



Title	Growth Rate of Spruces Related to the Thickness of Permafrost Active Layer near Inuvik, Northwestern Canada
Author(s)	SAKAI, Akira; YOSHIDA, Shizuo; SAITO, Mitsuru; Zoltai, S.C.
Citation	Low temperature science. Ser. B, Biological sciences, 37, 19-32
Issue Date	1980-03-15
Doc URL	http://hdl.handle.net/2115/17844
Type	bulletin (article)
File Information	37_p19-32.pdf



[Instructions for use](#)

Growth Rate of Spruces Related to the Thickness of Permafrost Active Layer near Inuvik, Northwestern Canada¹

Akira SAKAI², Shizuo YOSHIDA², Mitsuru SAITO³
and S. C. ZOLTAI⁴

酒井 昭・吉田 静夫
斎藤 満・エス・スイ・ゾルタイ

Abstract Growth rate of white spruce (*Picea glauca*) and black spruce (*Picea mariana*) occurring at different topographical sites near Inuvik was studied with special reference to the thickness of active layer (the annual layer of thaw). An important effect of permafrost in interior Alaska and Northwestern Canada is that of holding water near the ground surface, although the annual precipitation in this region is below 250 mm. Thus, topography such as aspect and slope is of special importance in the distribution of vegetation and soils. The best sites for tree growth are on south-facing slopes and river alluvium where the soils are well-drained and have a thick active layer. The growth rate of white spruce at different topographic sites was related to the thickness of active layer. In many white spruce height growth reached a maximum at the age of 20 to 40 years, and then abruptly decreased, remaining at low levels. However, in black spruce such conspicuous change was not observed in the growth rate which remained at low levels for about 100 years and then increased gradually.

Introduction

The northern region of the boreal forest zone of interior Alaska and northwestern Canada comprises woodlands of primarily open, slow-growing black spruce with occasional dense, well-developed forest stands and treeless bogs. This type of regional vegetation is referred to "taiga", and is differentiated from the closed-canopied, fast-growing forests of the more southerly region of the zone. The distribution of various features such as forests, bogs, and shrubs is closely related to the aspect of slope, presence or absence of permafrost, thickness of active layer, drainage, and to the past history

¹ Received for publication October 25, 1979. Contribution No. 2192 from the Inst. Low Temp. Sci. This study was supported by Grant-in Aid for Overseas Scientific Survey from the Ministry of Education, Joint Studies on Physical and Biological Environments in the Permafrost, Alaska and Canada, June to July, 1974.

² The Institute of Low Temperature Science, Hokkaido University, Sapporo, 060

³ Hokkaido Forest Experiment Station, Bibai, Hokkaido, 079-01

⁴ Environment Canada, Canadian Forestry Service, Northern Forest Research Center, Edmonton, Alberta, Canada

of flooding or forest fires. Fires apparently have been prevalent throughout the history of development of the taiga (13).

There are two general types of tree succession in Alaska (10~13). They relate in large degree to drainage. On well-drained sites such as south-facing slopes and river banks, the usual forest vegetation consists of white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), or some combination of these species. In the successional sequence the initially dominant hardwoods are replaced by spruces. As the fall of balsam or aspen leaves diminishes and the litter of spruce accumulates, a continuous and thick moss mat develops under the stand. The insulating effects of this moss mat cause delayed thawing and cooler soil temperatures, eventually resulting in the development of permafrost. Permafrost prevents internal drainage and creates a wetter soil on which Sphagnum mosses may develop, favouring the growth of black spruce over white spruce. As succession continues, the permafrost layer rises closer to the surface. Finally, black spruce and Sphagnum mosses attain a climax stand, finding optimum conditions for their growth (10~12).

In Inuvik, Mackenzie Delta, located near the northern tree limit in arctic zone of Canada, the climate is more severe than in inland Alaska. However, tree vegetation near Inuvik is nearly the same as in Alaska (14). The thickness of active layer seems to be a decisive factor in determining vegetation and growth rate of trees occurring on the permafrost table (14). In the present study, the growth rate of spruce was studied at different sites near Inuvik with special reference to the thickness of active layer to contribute to our understanding of forest ecology on permafrost.

Description of vegetation

Well-developed white spruce (*Picea glauca*) stands occur along the river in the Mackenzie Delta (Fig. 1). White spruce stands are mostly associated with



Fig. 1. General view of Mackenzie Delta from the Caribou Hills

H: A hill near Reindeer Depot (Locality 14 on Fig. 7). White spruce (W) occurs along the river.

willow (*Salix alaxensis*) bush (2 m height) adjacent to river (Fig. 2). Willows are pioneering shrubs on freshly deposited alluvium on river flood plains (1). On southfacing slopes, the forests consist of white spruce or white birch (*Betula papyrifera*) stands (Fig. 3). On the other hand, on poorly drained sites, including north-facing slopes, flats and plateaus, where thick Sphagnum mat develops, the predominant forest species is black

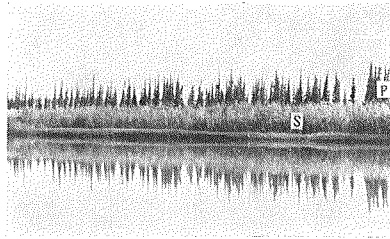


Fig. 2. White spruce stands associated with willow bushes along the river
 S: *Salix alaxensis*; P: *Picea glauca*
 Locality 13 on Fig. 7

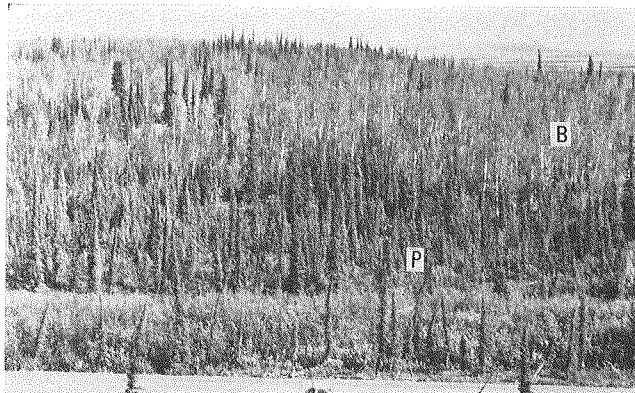


Fig. 3. Mixed forests consisting of white spruce and paper birch on the south-facing slope
 P: White spruce; B: Paper birch. Locality 7 on Fig. 7

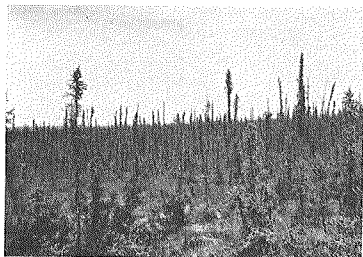


Fig. 4. Black spruce-Sphagnum vegetation
 Locality 11 on Fig. 7

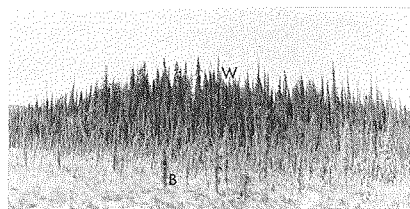


Fig. 5. White spruce on a loamy hill in black spruce-Sphagnum bog
 W: White spruce; B: Black spruce.
 Locality 10 on Fig. 7

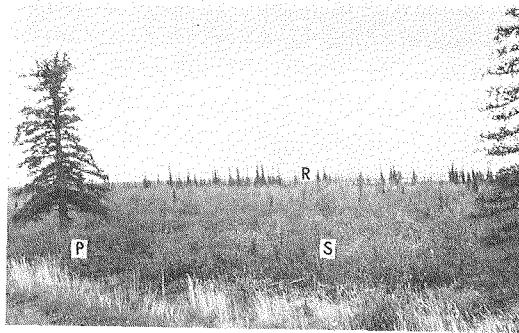


Fig. 6. General view of vegetation about 40 years after a fire near Inuvik

P: White spruce undisturbed by the fire (age: 140 years; height: 10 m, DBH: 23 cm). S: Mature willow bush. In the bush many fire-originated white spruces of about 35 years occur. R: White spruce growing near river bank. Locality 6 on Fig. 7

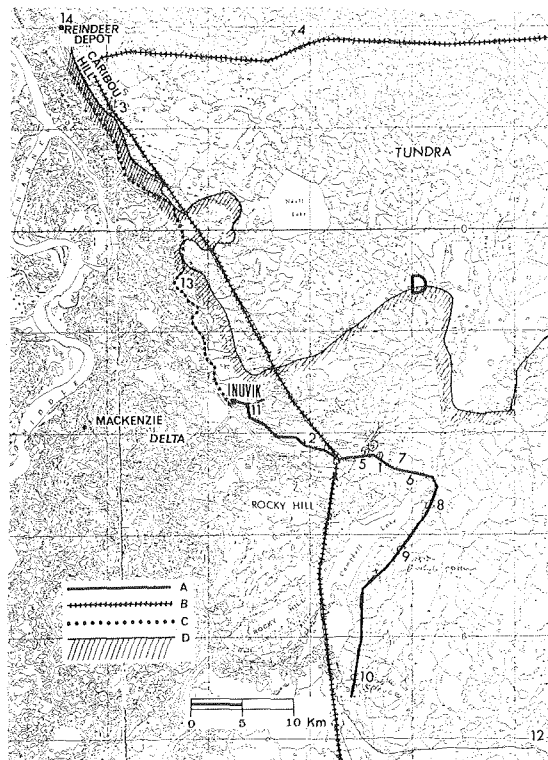


Fig. 7. Distribution of sample plots in the study area near Inuvik

Survey was made by car (A route), helicopter (B route) and motor boat (C route). Arctic tree line is shown by hatched line (D)

Table 1. Meteorological data of Inuvik

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
Mean temperature (°C)	-29.3	-29.4	-23.9	-14.6	- 0.8	9.8	14.5
Mean maximum temperature (°C)	-24.1	-23.9	-17.7	- 7.9	3.9	16.0	19.2
Mean minimum temperature (°C)	-34.5	-35.0	-30.0	-21.2	- 5.6	3.7	7.4
Number of day sub-zero temperature	31	28	31	30	26	7	1
Mean precipitation (mm)	20.4	10.4	16.5	13.9	17.5	12.9	34.3
	Aug.	Sep.	Oct.	Nov.	Dec.	Ann.	
Mean temperature (°C)	10.3	2.7	- 7.2	-20.6	-27.7	- 9.7	
Mean maximum temperature (°C)	15.5	6.8	- 3.8	-16.5	-22.0	- 4.5	
Mean minimum temperature (°C)	5.0	1.7	-10.7	-24.7	-32.0	-14.9	
Number of day sub-zero temperature	3	21	30	30	31	269	
Mean precipitation (mm)	46.2	21.1	33.8	14.7	18.5	260	

1941-1970, Warmth index: 18.4

spruce (*Picea mariana*) (Fig. 4). In the wettest sites larch (*Larix laricina*) is associated with black spruce. On small loamy hills, often surrounded by black spruce-Sphagnum bogs, well developed white spruce stands were observed on well-drained sites (Fig. 5). Fig. 6 shows a general view of vegetation about 40 years after a fire. A few large white spruce survived the fire. These were about 140 years old, 10 m in height and 23 cm at DBH. Many small white spruce of about 35 years age were observed among the mature willow bushes. The willows and young white spruce probably originated after the fire.

Field work and methods

Field work was performed near Inuvik by helicopter, car, and motor boat in early and mid-July, 1974. Distribution of sample plots in the study area is shown in Fig. 7. A sample area at each location was delimited, and then DBH and tree heights were measured. One to three trees were selected and felled. After recording of DBH and height, the fresh weights of stem bole and branches taken at one meter intervals along the stem bole were determined separately. Stratified clip discs of each sample were taken to be used for stem analysis. The thickness of active layer was determined by digging, and soil temperature readings were taken at various intervals. Meteorological data is presented in Table 1.

Results

The thickness of active layer and the soil temperature varied with topography, aspect, and drainage when surveyed in mid-July near Inuvik (Fig. 8). To demonstrate the effect of aspect, the growth rate and soil conditions of stands on south- and north-facing slopes on opposite sides of a road were compared. On the south-facing slope with about 10° gradient descending to a lake, well-developed mixed forest of white spruce and paper birch was established after a fire 60 to 70 years ago. On the south-facing slope the forest floor was covered by mosses and lichens. In contrast, on the north-facing slope, with about 5° gradient which gradually becomes flat, there were open black spruce stands, 2 to 3 m height. The ground surface was covered by up to 15 cm thick Sphagnum, and by dwarf shrubs, mainly *Vaccinium vitis-idaea*, *V. uliginosum* and *Ledum palustre*. As shown in Table 2, the soil on the well-drained south-facing slope has thawed to a depth of 50 cm

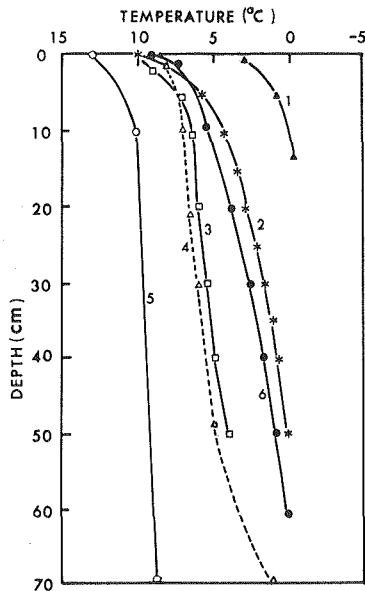


Fig. 8. Thickness of active layer and soil temperature in different vegetations near Inuvik

1. Black spruce stand on a plateau. July 15th (air temperature 19.5°C); Locality 11 on Fig. 7
2. Mixed forest consisting of white spruce and white birch. July 13th (air temperature 22°C); Locality 1 on Fig. 7
3. White spruce stand along a stream. July 7th (air temperature 12°C); Locality 8 on Fig. 7
4. Sparse stand of white spruce on the south-facing slope. July 15th (air temperature 18.2°C); Locality 11 on Fig. 7
5. Treeless area after fire on south-facing slope (30° gradient). July 8th (air temperature 15°C); Location: Midway, between Locality 2 and 11 on Fig. 7
6. Dahurian larch forest 350 km northeast of Yakutsk. August 12th, 1972 (air temperature 120°C), (8)

Table 2. Comparison of tree growth and soil conditions on south- and north-facing slopes (July 13, air temperature 22°C)

Slope	Tree species	Tree age (year)	Tree height* (m)	DBH* (cm)	Active layer (cm)	Soil temperature (°C)	Acidity of soil pH
South-facing slope	<i>Picea glauca</i> <i>Betula papyrifera</i>	60 to 80	9	12.3	50	4.5 (10 cm)	6.2 (10 cm)
North-facing slope	<i>Picea mariana</i>	150	3	3.7	5	0.6 (5 cm)	5.1 (5 cm)

* Mean value for 20 trees

The south-facing slope (10°), the north-facing slope (5°). Locality 1 in Fig. 7

on July 13, while on the north-facing slope the soil remained frozen under the well-developed organic layer, except for a few centimeters at the ground surface. Sharp contrasts in tree growth, vegetation, and soils appear to be related to the thickness of active layer and drainage. Stem analyses of representative trees for the south- and north-facing slopes are shown in Fig. 9. The total growth and 10-year periodic mean annual height increment are compared in Fig. 10.

Well-developed white spruce stands were observed along a stream flowing through an open bog with scattered stunted black spruces (Fig. 11). White spruce stands showed better growth within about 10 m of the stream and the biggest tree was 33 cm in DBH. A cut stump of 43 cm in diameter at stem base was also observed there. Tree height ranged from 10 to 14 m, and the mean DBH for 20 trees was 17.1 cm. The height of white spruce decreased with increasing distance from the stream bank (Fig. 11). The thickness of active layer was about 1 m at a distance of about 10 m from the stream, and the soil temperature 10 cm below the ground was 7.7°C on July 7th, 1974. The thickness of the active layer decreased with increasing distance from the stream. Some 30 m from the stream the active layer was only 5 cm thick under a ground cover of Sphagnum and thin peat in silty soil. The stand is transitional between a Sphagnum bog with open black spruce and well developed white spruce stands. Some representative

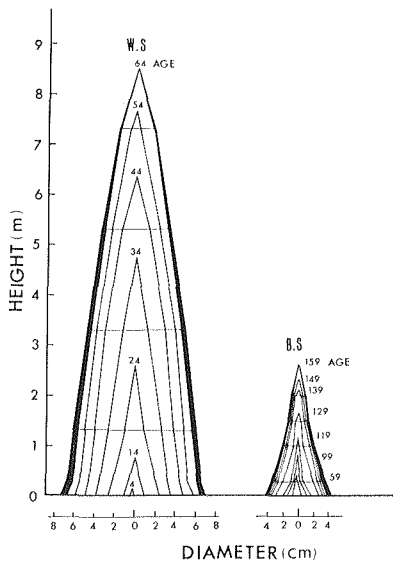


Fig. 9. Stem analyses of white and black spruce on south- and north-facing slopes near Inuvik

Locality 1 on Fig. 7. Refer to Table 2. W.S: White spruce; B.S: Black spruce

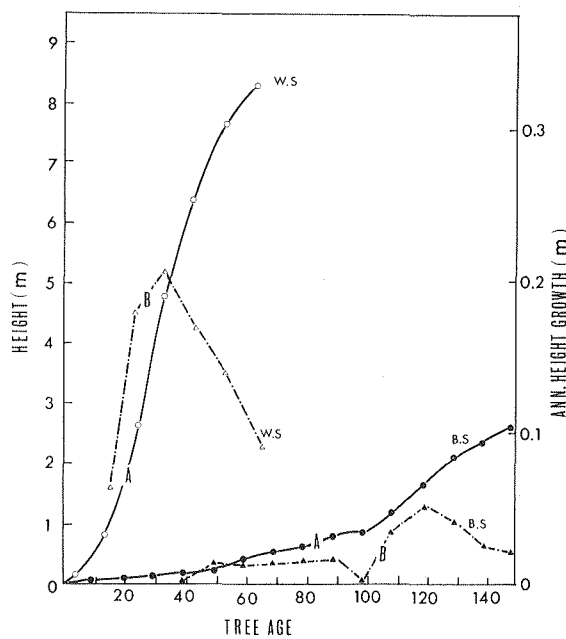


Fig. 10. Growth rate of white and black spruce on south- and north-facing slopes

The same trees shown in Fig. 9. A: Total growth; B: 10-year periodic mean annual height increment

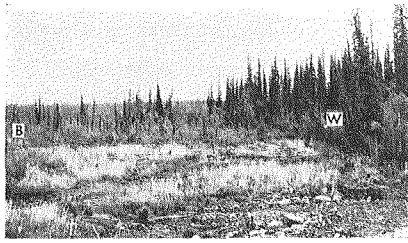


Fig. 11. Well developed white spruce stand along a stream flowing through an open bog with scattered stunted black spruce

W: White spruce; B: Black spruce. Locality 8 on Fig. 7. Stream is 5 m wide, water temperature 5.8°C on July 7th.



Fig. 12. A few clumps of white spruce in sheltered locations in treeless tundra

Locality 4 on Fig. 7. South-facing slope. Tree height: 4 to 6 m; Age: over 150 years

trees in two plots were felled and tree analyses were performed. The growth rate of white spruce and soil conditions at these plots are shown in Table 3.

North of Inuvik the tree line reaches where small stands of white spruce become increasingly separated by treeless tundra until only a few patches of spruce remain in sheltered locations. This transitional zone is 40 to 100 km wide, depending upon the topographic conditions, followed by the completely treeless tundra to the north. A patch of white spruce was examined on a south-facing slope in treeless tundra (Fig. 12), about 40 km north of Inuvik, at the climatic limit of white spruce in North America. The tree heights ranged 4 to 6 m and most of the spruce were over 150 years old. One of the surveyed trees was 236 years old, 6.1 m in height and about 10 cm at DBH. The soil was thawed to a depth of 25 cm on July 5th. The growth rate and stem analysis are shown in Figs. 13 and 14. The 10-year periodic mean annual increment in tree height reached a maximum at 25 years and remained at the same level for 10 years, and then decreased abruptly at 50 years. The growth rate in tree height is

Table 3. Comparison of growth rate of white spruce and soil conditions at two plots 8 and 30 m from a stream, respectively

Tree number	Tree age (year)	Forest floor	Active layer (cm)	Soil temperature (°C)	Tree height (m)	DBH (cm)
No. 19 (8 m from the stream)	143	litter (1-2 cm)	100	6.9 (10 cm)	9.8 (9.0)*	13.4 (9)*
No. 21 (30 m from the stream)	88	Sphagnum (Soil: silt)	5	1.0 (5 cm)	4.5	5.5

Locality 8 on Fig. 7

* Tree height and DBH of tree No. 9 at 88 years (in brackets) were calculated from data obtained by tree analysis.

greatly suppressed because of climatic stresses on trees growing on permafrost (Fig. 13). Thus, the shape of these trees resembles an isosceles triangle.

The growth rates of white and black spruces were compared at plot No. 5 (Fig. 7), situated on a south-facing slope with 10° gradient (tree density: 3,400/ha). This mature, nearly even-aged mixed coniferous forest consisted of white spruce (70%) and black spruce (30%). The forest floor was covered with a thick mat of Sphagnum mosses and many black spruce seedlings occurred. These data indicate that soil conditions have become favourable for the growth of black spruce over white spruce. The DBH of white spruce in this forest varied greatly, ranging from 6.7 to 20 cm, though their age was nearly the same. The average DBH of white spruce was 10.9 cm. In general, white spruce was much taller than black spruce of the same age. Two pairs of white and black spruces, growing side-by-side, were cut and the growth rate of one pair was compared (Table 4).

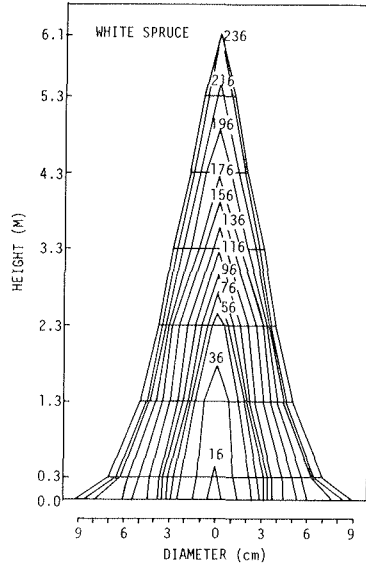


Fig. 13. Stem analysis of white spruce from a small clump in treeless tundra
Location: as Fig. 12

As shown in Fig. 15, the height growth rate of white spruce reached a maximal value at 30 years and then abruptly decreased to 50 years. Thereafter, the growth rate remained nearly the same. On the other hand, in black spruce such a great change in growth rate was not observed. High

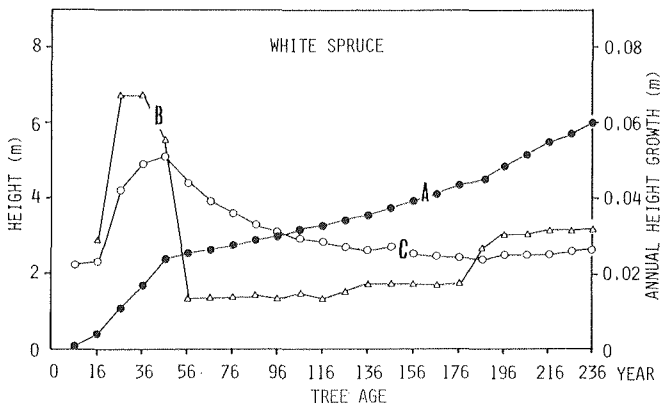


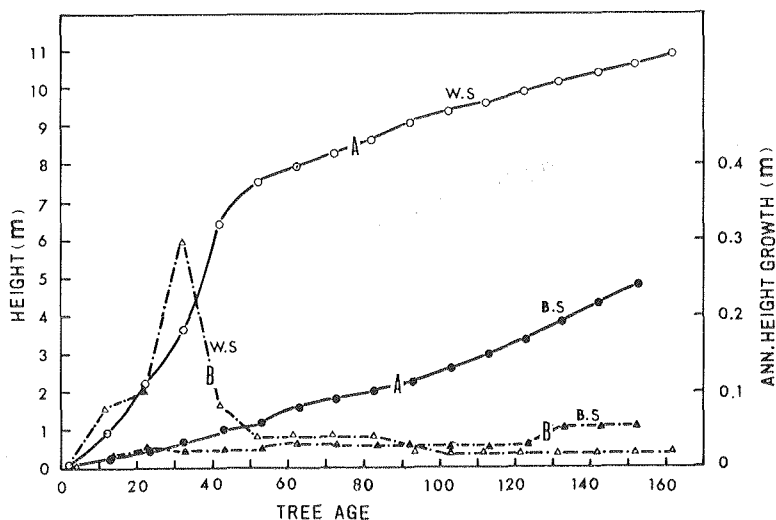
Fig. 14. Growth rate of white spruce from a small clump in treeless tundra

The same tree as Fig. 12. A: Total high growth, B: 10-year periodic annual increment of tree height, C: Annual increment

Table 4. Comparison of growth rate of white and black spruce growing side-by-side on the same plot

Tree species and number	Tree age (year)	Tree height (m)	DBH (cm)	Stem volume (m ³)	Growth in the last 10 years		
					Tree height (m)	DBH (cm)	Stem volume (%)
No. 16 (<i>Picea glauca</i>)	161	11.0	9.3	0.035	0.25	0.06	0.39
No. 17 (<i>Picea mariana</i>)	153	4.9	4.4	0.006	0.55	0.42	2.04

Locality 5 on Fig. 7

**Fig. 15.** Comparison of high growth rate of white and black spruces growing side-by-side on the same stands

Locality: 5 of Fig. 7. A: Total growth; B: 10-year periodic mean annual height increment; W. S: White spruce (No. 16); B.S: Black spruce (No. 17)

growth rate of the stem volume in the white spruce was also observed between the ages of 40 to 90 years, followed by a gradual decrease in stem volume. However, in black spruce, the growth rate remained at low levels for 120 years and then gradually increased. As shown in Table 4, in the last 10 years the growth rates of tree height, DBH and stem volume of black spruce greatly surpassed those of white spruce.

A conspicuous difference in the pattern of growth rate became evident between white and black spruces. The slow but steady growth appears to be characteristic for black spruce, unlike white spruce which has a fast growth rate at younger ages. Growth rates of white spruce growing at different locations near Inuvik were summarized in Table 5. Growth rate of white spruce in a clump in the treeless tundra was the lowest among the white spruce sampled near Inuvik. The stem volume at 64 years was only one-25th of that of white spruce growing in more favourable location

Table 5. Growth rate of white spruce growing at different locations near Inuvik

Locality of plot and tree number	Conditions of location and vegetation	Active layer (cm)	Tree age (year)	Tree height (m)	DBH (cm)	Growth* at 64 years		
						Tree height (m)	DBH (cm)	Volume (m ³)
No. 2 (1 on Fig. 7)	South-facing slope (10°), White spruce and Paper birch	50 (July 7)	64	8.5	12.3	8.5	12.3	0.05
No. 19 (8 on Fig. 7)	Nearness of stream, White spruce	100 (July 7)	143	9.8	13.4	6.2	7.0	0.02
No. 24 (9 on Fig. 7)	Muskeg	10 (July 7)	62	4.6	6.2	4.6	6.2	0.01
No. 21 (11 on Fig. 7)	Bog	5 (July 7)	88	4.5	5.3	2.7	4.0	0.002
No. 12 (4 on Fig. 7)	Patch in tundra	25 (July 5)	236	6.1	10.0	2.6	3.4	0.002
Rose Creek Forest Reserve (Alaska)**	South-facing slope (25°)	No permafrost	120	25	31.2	—	—	—

* Calculated from the data obtained by tree analysis

** 20 km south-west from Fairbanks (unpublished data by Sakai and Yoshida)

farther south (Location No. 2). The low values for growth rate which probably represents near-minimum values for conifers, are clearly related to the severe climate in treeless tundra during growing season. The low growth rate of white spruce occurring on north-facing slopes, bogs and muskegs may be related to the effects of topography (reduced incoming radiation, or poor drainage) that favours the development of an insulating organic mat. The result is cool soil temperatures, making the bio-climate similar to that of the forest patches in the tundra. The thickness of active layer is a reliable indicator of conditions that influence the distribution and growth of trees.

Discussion

In the Mackenzie Delta at Inuvik, Heginbottom (2) reports that by the second summer after a fire in a black spruce forest, thaw was 9 cm deeper in burned than in unburned stands and 35 cm greater on the fire lines where the organic layer had been completely removed. For the same fire and area, Mackay (7) reports a 42% increase in active layer thickness 2 years after the burn. Heilman (4, 5) shows that much of the soil nitrogen, potassium and calcium is tied up in lower organic layer, which in permafrost soils remain frozen the year around and is thus unavailable to plants. As the succession proceeds from birch-alder stands to Sphagnum-black spruce stands, Heilman (4, 5) finds that the foliar level of nitrogen decreases with age of successional stand and potassium and phosphorus actually are deficient as

the nutrients become unavailable in the frozen or cold organic layer. He concludes that the removal of low-density and low-nitrogen-content layers by fire and the subsequent deeper thawing of the underlying soil result in a concentration of available nutrients in the warmest portion of the soil profiles. The greater productivity of spruces on the south-facing slopes having deep active layers may be explained by a combination of factors such as good drainage, high soil temperature, availability of nutrient, well developed soil, etc.

Black spruce is a widely ranging species in North America, growing on both organic and mineral soils. In the south, it is confined largely to peat bogs, wet clay loams and clays on long gentle slopes or lowlands. As a rule, the best swamp and bog stands are near the edges of the peatland, particularly along upper slope margins of a sloping peat surface. In northern Minnesota, the best black spruce forests occur on dark brown, moderately well decomposed peats, although upper 15 cm may be relatively raw Sphagnum peat (9). Black spruce seedlings germinate and become established readily on Sphagnum moss, perhaps because it is almost constantly moist. Feathermosses generally provide a poorer seedbed than Sphagnum. In northern Minnesota, establishment of black spruce is generally successful on Sphagnum, burned peat, and on the compacted peat and moss of skid road (3). The feathermosses dry up and die when spruce forests are clear-cut and are generally poor for the establishment of seedlings (3). Root development is characteristically shallow in black spruce. Although taproots are absent, sinker roots, 25 or 30 cm long, may develop on older trees. In bogs with rapidly growing moss, adventitious roots often develop on the stem of black spruce seedlings. As many as 4 or 5 layers of roots may form in this manner, through a depth of 50 cm (6). On the older trees the roots below a depth of 35 cm are usually dead (9). In black spruce, vegetative reproduction by layering is common, particularly in swamps and bogs, and is the major source of reproduction in open Sphagnum-Chamaedaphne muskegs (9). Tremendous quantities of spruce seeds drop to the ground during the first and second summer after a fire, because the semi-serotinous cones of black spruce are opened by the heat of the fire. Various characteristics indicated above strongly suggest that black spruce is well adapted species to poorly-drained soils on permafrost.

In West Siberia, evergreen conifers are predominant as in Alaska and Canadian taiga, but in East Siberia, Dahurian larch (*Larix dahurica*) is the predominant tree species over wide regions. Siberian spruce (*Picea obovata*) was observed only along river courses (8).

In dense larch forests underlain by huge ice wedges, about 350 km northeast of Yakutsk, the active layer thickness was 60 cm in the forest on August 12th, 1972, and the soil temperature and water content at 30 cm depth were 2.5°C and 12.5% (D. W), respectively (8). The bark volume

percent of stem discs of Dahurian larch trees amounted to as high as 27 to 36%, though the bark volume percentage of black and white spruces and larch (*Larix laricina*) in Inuvik were only 5 to 7%. The high proportion of bark clearly demonstrates an adaptation of Dahurian larch trees to arid climates. The acidity of the soil in Dahurian larch forest, about 350 km north east of Yakutsk, ranged 8 to 9 at 30 to 60 cm depth, which also suggests arid climate.

In the taiga of North America, an important function of permafrost is that of holding ground water near the surface. The permafrost forms an impervious layer, preventing internal water drainage. Thus, the presence of extensive wet areas in a region with low precipitation is largely the result of the underlying permafrost. Variations in the thickness of the active layer, caused by better surface drainage on steeper slopes, more permeable materials, or the nearness of a stream, or by warmer soil temperatures on south-facing slopes create soils with improved internal drainage (14). On such sites white spruce is established, growing at a much faster rate than white or black spruce on waterlogged soil with thin active layer.

Acknowledgments

We wish to express our gratitude to Dr. Y. Hiratsuka, Canadian Forestry Service, Environment Canada, Northern Forest Research Center, Edmonton, Alberta, for his cooperation in the field work.

Literature Cited

- 1) Gill, D. 1973 Floristics of a plant succession sequence in the Mackenzie Delta, Northwest Territories. *Polarforschung*, 43: 55-65.
- 2) Heginbottom, J. A. 1973 Some aspects of surface disturbance on the permafrost active layer at Inuvik, N. W. T. Environ. -Soc. Program, North. Pipelines, Task Force North. Oil Develop., Gov. Canada, Rep. 73-16, 29 pp.
- 3) Heinselman, M. L. 1959 Natural regeneration of swamp black spruce in Minnesota under various cutting systems. U. S. Dept. Agr. Prod. Res. Rep. 32, 22 pp.
- 4) Heilman, P. E. 1966 Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology*, 47: 826-831.
- 5) ——— 1968 Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. *Ecology*, 49: 331-336.
- 6) Le Barron, R. K. 1945 Adjustment of black spruce root systems to increasing depth of peat. *Ecology*, 26: 309-311.
- 7) Mackay R. 1970 Disturbances to the tundra and forest tundra environment of the western Arctic. *Can. Geotech. J.*, 7: 420-430.
- 8) Sakai, A. 1973 Ecological characteristics of forests in Yakutia Plain. *Low Temp. Sci., Ser. B* 31: 49-66.
- 9) USDA Forest Service 1965 Silvics of forest trees of the United States. Agr. Handbook No. 271, 762 pp, Washington, D. C.
- 10) Viereck, L. A. 1966 Plant succession and soil development on gravel outwash on the Muldrow Glacier, Alaska. *Ecology. Monogr.*, 36: 181-199.

- 11) Viereck, L. A. 1970 Forest succession and soil development adjacent to Chena River in interior Alaska. *Arct. Alp. Res.*, 2: 1-26.
- 12) ——— 1970 Soil temperature in river bottom stands in interior Alaska. Proc. of the Helsinki Symp. UNESCO, Ecology and Conservation Series No. 1, 223-233.
- 13) ——— 1973 Wildlife in the taiga of Alaska. *J. Quater. Res.*, 3: 465-495.
- 14) Zoltai, S. C. and W. W. Pettapiece 1973 Terrain, vegetation and permafrost relationships in the northern part of Mackenzie Valley and Northern Yukon. Environ.-Soc. Program, N. Pipelines, Task Force N. Oil Develop., Gov. Canada, Rep. 73-4, 105 pp.