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Genetic variation in Saghalien fir from different areas of Hokkaido

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Introduction

Saghalien fir (*Abies sachalinensis*) is widely distributed throughout Hokkaido, the southern Kuriles and Saghalien. This fir is the most hardy among 5 species of *Abies* native to Japan and one of the most important forest tree in Hokkaido. In suitable habitats, it is also one of the most planted species for timber production. The selection of the best seed sources for planting is of economic interest.

Only a little information, e. g. MARUOKA (1966) and TAMARI (1965), is available so far on the geographic variations of Saghalien fir in Hokkaido. They observed the difference in early growth, the date of bud opening and the frequency of occurrence of secondary shoots between the seedlings from western and eastern parts of Hokkaido. This study was performed to determine the genetic variability of Saghalien fir among different areas in Hokkaido and to supply seed source information applicable to planting in different areas in Hokkaido.

Materials and Methods

In our studies we used Saghalien fir seedlings from natural forest sites of seven areas, including 117 individual mother trees. The number of trees from which seeds were collected and climatic and geographic data pertaining to the sites of their origin are given in Table 1 and the locations of collection areas are shown in Figure 1. Each collection consists of seeds from 18 to 39 average mother trees from an area of several acres.

The seeds collected in September 1964 were sent to our Station. After measuring the length of 10 cones and the weight of 1000 seeds from each mother tree, the percent germination was averaged for three replicates of 100 seeds. The seeds were buried in snow for promoting germination during this winter.

On May 11 and 12, 1965, the seeds were sown in our nursery. As the number of seeds collected from each mother tree was different, the plot size of each mother tree's seed

bed was different varying 100 cm² to 300 cm². Germination began from May 24 to May 30, and ended on June 10.

In the mid June, cotyledon number of seedlings was measured. At the end of the growing season, in mid September, 10 seedlings were dug up at random from the plots of each mother tree and site, taking care not to cut the roots. In the case of three sites, Nemuro, Sapporo and Rishiri, however, 60 seedlings were dug up. The height, root length (length of main root), diameter (at ground surface), dry weight of seedlings with shoots and roots (after drying at 110° C for 5 hours) and needle number (excluding cotyledon) were measured with one year seedlings.

In September, 1966, at the end of the second growing season, the seedlings were first transplanted. We sampled at random the seedlings from each plot and set up test plot by the method of split plot. The randomized block design with 4 replications was used. Each block consisted of seedlings from 117 mother trees from 4 sites and seedlings from mixed seed of mother trees from the other 3 sites. One plot for test of variance among mother trees included 64 seedlings per 1 m² and the plot for test of variance among sites using only mixed seed of mother trees included 786 seedlings in 12 m². After transplanting, the height and number of branches were measured in October, 1966, sampling 20 seedlings per plot. The height and diameter of 3-year seedlings were measured in September, 1967. The height and the frequency of occurrence of secondary shoots were measured in October, 1967 and 1968. We classified the Saghalien fir secondary shoots according to the method studied for Jack pine (RUDOLPH, 1964), namely (1) Lammas growth (developing terminal bud), (2) Prolepsis (developing lateral bud), (3) Lammas growth and Prolepsis. In the case of Saghalien fir, Prolepsis shoots are very frequent, and Lammas growth very few. We considered the mean value of the length of secondary shoots of 10 seedlings taken at random from each plot as a length of secondary shoot of each mother tree.

To clarify the geographical variation of Saghalien fir in Hokkaido, in early March of 1969, one month before the

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Table 1. — Geographic and climatic data of 7 localities.

	Latitude	Longitude	Altitude	Mean annual temperature	Mean winter temperature (Jan. and Feb.)	Mean summer temperature (June, July and Aug.)	Mean snow depth*** (Jan. and Feb.)	Number of mother trees tested
	°N	°E	(m)	°C	°C	°C	(cm)	
1 Hiyama (W)*	41 53	140 12	80	8.5	−3.7	19.7	44	18
2 Shintoku (E)*	43 17	142 55	300	6.9	−6.9	19.2	23	24
3 Kiyosato (E)	43 48	144 35	160	6.5	−8.2	18.3	33	36
4 Hidaka (W)	42 55	142 30	640	6.0	−7.7	15.5	43	39
5 Sapporo (W)	43 01	141 33	50	7.5	−6.3	19.1	51	30**
6 Nemuro (E)	43 15	145 30	40	5.7	−4.8	13.1	10	30**
7 Rishiri (W)	45 13	141 51	170	7.6	−5.0	19.8	67	30**

* W, E: indicate the western or the eastern part of Hokkaido.

** Seeds collected from 30 trees at each locality were mixed.

*** Mean value for 25 years.

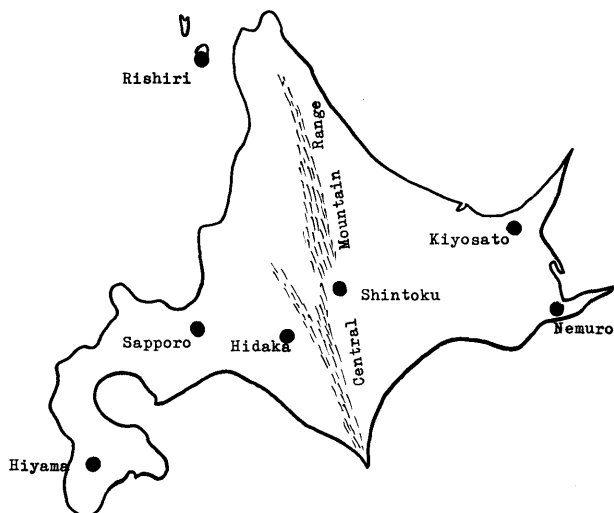


Fig. 1. — Locations of the 7 sites from which Saghalien fir seed used in this study were collected.

unfolding of winter buds, the number of layers of winter bud scales was investigated using 50 branches taken from 4-year seedlings, which were grown from the seeds of 10 mother trees from 7 sites. We used the main branches from the south side of seedlings planted on the south side of seed beds, in order to minimize variations due to the condition of the buds.

The variations in the dates of bud opening and winter bud formation among mother trees and sites were also investigated. The date at when the terminal bud scale had

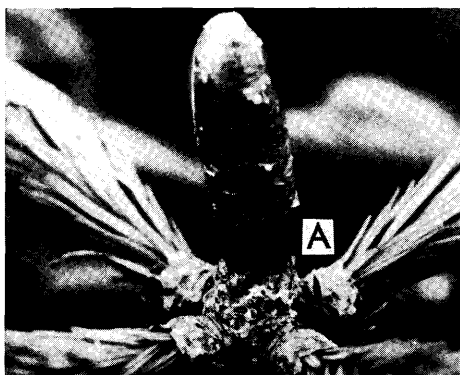


Fig. 2. — The bud opening of Saghalien fir seedlings. — The date at when terminal bud scale had just torn away at the base (A) was regarded as the time of bud opening.

just torn away at the base as shown in Figure 2 was regarded as the time of bud opening. And the date at when winter terminal buds became noticeable with naked eye after cessation of growth of shoots was regarded as the time of terminal bud formation. The dates of the bud opening and winter bud formation were determined with 20 seedlings sampled at random from each plot every day from May 1 to May 31, 1969 and with 10 seedlings every day from July 1 to July 31, 1969 respectively.

Results

The data on traits measured during the 5 years since 1965 are summarized in Table 2.

1. Cone and seeds

The measuring of cone length from Shintoku was not possible because the cones were broken. A great difference was observed in cone-length among mother trees of each site, especially in Hiyama and Hidaka. Of the 3 sites, Hiyama cones were the longest, on an average 6.9 cm, Kiyosato was next with 6.4 cm and Hidaka cones were the shortest 6.1 cm (Table 2). Nearly the same trend was observed in the weight per 1000 seeds (Table 2), seeds from Hiyama were the heaviest, on an average 12.3 g, Shintoku seeds were the lightest 9.3 g. Percentage of the seed germination ranged from 20 to 30 for each site. Thus, in the size of seed as well as the percentage of seed germination, a considerable difference was observed among the mother trees of each site.

2. Cotyledons

The relative frequencies of cotyledon numbers 2 to 7 at different sites are presented in Table 3. Most of Saghalien firs had 4 cotyledons, amounting from 80 to 90% of the seedlings tested. However, a great difference among the sites was observed in the frequency of 3 or 5 cotyledons. In seedlings from Hiyama, Sapporo and Nemuro there were more than twice as many with 3 cotyledons as with 5 cotyledons. In contrast, among the seedlings from Shintoku, Kiyosato and Hidaka there were more than twice as many with 5 cotyledons as with 3 cotyledons. The largest number of cotyledons were observed in the seedlings from Hidaka (mean 4.07) and the smallest in the seedlings from Sapporo (mean 3.87). The mean cotyledon number of seedlings from Hiyama was nearly equal to those from Nemuro, but the variance of Hiyama was almost twice as much as those of Nemuro. In the number of cotyledons, the variances among mother trees as well as progenies of the same mother tree from Hiyama were larger than that of any

Table 2. — Data on traits of seedlings from 7 sites.

Site of seed origin	Cone length (mm)	Seed weight (g)	Seed germination (%)	Cotyledon number	Height (cm)			Diameter (mm)		Total dry weight (g)	Needle number		Branch number			Frequency of occurrence of secondary shoots (%)			Length of secondary shoots (cm)	
					1 year	2 years	3 years	4 years	1 year		3 years	1 year	3 years	1 year	3 years	4 years	3 years	4 years	3 years	4 years
Hiyama (W)	69.2	12.3	29.9	3.92	4.45	12.00	18.03	33.4	1.47	4.26	0.091	19.7	2.4	64.6	39.8	4.1	8.9			
Shintoku (E)	9.3	9.3	25.8	4.05	3.90	9.86	15.66	27.8	1.28	4.27	0.064	13.0	2.3	39.5	14.3	3.9	4.8			
Kiyosato (E)	63.7	10.7	29.2	4.05	3.95	9.32	14.29	23.9	1.24	4.01	0.063	12.7	2.3	43.2	19.2	3.3	3.6			
Hidaka (W)	60.8	10.2	22.1	4.07	3.74	9.42	14.42	25.8	1.27	3.85	0.066	12.3	2.2	41.8	18.5	3.4	5.0			
Sapporo (W)				3.87	4.01	10.17	15.30	27.2	4.01	4.01	0.068	16.4	1.5	51.2	33.5	3.0	7.1			
Nemuro (E)				3.93	3.57	7.51	12.09	19.5	3.70	3.70	0.054	12.5	0.9	21.6	21.1	2.5	7.0			
Rishiri (W)				4.04	4.08	9.56	13.95	23.0	3.72	3.72	0.070	16.1	1.3	39.7	23.8	2.4	6.0			

other of the 4 sites. Using progeny means, analysis of variance was carried out for the number of cotyledons. Hiyama was significantly different at 1 percent level from other 3 sites (Shintoku, Kiyosato and Hidaka). The result of statistical analysis of each site suggests that there is a significant difference among individual mother trees from the same site, especially in Hiyama.

3. Height at 1-year, root length, total dry weight and needle number

The maximum height of 1-year seedlings was from Hiyama (mean 44.5 mm) and the minimum was from Nemuro (mean 35.7 mm) (Table 2). The same trend was observed in the needle number of 1-year seedlings, the difference in needle number between the maximum and the minimum amounting to 7.4 (Table 2). Only a slight difference was observed in the root length of 1-year seedlings. However, a marked difference was observed in total dry weight of 1-year seedlings among 7 sites. The results of statistical analysis using progeny means of mother trees from 4 sites indicated that in height, needle number and total dry weight of 1-year seedlings, Hiyama was significantly different at 1 percent level from other 3 sites. In the case of root length it was impossible to demonstrate a significant difference between the 4 sites.

4. Height at 3-year and the frequency of occurrence of secondary shoots

The site differences in height of 3-year seedlings were compared with those of 1-year seedlings (Table 2). It was found that the difference in height between sites became greater as the age increased. The variance of the height of seedlings from Hiyama was larger than that from any other sites. And the variance among mother trees as well as among progenies of the same mother tree was larger for Hiyama than for any other of the 3 sites (Table 2).

The variance in the frequency of occurrence of secondary shoots among mother trees within the same site was observed to be much greater than that in the height. Its maximum was 64.6% of the seedlings from Hiyama, next was 51.1% from Sapporo and the minimum was 21.6% from Nemuro. The result of analysis of variance of height at 3-year and the frequency of occurrence of secondary shoots for the 4 sites (Hiyama, Shintoku, Kiyosato and Hidaka) from which were collected from individual mother trees indicated that they were significantly different at 1 percent level among the 4 different sites and among mother trees within the same site. In the case of height there was interaction between mother trees and replicates. The F value for the height of seedlings among 4 sites was almost twenty times the F value for the height of seedlings among individual mother trees. The F value for the frequency of occurrence of secondary shoots of seedlings among mother trees was much larger than that among 4 sites. Analysis of variance was also carried out to study the variations among 7 sites, namely 4 sites tested above and 3 sites of Sapporo, Nemuro and Rishiri, from which only mixed seeds were collected. The results showed that they were significantly different at 1 percent level among 7 sites. To know the significance of difference between the eastern and western parts in Hokkaido, the partition of sum of squares was done for height and frequency of occurrence of secondary shoots. The result of analysis showed that there was a statistically significant difference in these silvic characters between trees from the eastern and western parts of Hokkaido separated by the central mountain range, and among the sites in each region.

Table 3. — Relative frequencies of seedlings with different cotyledon numbers and the variance of cotyledon number among Saghalien fir progenies sown in 1965.

Site of seed origin	Number of seedlings measured	Cotyledon number						variance of cotyledon number
		2 (%)	3 (%)	4 (%)	5 (%)	6 (%)	7 (%)	
Hiyama	5315	3 (0.06)	696 (13.10)	4326 (81.38)	289 (5.44)	1 (0.02)		0.203
Shintoku	4841	1 (0.02)	163 (3.37)	4246 (88.04)	413 (8.53)	2 (0.04)		0.121
Kiyosato	6045		249 (4.10)	5268 (87.15)	527 (8.72)		1 (0.02)	0.099
Hidaka	4580		150 (3.27)	3957 (86.40)	470 (10.26)	3 (0.07)		0.119
Sapporo	600		95 (15.08)	489 (81.50)	15 (2.50)	1 (0.17)		0.173
Nemuro	777		78 (10.04)	677 (87.13)	22 (2.83)			0.107
Rishiri	901		56 (6.21)	755 (83.80)	90 (9.99)			0.142

5. Correlation between characters

All phenotypic correlations between the traits of one year seedlings are shown in Table 4. These correlations were calculated using progeny means of individual mother trees from each site (Hiyama, Shintoku, Kiyosato and Hidaka).

Height, diameter and needle number were positively and significantly correlated with total dry weight in each site, and there were weak and positive correlations between seed weight and root length, and total dry weight, although these were not significant in all sites.

The correlations between frequencies of occurrence of

Table 4. — Correlation coefficients between characters of one-year-old seedlings based upon 18 to 39 single tree progenies from 4 localities.

		II	III	IV	V	VI	VII	VIII	IX
I Cone length	A	0.41	—0.02	—0.14	0.08	0.05	0.32	0.34	0.07
	B	—	—	—	—	—	—	—	—
	C	0.43**	—0.04	—0.21	0.27	0.20	0.29	0.28	0.02
	D	—0.15	—0.01	0.05	0.07	—0.05	0.00	0.24	0.25
II Seed weight	A		—0.17	0.20	0.21	0.44	0.06	0.38	—0.32
	B		0.06	0.21	0.34	0.18	0.55**	0.77**	0.23
	C		0.28	0.08	0.19	0.04	0.19	0.33*	0.22
	D		0.46**	0.08	0.27	—0.04	0.27	0.26	0.22
III Seed germination	A			0.27	0.40	0.41	0.08	0.18	0.24
	B			—0.27	0.26	0.19	—0.21	0.09	0.32
	C			—0.22	0.06	0.14	0.13	0.03	0.30
	D			—0.18	0.23	—0.14	—0.12	—0.30	—0.15
IV Cotyledon number	A				0.52*	0.51*	0.30	0.39	0.20
	B				—0.01	0.06	0.16	0.19	0.17
	C				0.29	0.30	—0.17	0.11	0.30
	D				—0.22	—0.04	0.26	0.26	0.19
V Height	A					0.64**	0.46*	0.78**	0.56**
	B					0.21	0.19	0.53**	0.76**
	C					0.36**	0.11	0.50**	0.42**
	D					0.08	0.30	0.55**	0.17
VI Root length	A						0.34	0.41	—0.08
	B						0.08	0.52**	0.28
	C						0.33	0.40	0.11
	D						0.03	0.29	—0.10
VII Diameter	A							0.65**	0.35
	B							0.47**	0.42*
	C							0.40**	0.32
	D							0.60**	0.44**
VIII Dry weight	A								0.61**
	B								0.53**
	C								0.60**
	D								0.48**
IX Needle number	A								
	B								
	C								
	D								

A: Hiyama; B: Shintoku; C: Kiyosato; D: Hidaka.

* Significant at 5% level. ** Significant at 1% level.

secondary shoot in 3- and 4-year seedlings were calculated and they were positively and significantly correlated in most sites. (Hiyama $r = 0.56^{**}$, Shintoku $r = 0.24$, Kiyosato $r = 0.65^{**}$ and Hidaka $r = 0.57^{**}$).

The multiple correlations between height at 1, 2, 3-year and 4-year were calculated. For all sites they were very strong (Hiyama $r = 0.9990$, Shintoku $r = 0.9994$, Kiyosato $r = 0.9990$ and Hidaka $r = 0.9990$) as expected.

6. Number of layers of the winter bud scales

As shown in Table 5 and Figures 3 and 4, the mean number of layers of winter bud scales of seedlings from Hiyama was the lowest (5.9), and that from Shintoku was the highest (8.1). The Saghalien firs from Hiyama, Sapporo and Hidaka located in the western parts in Hokkaido had a far lesser winter bud scales than those of Shintoku, Kiyosato and Nemuro in the eastern parts of Hokkaido. Analysis of variance of number of layers of bud scales among the 4 sites (Hiyama, Shintoku, Kiyosato and Hidaka) proved to be a significant difference at 1 percent level among different sites and among mother trees within the same site. The result of analysis of variance which was done in order

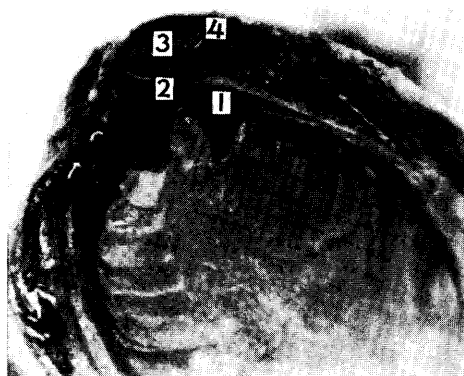


Fig. 3. — Winter bud scales of a seedling from Hiyama (4 layers).

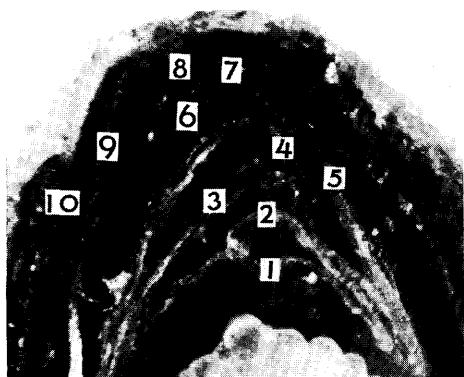


Fig. 4. — Winter bud scales of a seedling from Nemuro (10 layers).

Table 5. — Number of layers of winter bud scales of seedlings from 7 localities.

Site of seed origin	Average number of layers of winter bud scales
Hiyama	5.9 ± 1.2
Shintoku	8.1 ± 1.6
Kiyosato	7.2 ± 1.1
Hidaka	6.2 ± 1.1
Sapporo	6.2 ± 0.9
Nemuro	7.5 ± 1.4
Rishiri	7.3 ± 0.9

to study the variation among 7 sites showed that the differences between sites were highly significant.

7. Length of growing season

Marked variations in date of bud opening and winter terminal bud formation among 7 sites and mother trees within same sites were observed. The dates of bud opening were earlier in seedlings from western localities except Hiyama, and later in those from eastern localities. Dates of bud opening were the latest in seedlings from Nemuro located in the far eastern part of Hokkaido and were the earliest in those from Rishiri in the far northern part in Hokkaido. The terminal bud formation in the seedlings from the western localities except Hiyama was earlier than in those from the eastern localities. Thus, the length of growing season, from bud opening to winter bud formation was nearly the same among all sites studied.

Discussion

A large difference in cone length, seed germination and seed weight was observed among the sites and among mother trees. These traits may be under hereditary control, though they seem to be influenced by the age and nutritional and physiological conditions of mother trees and climatic conditions of the year of seed collection. The multiple correlations between height at 1, 2, 3-year and at 4-year were very strong, and the height-rank of the progeny from mother trees remained nearly constant from first to fourth in each site. These results also suggest that the early growth depends on heredity, though it should be more or less influenced by environmental conditions.

The result obtained in 1, 2, 3- and 4-year seedlings showed that the growth of seedlings from the western parts of Hokkaido was faster than those from eastern parts. The seedlings from Hiyama near the southern limit of its natural range grew best and those from Nemuro located in the far eastern part of Hokkaido grew slowest. It was also observed that in 3- and 4-year seedlings, the frequency of occurrence of the secondary shoots from the western localities was much higher than that from eastern localities.

WRIGHT and BULL (1963) reported that seedlings of Scotch pine grew faster in central European varieties and grew slower in northern Europe and Siberia, and that the trees from cooler climates and from drier climates grew more slowly. Genys (1968) reported that height, diameter, secondary growth and needle length of the Eastern White pine changed gradually more or less from north to south, and that climate was apparently one of the main factors that acted strongly in the natural selection and formation of different geographic strains. It is interesting that the same trend in geographic variations of many traits was observed in Saghalien fir growing in Hokkaido (total area: 80,000 km²), northernmost island of the Japan archipelago.

T. D. RUDOLPH (1964) reported in Jack pine that the abnormal shoot type is under genetic control, though their occurrence is modified by environmental factors. A positive significant correlation was observed by us also in the frequency of occurrence of secondary shoots between 3- and 4-year seedlings in most sites.

A remarkable difference in climate is observed between the eastern and western Hokkaido, which are divided into two parts by central mountain range as high as 2000 m above sea level. Cool summers, cold winters and few snow drifts are characteristic in eastern Hokkaido. Especially in the pacific coast areas, cool and foggy days prevail in sum-

Table 6. — Dates of bud opening in Saghalien fir seedlings from 7 localities.

Site of seed origin	Percentage of seedlings with opened bud			
	May 16	May 19	May 21 (%)	May 23
Hiyama	2.4	26.0	75.7	89.2
Shintoku	3.4	31.7	76.7	95.0
Kiyosato	3.4	37.5	76.7	87.7
Hidaka	14.3	61.2	90.9	96.9
Sapporo	11.5	58.3	92.5	97.5
Nemuro	1.9	8.3	31.0	71.3
Rishiri	15.0	75.8	95.8	100.0

Table 7. — Dates of terminal bud formation in Saghalien fir seedlings from 7 localities.

Site of seed origin	Percentage of seedlings with winter buds						
	July 7	July 9	July 11	July 14	July 16	July 18	July 21
Hiyama	1.9	5.8	11.1	22.2	32.5	55.6	78.6
Shintoku	6.5	8.5	13.1	27.9	42.1	66.3	85.6
Kiyosato	6.5	10.8	18.5	33.8	49.6	71.4	86.0
Hidaka	16.6	21.4	32.8	51.0	64.6	83.5	95.4
Sapporo	16.7	20.4	30.0	45.4	55.8	76.3	94.5
Nemuro	2.9	5.8	10.0	19.2	28.8	47.1	71.7
Rishiri	21.3	28.8	38.3	60.8	68.3	86.3	98.3

mer. Heavy snow drifts are most characteristic in western Hokkaido. The differences of mean annual and mean summer temperatures amount to 2.8 and 6.6° C respectively, between Hiyama and Nemuro. It is very interesting that Saghalien firs from eastern localities have more layers of winter bud scales than those of western localities. A question arises as to what kind of natural selection causes the variance in the scale layers of winter bud among sites. Recently we noticed that Saghalien firs from Kuriles island (Kunashiri) had many more layers of winter bud scales than those from Nemuro. It appears that more layers of winter bud scales can be observed in Saghalien fir from colder climates. It may therefore be postulated that the bud scales play a role to protect the buds from winter cold injury and winter desiccation. To clarify further the relation between number of bud scale and climate, an extensive study is required on the number of layers of bud scales of Saghalien fir from different climates, especially from Saghalien.

Summary

The available data may lead to the following conclusions.

1. In most of the traits bearing quantitative characters there was a significant difference among 7 localities in Hokkaido. Highly significant differences among mother trees within the same site were also observed. The degree of genetic variance was noticeable in the seedlings from Hiyama.

2. The multiple correlation in growth height between 1-, 2-, 3- and 4-year seedlings was very strong in each

locality. There was also a positive and significant correlation among the progeny of individual mother trees in the frequency of occurrence of secondary shoots 3- and 4-year seedlings. Thus, these traits may be under the control of the characteristics of mother trees.

3. Saghalien firs from the western part of Hokkaido have a less number of layers of winter bud scales than those from the eastern part.

4. The dates of bud opening were earlier in seedlings from the western localities except Hiyama and later in those from the eastern localities. The date of terminal bud formation followed the same tendency. Thus, the length of growing season was nearly the same in the seedlings of all sites

studied. In the dates of bud opening and terminal bud formation, the seedlings from Hiyama behaved like seedlings of the eastern part, although Hiyama is actually a western locality.

5. Significant difference was observed in cotyledon number, height, total dry weight, needle number, diameter of one year seedlings and in frequency of occurrence of secondary shoots in 3- and 4-year seedlings between the western and eastern parts of the central mountain range, and among the sites in each region. Height of Saghalien fir seedlings from the western parts in Hokkaido was much greater than those from the eastern parts. The remarkable difference observed in many traits between Saghalien firs from the 2 regions may be to the difference in climate between them and this may be one of the main factors acting the natural selection.

Key words: Saghalien fir, genetic variation, natural selection, Hokkaido.

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