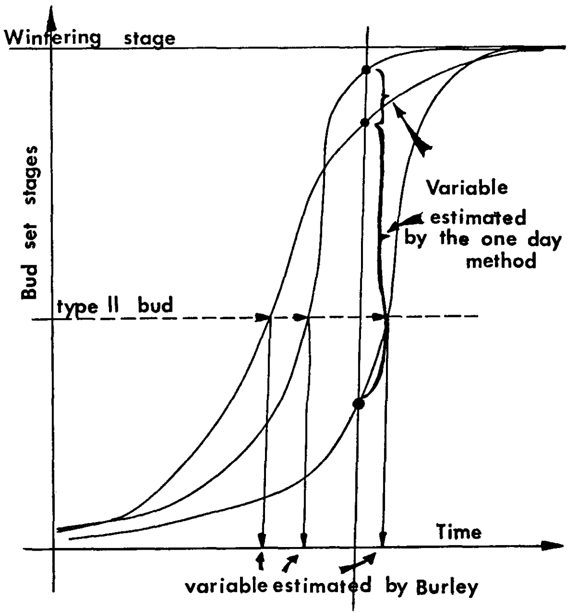

Figure 5. — Relationship between the one-day method to asses bud set and Burley's method.

The nature of the frequency distribution of bud flushing stages within different provenances of European beech (*Fagus sylvativa* L.) has been intensively studied by Galoux and Falkenhagen (Galoux, 1966). Two theoretical distributions, normal and log-normal, have been adjusted to the data accumulated for different beech progenies. Different numbers of bud stages: 5, 6 or 7 have been considered. The number of stages or classes to be distinguished is a problem in itself. Generally, the distribution was found to be skewed and not normal, rarely log-normal.

Our data confirm Burley's (1966 a) findings that seedlings from northern sources form their buds before the southern provenances, findings based on the study of the formation of a certain type of bud (Type II). However, some of his observations on the Type III bud could contradict his relationships based on his Type II bud.

However, our research does not confirm Burley's contention that flushing rate is not related to the place of origin of the Sitka spruce provenances. It is also important to note that Burley did not study the relationship between the number of leaf primordia and internodes and the next year's shoot growth. According to Romberger (1963), for some species of *Pinus* or *Picea*, the number of internodes telescoped in the terminal bud determines the total shoot growth of the next growing season. It is not known if Sitka spruce has terminal buds with predetermined shoots and fully preformed needles and internodes. In the nursery, the Sitka spruce provenances grew continuously until fall. No repeated flushes have been noticed by us, which would indicate (Kozlowski, 1971) that Sitka spruce has no shoots preformed in the dormant buds, at least at a juvenile stage. It is possible that adult Sitka spruce trees present buds with predetermined shoots.

Bud set in trees is considered by many authors as often set in motion by declining photoperiod during late summer through some "phytochrome" mechanism (Romberger, 1963; Kozlowski, 1971). The data presented here do not support this theory, because at the time of measurements, the differences between the photoperiods at latitude 50⁰ and 58⁰ are too small to explain the differences in bud setting expressed by the provenances growing at Surrey (the differences were less than 6 minutes). Perhaps the mechanism triggering the onset of dormancy is set in motion earlier, during the summer. The same holds true for bud flushing as observed in the nursery. Thus, it is difficult to attribute the differences in bud flushing and bud set observed in the nursery as due to different adaptations to different photoperiods at the place of origin of the provenances.

However, the thermal energy accumulated over the growing season varies much in quantity and rate of accumulation with latitude. The effect of altitude could be the same. Note that the correlation of bud burst with altitude is +0.42**. The analysis of *table 2* also offered some evidence that the differences in bud flushing observed in this study are related to the thermic conditions of the place of origin, probably with the local late frost distribution as already observed by Schober (1962).

There was a covariance structure between bud set 72 and bud burst, bud set 2 and needle colour. As there traits are strictly heritable, it is possible that genetic correlations exist between these traits, positive or negative. Therefore, in a selection experiment, care should be taken of the correlated responses when selecting for a given trait such as late flushing or early bud setting.

Burley (1966 b) has observed genetic variation in needle and hypocotyl colour of different Sitka spruce provenances. The bluish bloom occurring on plum fruits, eucalypt leaves and needles of blue spruce, is well known and has been linked with cuticular wax structures. The pattern of variation detected by Burley (1966 b) for needle colour in Sitka spruce is similar to the pattern described in this study.

For both EPL and HET, the components of variance differ according to the region.

The components of variance estimated for HET indicate that, generally, the genetic variance between provenances is larger than the tree to tree within provenance genetic variation, while in the case of EPL, the within provenance variation can be larger than the between variation.

The residual variance is the largest component. This large component might suggest that the within progeny group genetic variation is quite large, attesting a genetic plasticity in harmony with the idea that Sitka spruce might be an "opportunistic" species. However, in the absence of data on the frequency of self-pollination and the inbreeding processes taking place in Sitka spruce, no definite interpretation is possible.

That the narrow sense heritability, *i.e.*, the additive genetic variance could be small for growth traits is confirmed by the results of the diallel cross performed on Sitka spruce (Samuel *et al.*, 1972).

Therefore, family selection would be appropriate (Falconer, 1964). The general combining ability seems to be low, therefore specific combining ability should be used through crossing between outstanding individuals and populations.

Summary

A total of 542 single-tree progenies of Sitka spruce, grouped into 38 provenances, were sown in April 1971 in a randomized complete block design with four replications and 24 seedlings per replication, or 96 seedlings per progeny. The seeds were sown in styro-blocks and treated by the most recent methods in use in British Columbia, Canada.

Germination rate, bud set, length of epicotyl and survival after the first growing season were assessed in 1971. The seedlings were transplanted at 6 × 6-inch spacing in plain soil seedbeds in May 1972, each progeny being kept separate and having the same statistical design as in 1971. There was a general pattern of clinal variation in bud burst, bud set, colour of the needles and epicotyl length at the end of the first year. Bud burst was negatively correlated with longitude ($r = -0.50$). Bud set appeared to be under strict genetic control as attested by the second estimation of this character at the end of the second growing season (with latitude: $r^2 = 0.77$). Latitude and altitude of the place of origin of the provenances explained 65% of the total variation in epicotyl length. Total height after the second growing season showed the same relationship as epicotyl length. Components of variance and their standard error were calculated for epicotyl length and total height. Depending on the sub-region, the genetic variance among provenances was generally larger than the tree to tree genetic variation. The narrow sense heritability, on an individual basis, and its standard error, for total height, were estimated on a sub-region basis. Heritability was found to be generally close to 0.10, but affected by a large standard error.

Key words: Picea sitchensis (Bong.) Carr., Provenance and Progeny variation. 1970. I.U.F.R.O. collection.

Zusammenfassung

Im April 1971 wurden 542 Einzelbaumabsaaten aus 38 Herkünften von *Picea sitchensis* in einer Blockanlage mit 4 Wiederholungen durchgeführt. Nach dem Auflaufen der Sämlinge wurden das Pflanzenprozent, die Knospenbildung,

die Epikotyllänge und das Überstehen der ersten Vegetationsperiode festgestellt bzw. gemessen. Im Mai 1972 wurden die Pflanzen in gleicher Blockanordnung verschult. Nach dem ersten Jahr zeigte sich eine allgemeine Tendenz zu klinaler Variation beim Austreiben, bei der Knospenbildung, bei der Nadelfarbe und der Epikotyllänge. Insbesondere nach der zweiten Vegetationsperiode ergaben sich deutliche Zusammenhänge bei der Knospenbildung, Epikotyllänge und Gesamthöhe jeweils bezogen auf den Herkunftsort einer Provenienz. Die genetische Varianz war zwischen den Nachkommenschaften größer als zwischen den Einzelbäumen.

Literature Cited

Andersson, R. L. and Bancroft, T. A.: Statistical theory in research. McGraw Hill Co., New York. 400 pp. (1952). — Becker, W. A.: Manual of procedures in quantitative genetics. The programme in genetics. Washington State University, Washington. 128 pp. (1967). — Burley, J.: Provenance variation in growth of seedling apices of Sitka spruce. For. Sci. **12** (2): 170—4 (1966 a). — Burley, J.: Variation in colour of Sitka spruce seedlings. Quart. Jl. For. **60** (1): 51—4 (1966 b). — Draper, N. R. and Smith, A.: Applied regression analysis. J. Wiley & sons, Inc. New York and London. 407 pp. (1966). — Driscoll, J. O.: I.U.F.R.O. S2-02-12. Sitka spruce provenance working plan for international ten-provenance experiment. Stencilled notes. Forest and Wildlife Service. Dublin 2. Ireland. 68 pp. (1972). — Falconer, D. S.: Introduction to quantitative genetics. Oliver & Boyd. Edinburgh & London. 356 pp. (1964). — Falkenhagen, E. R.: La génécologie forestière: une introduction. Annales de Gembloux **74**: 181—192 (1968). — Falkenhagen, E. R.: A study of the phenotypic and genotypic variation of 542 single tree progenies of 38 provenances of the 1970 I.U.F.R.O. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) collection. Ph. D. thesis. Faculty of Forestry. University of British Columbia. Vancouver, Canada. 235 pp. (1974). — Falkenhagen, E. R.: Composantes de variance pour un modèle déséquilibré à trois facteurs hiérarchisés et croisés. Biométrie-Praximétrie XVI (1-2), 50—57 (1976). — Falkenhagen, E. R. and Nash, S. W.: Multivariate classification in provenance research. A comparison of some statistical techniques; in press, Silvae Genetica (1977). — Galoux, A.: La variabilité génécologique du hêtre commun (*Fagus sylvatica* L.) en Belgique. Station de recherches des Eaux et Forêts. Groenendaal-Hoeillart. Travaux. Série A. No. 11. 121 pp. (1966). — Kozlowski, T. T.: Growth and development of trees. Vol. 1. Academic Press. New York and London. 443 pp. (1971). — Mahamunulu, D. M.: Sampling variances of the estimates of variance components in the unbalanced 3-way nested classification. Ann. Math. Stat. **34**: 521—527 (1963). — Matthews, R. G.: Container seedling production: a provisional manual. Pacific Forest Research Centre. C.F.S. Information report. B.C. — X-58. 57 pp. (1971). — Namkoong, G.: Inbreeding effects on estimation of genetic additive variance. Forest Science **12** (1): 9—13 (1966). — Romberger, J. A.: Meristems, growth, and development in woody plants. U.S. D.A. techn. bull. 1293. 212 pp. (1963). — Samuel, C. J. A., Johnstone, R. C. B. and Fletcher, A. M.: A diallel cross in Sitka spruce. Assessment of first year character in an early glasshouse test. Theoret. Appl. Genet. **42**: 53—61 (1972). — Schober, R.: Die Sitka-Fichte. Schriftenreihe der Forstlichen Fakultät der Universität Göttingen. Bd. 24/75. 230 pp. — Stern, K.: Herkunftsversuche für Zwecke der Forst-pflanzenzüchtung erläutert am Beispiel zweier Modellversuche. Der Züchter **34** (5): 182—219 (1964). — Vegis, A.: Die Bedeutung von physikalischen und chemischen Außen-faktoren bei der Induktion und Beendigung von Ruhezuständen bei Organen und Geweben höherer Pflanzen. In: Handbuch der Pflanzenphysiologie. Band XV. Teil 2. 534—668. Springer-Verlag (1965). — Wright, J. W.: Genetics of forest tree improvement. FAO No. 16. 399 pp. (1962).

Female Sterility in Douglas-fir

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Introduction

In 1967, controlled pollinations were made on three young Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco which were located in a natural stand some 100 km southeast of Cowichan Lake on southern Vancouver Island, British Columbia. The trees were bagged at the beginning of April and pollinated May 9th, the pollen used for the crosses coming from single trees on the coastal mainland of the province, Oregon, Arizona and New Mexico. Cones were collected at the beginning of September together with wind-pollinated samples from each of the trees. There had been little damage from cone insects and the seed was extracted without any difficulty. It was then found that the more than 3500 seeds from tree 618 were all undeveloped and flat so that not one seed could be sown. The seeds from the other two trees, were perfectly normal with yields of 45.0 and 68.4 seeds per cone respectively and later produced 28.2 and 37.0 healthy germinants per cone in the nursery. The difference between normal fully formed seed and the typical flat seed from tree 618 is shown in *Figure 1.*

Figure 1. — Normal seed compared with flat undeveloped seed.

Seed Development on Clone 618

As this was the first occasion that this phenomenon had been observed in the course of extensive pollinations with Douglas fir, tree 618 was propagated to ascertain whether the clone would produce similar flat seed when grown in a different environment. Scions were accordingly removed and grafted at Lake Cowichan in 1968, the two surviving