Table 3. — Analysis of variance based on average height growth of sets of crosses using the method of Eberhart and Russell.

Source of variation	DF	SS	MS	
Sets	10	6.908	.6908	$MS^b{}_1$
Location + (Location x Sets)	88	707.736	8.0424**[a]	
Locations (linear)	1	667.482	667.482**	
Sets × location (linear)	10	3.182	.3182	MS_2
Pooled deviations	77	37.072	.4814	MS_3

[a] Significant at the .01% probabaility level.

[b] To test the significance of differences among sets of crosses.

F $\simeq MS_1/MS_3$ was used; to test the significance of differences among the regression coefficients, F $\simeq MS_2/MS_3$ was used.

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Supernumerary chromosome distribution in provenances of Picea sitchensis (Bong.) Carr.

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Introduction

Moir and Fox (1972) described the existence of supernumerary (B-) chormosomes in seven provenances of Sitka spruce from the central part of its geographical range. This B-chromosome is typical of supernumerary chromosomes in general in existing as a widespread polymorphism, with variable frequency, both in different individuals and different provenances. It is also heterochromatic, another frequent feature of such chromosomes. Indeed, this last property allows the B-chromosome status of a plant to be determined from non-dividing tissue. Generally, one cannot detect the presence, let alone the frequency, of B-chromosomes in a population for they do not have marked effects upon the external phenotype (exophenotype). However, where effects have been described, they frequently affect characters concerned with the fitness of individuals or populations (See Jones, 1975 for review). Small numbers of B-chromosomes sometimes increase fertility and vigour, e.g. fertility and viability were higher in Lilium *calosum* plants with 1 B than in those with O B'sKimura and Kayano (1961) and Rutishauser (1956) found that seed fertility increased with the presence of up to three euchromatic B-chromosomes of a specific type in the endosperm of *Trillium* grandiflorum. However, deleterious effects of B-chromosomes on the exophenotype have been described rather more frequently. The presence of a single B in

Plantago coronopus gave rise to male sterility (Daliwal and Hyde, 1960) and in *Lilium callosum* (Kimura and Kayano, 1961) pollen fertility and seed set were greatly reduced with as few as 2 B's. Muntzing (1963) studied diploid varieties of Swedish and Korean Rye. As B frequency increased in individuals, fertility decreased correspondingly irrespective of origin. On the other hand, straw weight was progressively reduced with increasing numbers of B's in the Swedish varieties but not in Korean Rye.

Effects observed in the exophenotype are probably the results of effects produced at a cellular or nuclear level (endophenotype) — see Rees and Jones (1968), Ayonoadu and Rees (1971). B-chromosomes often affect the number and position of chiasmata and thus genetical crossing-over. This usually results in increase in the rate of release of genetic variation (Ayonoadu and Rees, 1968; Malik and Tripathi, 1970; Barlow and Vosa, 1970; Zecevic and Paunovic, 1969).

In view of the widespread effects of supernumerary chromosomes on fitness characters in other plant species, it is vital to assess their effects in Sitka spruce. In this paper we have laid the foundations for such an investigation by recording the frequency of occurrence of B-chromosomes in some detail throughout the species range in the hope of shedding hight on the selective forces currently operating to control the supernumerary chromosome frequency. It will be of great importance for the exploitation of Sitka spruce to discover if this chromosome plays a positive adaptive role in natural populations.

Table 1. — The locations of the 43 provenances of *Picea sitchensis* and *Picea glauca* used in this study

Origin	Latitude (°N)	Longitude (°W)	Altitude (feet)
Val	61° 07'	146° 16'	100
Ken^{-}	60° 33'	151° 66'	50-60
21	59° 31'	139° 42'	40
22	59° 30'	135° 21'	0
23	58° 32'	134° 48'	50
Ala	58°	153°	25-250
25	56° 35'	132° 44'	0-50
26	55° 41'	128° 41'	800
28	55° 28'	132° 40'	0
Sun^{-}	55° 20'	120° 40'	3500-3700
32*	55° 10'	127° 52'	2200
36*	55° 01'	128° 19'	800
40*	54° 38'	128° 24'	450
41*	54° 24'	128° 57'	100
44*	54° 12'	130° 15'	0-100
45*	54° 12'	129° 55'	0
And^{-}	53° 48'	126° 42'	3350-3500
51	53° 03'	132° 04'	200
54	51° 56'	126° 53'	450-850
56^{+}	50° 36'	128° 06'	100-700
58	50° 23'	125° 57'	0
59^{+}	50° 03'	127° 02'	100
60	49° 53'	123° 15'	100
61^{+}	49° 50'	126° 40'	0
62^{+}	49° 23'	124° 37'	0
64	49° 07'	121° 56'	100
01	48° 45'	122° 38'	50-100
65^{+}	48° 35'	124° 24'	0-50
66^{+}	48° 23'	123° 52'	0
67	48° 07'	121° 45'	1000-1200
03	48° 04'	124° 18'	400-500
04	47° 42'	124° 25'	0-100
06	47° 21'	123° 09'	0-20
08	47° 05'	124° 03'	20
10	46° 22'	123° 47'	0-50
12	45° 49'	123° 46'	150
13	45° 20'	123° 53'	300-400
15	44° 07'	124° 07'	500
16	42° 51'	124° 27'	500
17	42° 30'	124° 25'	100
18	42° 15'	124° 23'	300
20	41° 40'	124° 11'	30-50
19	41° 08'	124° 09'	30-50

- - - *Picea glauca*, * — Skeena River area populations, + — Vancouver Island populations of *Picea sitchensis*.

Materials and Methods

(i) *Seed Origins.* The seed samples used in this work were derived from IUFRO collections made in North America in 1968, 1969 and 1970. At each site seeds were collected from up to 20 trees and subsequently bulked. In addition three pure *Picea glauca* (white spruce) seed lots (from Sundown Creek, Andrew Bay and Kenai Peninsula) were also investigated. Details of provenance locations and altitudes are given in *table 1.*

ii) *Cytological techniques.* Germination of seed was on damp sand at 20° C in plastic petri dishes. Fixation and slide preparation from the tap root of two-week old seedlings was essentially according to the procedure of Moir and Fox (1972) usually with the omission of a spindle inhibitor. However, a few seedlings were treated with 0.05% colchicine for 4 hrs. prior to fixation.

While in our earlier work (Moir and Fox, 1972) it was found that B-chromosome satus could be determined by casual observation of numbers of chromocentres in the interphase nuclei, difficulties arose in the present study in some provenances which proved to have high mean B-chromosome frequencies. Two of the 43 provenances with high mean B-chromosome frequencies were selected for more detailed study, provenance 66 on Vancouver Island and provenance 18 on the mainland. The B-chromosome con-

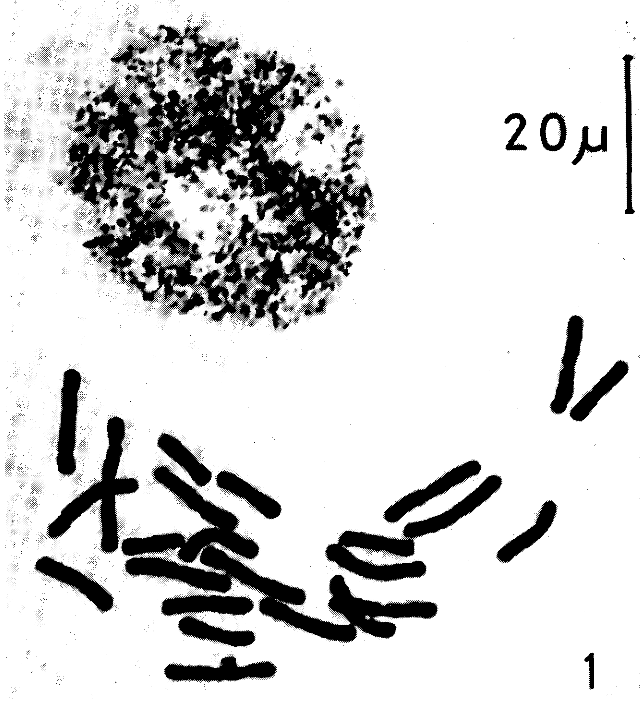

Fig. 1. — C-metaphase and interphase cells from origin 66 plant lacking B-chromosomes. Note the presence of 24 metacentric or sub-metacentric chromosomes all of similar size and the absence of large chromocentres in the interphase nucleus.

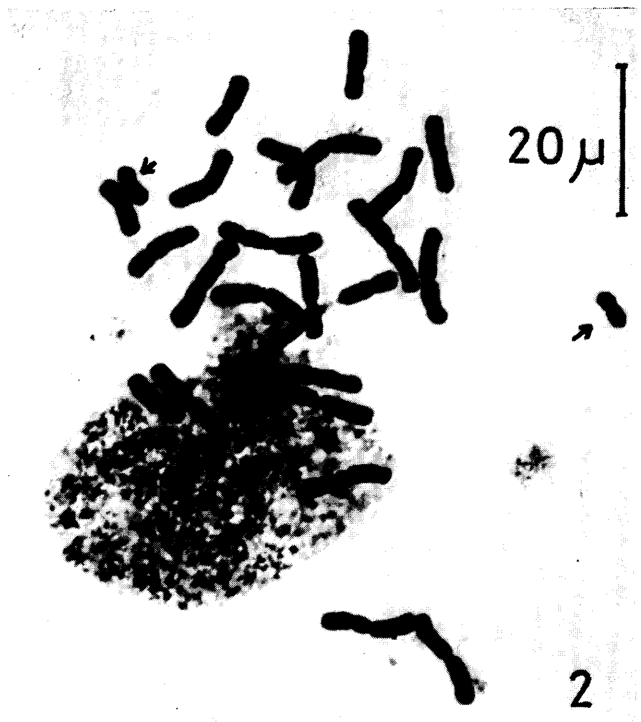

Fig. 2. — C-metaphase cell from origin 66 plant carrying two B-chromosomes. Note that one B-chromosome is sub-metacentric while the other is more or less metacentric. These chromosomes are in addition to the 24 much larger members of the A-chromosome set.

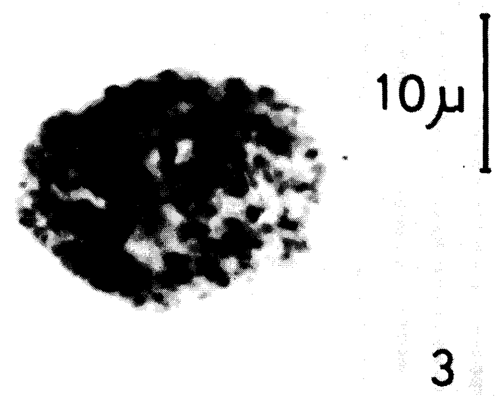

Fig. 3. — Interphase nucleus from origin 66 plant carrying two B-chromosomes. Note the presence of two large chromocentres.

stitution from each single root preparation was determined by scoring the distribution of chromocentre number in the first 100 interphase nuclei encountered.

Results

i) *Determination of B-chromosome status.*

B-chromosome status can usually be determined quickly by the inspection of chromocentre number in interphase nuclei of the root tip meristem *(Figs. 1—3)*. However, in some cases extensive counts were necessary. *Tables 2 and 3* contain data on frequency of chromocentres in the 60 roots sampled from origin 66 and 41 roots sampled from origin 18. In these tables plants are ranked according to increasing mean chromocentre scores and the estimated B-chromosome status is derived from the chromocentre class containing the highest proportion of cells. *Table 4* shows the mean chromocentre number and standard deviation for the plants of each B-chromosome class in origins 66 and 18.

ii) *Geographical distribution of B-chromosomes.*

The B-chromosome constitution of 50 or 75 seedlings from each provenance (excepting Andrew Bay *Picea glauca* where only 43 seedlings were available) was determined from chromocentre frequencies. This allows the population frequency of B-chromosomes to be estimated with some accuracy. It was clear that while all B-chromosomes are smaller than the smallest A-chromosome (Moir and Fox, 1972), some are metacentric and some sub-metacentric *(fig 2)*. Often it was difficult to decide if the centromere position in the B-chromosome was median or not since most plants were not treated with a spindle inhibitor. The actual frequency of sub-metacentrics was only estimated for provenance 66. Here 82.4% of B-chromosomes were metacentric and 17.6% sub-metacentric. However, a low frequency of sub-metacentric B's was also found in the mainland *Picea sitchensis* provenances and in the Sundown Creek and Andrew Bay *Picea glauca* provenance.

Fig. 4 illustrates the distribution of B-chromosome frequency in relation to the natural range of the species. Details of the provenance B-chromosome statistics are given in *table 5*.

Discussion

i) *The validity of the technique.*

The method used in this work to determine the B-chromosome status of a plant is indirect, depending as it does on counts of chromocentre numbers from interphase nuclei. However, extensive quantitative evidence from previous work (Moir and Fox, 1972) strongly supports its accuracy. In that paper no plant was observed with more than 2 B-chromosomes but in the present work some provenances contain plants with up to 5 B-chromosomes. The data in *tables 2 and 3* relating to provenances 66 and 18, both of which had high- B-chromosome frequencies, illustrate the difficulties that high B-chromosome frequency presents for this method. In both cases there is a clear discontinuity between distributions having mean chromocentre numbers near O/cell and 1/cell. Thus, as was found previously, the B-chromosome must be responsible for nearly all large chromocentres seen in interphase nuclei of this species. The real problem then is to estimate the number of B-chromosomes present, not their presence or absence. In both *tables 2 and 3* the individual plants are ranked according to increasing chromocentre mean. As the mean increases the number of classes represented in the distribution increases and the frequency of the most frequent class decreases. Since we do not know what factors are responsible for this variation in chromocentre number within plants, it was decided to allot each plant the B-chromosome status corresponding to the most frequent chromocentre class. Some mistakes will be made *e.g.* distributions 19, 21, 31 and 34 in *table 2* may have been wrongly assessed when one also takes into account the chromocentre mean but on the other hand no similar cases in transitions between adjacent B-classes are present in *table 3*. Provenance 66 had by far the highest B-chromosome frequency and so the few errors which may have been made here are probably not repeated elsewhere. This suspected low frequency of error is acceptable when one considers the rapidity of this indirect technique in comparison with the more direct method of chromosome counting in colchicine-metaphase cells.

ii) *Factors affecting B-chromosome distribution.*

In trying to understand the characteristics of the current geographical distributionn of supernumerary chromosomes in *Picea sitchensis* two major questions must be answered. (a) Is the B-chromosome of recent or ancient origin and, if the latter, in what ways may the migrational history of the species have affected its distribution?

(b) Is the B-chromosome adaptive, conferring clear advantages or disadvantages upon its possessors under certain circumstances, or is it a neutral character?

The *Picea* genus is believed to have been introduced from Asia into America via the Siberian-Alaskan land bridge during the middle of the Tertiary period and to have spread eastward and southward over the continent (Stebbins, 1971,

Table 2. — Chromocentre frequencies in 60 plants from origin 66. They are ranked according to increasing mean chromocentre frequency and the B-chromosome status is estimated from the most frequent chromocentre class.

Rank No.	Chromocentre class frequency					B Status	Rank No.	Chromocentre class frequency							B Status
	0	1	2	3	3			0	1	2	3	4	5	5	
1	100	-	-	-	-	0	31	-	36	30	28	6	-	-	1
2	100	-	-	-	-	0	32	7	20	41	30	2	-	-	2
3	100	-	-	-	-	0	33	-	13	72	12	1	1	1	2
4	100	-	-	-	-	0	34	6	26	33	29	3	3	1	2
5	100	-	-	-	-	0	35	3	23	30	36	7	-	-	3
6	98	2	-	-	-	0	36	4	22	29	39	6	-	-	3
7	94	6	-	-	-	0	37	1	20	33	38	7	1	-	3
8	75	21	4	-	-	0	38	3	18	29	35	13	2	-	3
9	14	69	17	-	-	1	39	8	17	25	36	12	2	-	3
10	5	86	8	1	-	1	40	2	14	43	28	11	2	-	2
11	8	77	13	2	-	1	41	6	17	29	31	12	3	2	3
12	6	79	11	4	-	1	42	4	16	32	36	9	2	1	3
13	14	63	20	2	1	1	43	5	15	22	50	7	1	-	3
14	6	75	15	4	-	1	44	1	16	29	36	15	3	-	3
15	6	70	21	2	1	1	45	-	13	28	45	13	1	-	3
16	9	54	29	6	2	1	46	-	13	28	49	4	6	-	3
17	12	46	27	9	6	1	47	1	9	24	55	8	3	-	3
18	8	33	51	6	2	2	48	1	8	23	58	8	2	-	3
19	8	44	27	13	8	1	49	4	8	15	56	11	5	1	3
20	4	36	50	6	4	2	50	1	9	29	37	22	2	-	3
21	9	42	29	11	9	1	51	3	11	17	33	29	7	-	3
22	8	29	47	14	1	2	52	2	13	21	28	29	6	1	4
23	6	31	45	11	7	2	53	2	11	20	41	13	7	6	3
24	10	24	46	14	6	2	54	-	9	21	38	29	3	-	3
25	6	27	53	12	2	2	55	1	7	15	28	39	7	3	4
26	-	32	50	14	4	2	56	1	6	17	28	30	17	1	4
27	6	29	42	14	9	2	57	-	5	18	26	40	9	2	4
28	3	25	52	16	4	2	58	-	7	17	22	41	13	-	4
29	-	18	72	9	1	2	59	1	5	11	20	41	15	7	4
30	1	29	49	14	7	2	60	1	6	7	14	20	29	23	5

Table 3. — Chromocentre frequencies in 41 plants from origin 18. They are ranked according to increasing mean chromocentre frequency and the B-chromosome status is estimated from the most frequent chromocentre class.

Rank No.	Chromocentre class freauency					B Status	Rank No.	Chromocentre class frequency					B Status
	0	1	2	3	3			0	1	2	3	3	
1	100	-	-	-	-	0	22	12	67	18	2	1	1
2	100	-	-	-	-	0	23	6	71	23	-	-	1
3	100	-	-	-	-	0	24	13	61	24	-	2	1
4	100	-	-	-	-	0	25	4	76	16	4	-	1
5	100	-	-	-	-	0	26	11	63	17	5	4	1
6	100	-	-	-	-	0	27	3	71	19	5	2	1
7	100	-	-	-	-	0	28	6	62	26	5	1	1
8	100	-	-	-	-	0	29	6	57	30	4	3	1
9	100	-	-	-	-	0	30	2	66	24	5	3	1
10	100	-	-	-	-	0	31	11	36	45	5	3	2
11	99	1	-	-	-	0	32	4	40	46	8	2	2
12	98	1	1	-	-	0	33	2	35	52	10	1	2
13	96	2	2	-	-	0	34	4	27	57	11	1	2
14	97	-	3	-	-	0	35	3	27	58	11	1	2
15	91	6	3	-	-	0	36	6	17	65	11	1	2
16	15	72	12	1	-	1	37	-	21	68	7	4	2
17	10	81	8	1	-	1	38	3	23	50	20	1	2
18	12	71	15	2	-	1	39	3	17	59	18	3	2
19	9	78	10	2	1	1	40	-	17	57	25	1	2
20	9	72	18	1	-	1	41	4	18	29	44	5	3

Table 4. — Mean chromocentre number per cell and standard error for the different B-chromosome classes in origins 66 and 18.

Origin	Root B Status	Chromosome Mean ± S.E.	Coefficient of Variation
66	1	1.35 ± 0.85	62.29%
	2	1.92 ± 0.92	48.07%
	3	2.59 ± 1.08	41.58%
	4	3.34 ± 1.24	36.97%
	5	4.38	-
18	1	1.18 ± 0.65	55.14%
	2	1.83 ± 0.75	40.90%
	3	2.37	-

p. 188; Wright, 1955). Wright (1955) proposed that *Picea jezoensis* was the link between the Old and New World, with Sitka being the first of the *glauca-engelmannii-sitchensis-pungens* (*i.e.* White, Engelman, Sitka, Blue Spruce) complex to arise from it. However, Fowler (1966) with fossil evidence of a newly-discovered, extinct spruce species, proposed that *Picea glauca* was the link. This would imply a more recent origin for Sitka.

The north american spruces are certainly very closely related, often forming hybrids in overlapping parts of their ranges (Roche, 1969) and under cultivation (Wright, 1955). Their karyotypes are identical in chromosome number and very similar in chromosome shape and size (Burley, 1965; Moir and Fox, 1972; Moir, 1975; Teoh personal com-

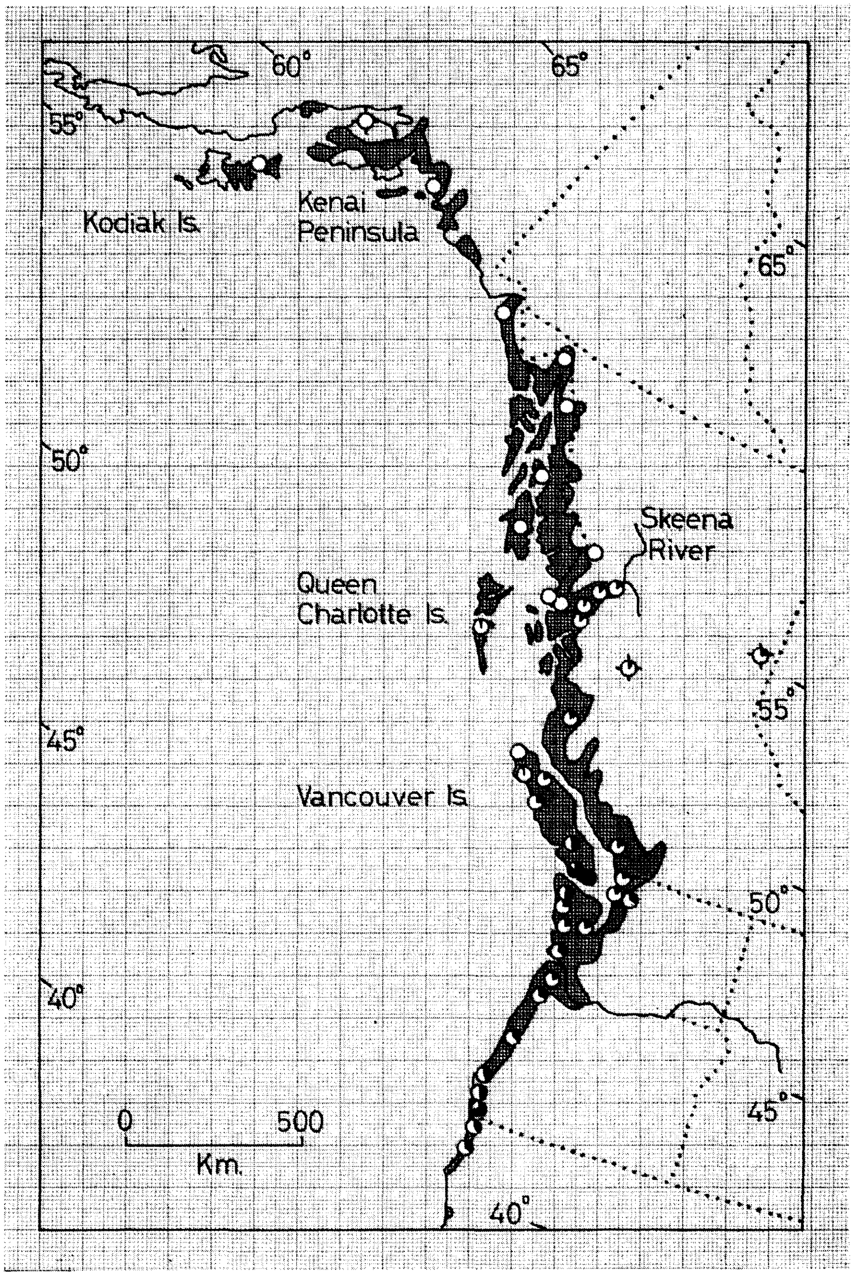

Fig. 4. — Distribution of B-chromosome frequency in provenances of *Picea sitchensis* in relating to the natural range. Cross-hatched area — natural range of *Picea sitchensis*. Symbols indicate B-chromosome frequency 360° black area = 1.0 B-chromosomes/plant. Origin 66 had a frequency of 1.52 B-chromosomes/plant but is still indicated by the symbol appropriate to 1.0/plant. The *Picea glauca* populations are indicated by the modified symbol ⌖

Table 5. — Provenance frequency of B-chromosomes.

Origin	B-chromosome frequency					Total Plants	Mean B Chromosome per plant
	0	1	2	3	4		
Val	50					50	0
Ken$^-$	50					50	0
21	75					75	0
22	75					75	0
23	75					75	0
Ala	50					50	0
25	75					75	0
26	50					50	0
28	50					50	0
Sun$^-$	42	4	4			50	0.24
32*	48	8				50	0.16
36*	69	3	1	2		75	0.15
40*	69	6				75	0.08
41*	46	1	3			50	0.14
44*	75					75	0
45*	75					75	0
And$^-$	39	4				43	0.09
51	72	3				75	0.04
54	42	7	1			50	0.18
56$^+$	50					50	0
58$^+$	43	5	1	1		50	0.20
59$^+$	74	1				75	0.01
60	44	3	3			50	0.18
61$^+$	38	9	3			50	0.30
62$^+$	38	26	10	1		75	0.52
64	41	8	1			50	0.20
01	43	5	2			50	0.18
65$^+$	34	20	17	4		75	0.88
66$^+$	11	28	22	13	1	75	1.52
67	37	8	5			50	0.36
03	44	24	5	2		75	0.53
04	39	9	2			50	0.26
06	42	5	3			50	0.22
08	42	5	3			50	0.22
10	35	12	3			50	0.36
12	61	13	1			75	0.20
13	35	14	1			50	0.32
15	48	24	3			75	0.40
16	47	23	4	1		75	0.45
17	32	12	5	1		50	0.50
18	32	33	10			75	0.71
20	34	12	4			50	0.40
19	52	19	4			75	0.36

- -*Picea glauca*, * — Skeen River area populations, + — Vancouver Island Populations of *Picea sitchensis*.

munication). Further, the DNA content of the haploid complement is virtually the same in *sitchensis, glauca* and *engelmannii* (Rees and Teoh, 1976; Moir, 1975). Finally, on morphological grounds and its presence in hybrids, the B-chromosome found in *sitchensis* (Moir and Fox, 1972) looks identical to that present in *glauca* (Moir, 1975 and this paper; Teoh, personal communication) and *Picea obovata* (Kruklis, 1971), and Old World species with an extensive distribution. It seems possible therefore that the B-chromosome present in the north american spruce species had a common origin in the Old World prior to the colonisation of North America. In view of the frequent occurrence of hybrid swarms between the North American spruce species and the occurrence of the same morphological types of B-chromosomes in *Picea sitchensis* and *Picea glauca* with similar frequency (see Results) it seems likely that-B-chromosomes will have been passed from one species to another on numerous occasions.

During the Pleistocene upheavals in America, when the ice sheet repeatedly advanced and retreated, *Picea* was forced to migrate in different directions and it underwent range restrictions and fragmentation (Daubenmmire, 1968). From pollen data analysis, several researchers (*e.g.* Hulten, Halliday and Brown — see Roche, 1969) concluded that all four *Picea* species of the complex survived the late Pleistocene era in the south, afterwards invading the north. According to Daubenmire (1966) the final ice-sheet extended over the whole of Vancouver Island and the north eastern part of the Olympic Peninsula, Washington. Other workers believe that *Picea* also took refuge in nunatak habitats in the corner of Graham Island, Queen Charlotte Islands (Day, 1957), in west central Yukon and on the eastern slopes of the Rocky Mountains, British Columbia (see Roche, 1969). It is likely therefore that the most southerly populations of present day *sitchensis* are the oldest. What is certainly beyond doubt is that north of Juneau, Alaska, *Picea sitchensis* populations are much younger than the rest of the range (Daubenmire, 1968). Now it is also true, in general, that the most southerly populations of *Picea sitchensis* also have the highest B-chromosome frequency *(fig. 5).* With the retreat of the last ice-sheet and the recolonisation of more northerly habitats the B-chromosome would be expected to spread north. Thus to account for the absence of B-chromosomes from the northern part of the contemporary *sitchensis* range on migrational grounds it would be necessary to propose a separate colonisation of this area, possibly from nunatak habitats, by plants totally lacking B-chromosomes. In view of the likely ancient origin of the B-chromosome, its spread to North America via Alaska, and the presence of presumed homologous B-chromosomes in *Picea glauca* as far north as Yukon (Teoh, personal commnunication) this argument seems improbable. The alternative to this proposal is that the B-chromosome is adaptive and its absence from the northern half of the species range is due to its possession being disadvantageous there.

Darlington (1956) believed that B-chromosomes boosted the variability of a species and should be found in the marginal, inbreeding populations of a species range. However, since that time, only work on *Brachyome* (Carter and Smith-White, 1972) has tentatively supported this idea, the majority of reports (see Hewitt, 1974) indicating that B-chromosomes are found with highest frequency in the central, stable, outbreeding populations. The current situation in *Picea sitchensis* does not fit easily with either of these hypotheses. It reaches zero frequency near the centre of the species range, is admittedly absent from the pioneering populations in the extreme north west but is present with relatively high frequency in the most extreme southerly populations which, while they are old, are definitely marginal.

As was pointed out in the Results section above, the distribution of B-chromosomes is clearly non-random, not being found at all in pure *Picea sitchensis* north of the Queen Charlotte Islands. However before considering the climatological factors which may be correlated with B-chromocentre frequency, the question of introgression with *Picea glauca* in the Skeena River area must be dealt with.

Natural hybrids between *Picea sitchensis* and *Picea glauca* were first seen on Kenai Peninsula, Alaska, by Little (1951). They were then noted in Copper River Valley, Alaska by Shepherd (1962). In the Skeena River area, including the Nass River and the upper reaches of the Fraser River, similar hybrids have been found. Roche (1969) only recognises them in populations east of Terrace (approximately origin 36 eastward — see *fig. 4* and *table 1)* but Daubenmire (1968) described hybrids west of Terrace also though the morphological characters of the trees at the estuary of the Skeena River fitted into a general north-south cline in the rest of the range of *Picea sitchensis.*

Further evidence for hybridisation in this area comes from the work of Hanover and Wilkinson (1970) on the composition of leaf oils. Their hybrid studies (at approximately origins 41 and 36 — see *fig. 4* and *table 1)* confirm Daubenmire's (1968) findings of hybrids down-river as well as upriver of Terrace.

The presence of B-chromosomes in all four provenances (41, 40, 36 and 42) from the Skeena River Valley, the absence of B-chromosomes from the two pure *Picea sitchensis* provenances nearest to the River mouth (45 and 44) and the presence of B-chromosomes in pure *Picea glauca* in the region *(fig. 4* and Teoh — personal communication) suggest that the B-chromosome in this area is probably derived from *Picea glauca* and not *Picea sitchensis.* B-chromosomes are found in the populations which are probably the oldest. However, the Skeena River populations must be very young yet they still contain B-chromosomes. Perhaps the age of populations is not of great consequence for their possession of B-chromosomes.

B-chromosome distribution in other organisms has been found to be correlated with altitude (Malik and Tripathi, 1970), humidity (Frost, 1958), rainfall (Hewitt and Brown, 1970) and soil type (Bosemark, 1967). However, in seeking correlations with specific climatological and edaphic factors for the *Picea glauca* B-chromosome one is faced with the problem of insufficient detailed information of this kind. Using data contained in the works of Brydon and Hare (1974) and Walter *et al.* (1975), some tentative general correlations with climate do seem to emerge. Firstly, the northern border of the B-chromosomes' distribution corresponds more or less to the limit of persistent frost, *i.e.* regions which suffer persistent frost do not contain B-chromosomes. Secondly, the parts of the *Picea sitchensis* range with the highest B-chromosome frequencies also have the lowest mean annual precipitation. Thirdly, the high B-frequency areas also have high mean hours of sunshine, especially in summer.

The highest B-chromosome frequency recorded in this work was for provenance 66 in the south-east corner of Vancouver Island. The uniqueness of the climate of this area has been noted by Kerr (1951) who named it a "summer-dry climate". It is the only place in Canada which is similar to a Mediterranean regime and possesses an unusual flora, including Garry Oak *(Quercus garryana)* and Madrona *(Arbutus menziesii)* which are adapted to high summer sun and low summer rainfall. This climate also extends to a few adjacent areas on the mainland. In conclusion there does appear to be a correlation between climatic factors and the frequency of B-chromosomes but the causal relationship between them is not clear. The evidence presented here, while suggesting that the possession of B-chromosomes is not a neutral character in *Picea sitchensis,* does not indicate if it confers positive advantages upon the populations that contain it or if it is indeed a chromosomal parasite which may only be tolerated in populations growing under very favourable conditions. The fact that this B-chromosome, like many others — see Battoglia 1964, possesses an accumulation mechanism in the female germ line (Moir, 1975) suggests that there must be a corresponding selection against it at some other point in the life cycle. It will be of great importance for the commercial exploitation of this species to discover what role this major genetic polymorphism plays.

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Summary

1. Supernumerary (B-) chromosome frequency was determined for 40 provenances of *Picea sitchensis* from the whole of the species range. In addition three provenances of *Picea glauca* were investigated.
2. The technique for estimation was indirect, employing chromocentre counts from interphase nuclei in the root meristem. Difficulties involved in the use of this technique for high B-frequency populations are discussed.
3. B-chromosomes were found in all but one pure *Picea sitchensis* provenance below 53^{0} N but in no pure provenance above that latitude.
4. The B-chromosome is usually metacentric and smaller than the smallest A-chromosome. A small proportion of B-chromosomes in *Picea sitchensis* is sub-metacentric and this dimorphism was also found in two provenances of *Picea glauca.*
5. In a *sitchensis* × *glauca* hybrid swarm from the Skeena River area B-chromosomes were present and appeared to be derived from *Picea glauca.*
6. The similarity of the *sitchensis* and *glauca* B-chromosomes to that described in the Old World species *Picea obovata* leads to the suggestion that they originated before the colonisation of North America by the genus *Picea.*
7. Population B-chromosome frequency is variable and is particularly high in the south-eastern part of Vancouver Island and some adjacent parts of the mainland.
8. B-chromosomes seem only to be present in populations south of the line of persistent frost.
9. The highest B-chromosome frequencies are found in areas of low rainfall and high summer insolation.

Key words: Sitka spruce, supernumerary chromosomes, population varation, interspecific hybridization.

Zusammenfassung

Bei 40 Provenienzen von *Picea sitchensis* aus dem gesamten Verbreitungsgebiet der Art wurde die Frequenz der überzähligen B-Chromosomen bestimmt, desgleichen bei 3 Provenienzen von *Picea glauca.* Die Bestimmung erfolgte indirekt.

Im Teilungsgewebe der Wurzel wurden die Chromozentren der Interphasekerne gezählt. B-Cromosomen wurden bei allen *P. sitchensis*-provenienzen unter 53^{0}N gefunden, ausgenommen bei einer Provenienz, die keine Mischung war. Bei einem Hybridschwarm von *sitchensis* und *glauca* in der Nähe des Skeenaflusses wurden B-Chromosomen gefunden die sich wahrscheinlich von *P. glauca* ableiten lassen. Die Ähnlichkeit der B-Chromosomen von *P. glauca* und *P. sitchensis* mit solchen von *Picea obovata* scheint darauf hinzuweisen, daß die Ausbreitung der Art von Nordamerika her erfolgt ist. Die Frequenz der B-Chromosomen ist veränderlich und im Südosten von Vancouver Island sowie auf dem angrenzenden Festland besonders hoch. Es scheint B-Chromosomen nur in solchen Populationen zu geben, die ihre Verbreitung südlich der Dauerfrostgrenze haben. Die höchste Frequenz wurde in Gebieten mit geringem Niederschlag und hoher Sonnenscheindauer gefunden.

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Über Austrieb und Zuwachs von Fichtenklonen in verschiedener Seehöhe[1])

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Einleitung

Die Variabilität der Fichte *(Picea abies* (L.) Karst.) ist aufgrund ihres weiten Verbreitungsgebietes entsprechend groß, da diese Holzart sich sowohl an gemäßigte wie an kalte Klimate z. T. sehr unterschiedlicher photo- und thermoperiodischer Verhältnisse anpassen mußte. Das äußert sich nicht nur in morphologischer Hinsicht (Holzer 1964, 1967, Schmidt-Vogt 1972), sondern vor allem in der physiologischen Reaktion der Sämlinge verschiedener Herkünfte im Zuge von Nachkommenschaftsprüfungen in Kulturkammern (Dormling *et al.* 1968, 1971, Heide 1974, Holzer 1966, 1975) oder im Pflanzgarten (Cieslar 1895, Krutzsch 1975, Holzer 1967, 1975). Auch langfristige Herkunftsversuche, wie der IUFRO-Fichtenversuch 1938 (Zusammenfassung bei Lines 1974) und der inventierende Fichtenversuch 1964—1968 (erste Ergebnisse bei Krutzsch 1975) lassen diese Tatsache erkennen und zeigen, daß bei Begründung von Fichtenwäldern der Herkunft des Pflanzenmaterials besondere Beachtung geschenkt werden muß (Holzer und Nather 1974).

Im zentraleuropäischen alpinen Gebirgsraum ist diese Herkunftsfrage besonders wichtig, da hier auf engem Raum durch die starke vertikale Gliederung die unterschiedlichsten Typen nahezu nebeneinander vorkommen (Holzer 1964, 1970). Um die physiologische Reaktion der einzelnen Typen näher erforschen zu können, wurden Versuche durch Verklonung entsprechend differierender Ausgangspflanzen angelegt (Holzer 1974), die eine eingehende Analyse der Umweltwirkung durch die unterschiedlichen Seehöhenklimate auf die genetisch gesteuerten physiologischen und phänologischen Reaktionen ermöglichen sollen (Ruden 1968, Burdon und Shelbourne 1974).

Neben den in dieser Arbeit behandelten Merkmalen Austrieb, Zuwachsperiode und Höhenzuwachs sind an diesem Material noch zahlreiche weitere Feststellungen in diesem Zusammenhang vorgesehen, deren Klärung jedoch noch einige Jahre in Anspruch nehmen wird.

Pflanzenmaterial, Versuchsgelände und Methodik

Als Versuchspflanzen dienten Stecklinge von Fichten, die im Jahre 1959 im Forstgarten Mariabrunn der FBVA Wien aus Einzelbaumsaatgut verschiedener Seehöhe von den Seetaler Alpen (Steiermark) und dem Höllengebirge (Oberösterreich) herangezogen wurden (siehe Holzer 1972, p 63 ff). Die Stecklinge wurden 1970 und 1971 geschnitten, im Sprühbeet bewurzelt und einzeln in Torftöpfen weiterkultiviert. 1973 kamen sie nach Innsbruck und wurden im

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[1]) Für die Arbeit wurden Teile einer Dissertation von F. Lechner verwendet, die an der Außenstelle für subalpine Waldforschung durchgeführt und bei der Universität Innsbruck eingereicht wurde.