

Small Openings in Trembling Aspen Forest: Microclimate and Regeneration of White Spruce and Trembling Aspen

**Arthur Groot, Derek W. Carlson¹,
Robert L. Fleming, and James E. Wood**

¹ BC Ministry of Forests, Research Branch
3015 Ord Rd., Kamloops, BC V2B 8A9

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ABSTRACT

In 1993 a study was established near Chapleau, Ontario (47°43' N, 83°11' W), in a 40-year-old trembling aspen (*Populus tremuloides* Michx.) stand to examine how microclimate influences the regeneration of white spruce (*Picea glauca* [Moench] Voss) and trembling aspen. Openings of the following sizes were created: 9-m- and 18-m-diameter circular openings, 9-m- and 18-m-wide east-west strips, and a 100-m x 150-m clear-cut. Solar radiation, air temperature, and soil temperature within the smallest opening were similar to that of the intact forest, whereas the microclimate of the north half of the 18-m-wide strips approached that of the clear-cut. The daytime vapor pressure deficit generally increased as the shelter provided by vegetation decreased. The soil was consistently drier under the intact forest than within openings, and control of the lower vegetation layer generally resulted in moister soil. The lower vegetation layer developed rapidly following harvesting, and within two growing seasons the clear-cut and uncut forest had similar levels of total (overstory and lower vegetation) leaf area index. First-year trembling aspen suckers were abundant (> 50 000 ha⁻¹) in the centers of all openings, except the 9-m circle. During the first growing season, white spruce stomatal conductance generally decreased from more sheltered to more exposed environments, likely as a result of increasing vapor pressure deficit. The dense, lower vegetation layer allowed only weak expression of the effects of overstory treatments on planted white spruce seedlings. Vegetation control within the strips resulted in substantially greater second-year height growth and diameter in planted white spruce seedlings. Excellent growth of white spruce was observed with vegetation control in the centers of the strips, likely as a result of a highly favorable microclimate (sufficient light, favorable soil temperature, lack of competition for moisture, moderate vapor pressure deficit, and protection from frost). Establishment of white spruce from seed was hindered by the dense, lower vegetation layer.

RÉSUMÉ

Une étude a été entreprise en 1993 près de Chapleau, en Ontario (47°43' N, 83°11' W), dans une tremblaie de 40 ans pour d'examiner l'influence du microclimat sur la régénération de l'épinette blanche (*Picea glauca* (Moench) Voss) et du peuplier faux-tremble (*Populus tremuloides* Michx.). On a créé dans le couvert des ouvertures des dimensions suivantes : trouées circulaires de 9 m et de 18 m de diamètre, bandes orientées d'est en ouest de 9 m et de 18 m de largeur et parterre de coupe à blanc de 100 m sur 150 m. Le rayonnement solaire ainsi que les températures de l'air et du sol étaient semblables dans la plus petite trouée et dans la parcelle boisée non perturbée, tandis que le microclimat de la moitié nord des bandes de 18 m de largeur se rapprochait de celui du parterre de coupe à blanc. Le déficit hygrométrique diurne augmentait généralement à mesure que diminuait l'effet abritant de la végétation. Le sol était fréquemment plus sec sous le couvert de la parcelle boisée non perturbée que dans les ouvertures créées dans le couvert et l'élimination de la strate de végétation inférieure indésirable se traduisait généralement par des sols plus humides. La strate de végétation inférieure s'est développée rapidement après la récolte et, en l'espace de deux saisons de végétation, le parterre de coupe à blanc et la parcelle boisée non perturbée présentaient des indices de surface foliaire totale (étage dominant et strate inférieure) similaires. Les drageons de peuplier faux-tremble d'un an étaient abondants (> 50 000/ha) au centre de toutes les ouvertures créées dans le couvert, sauf dans celle de 9 m de diamètre. Pendant la première saison de croissance, la conductance stomatique de l'épinette diminuait généralement des endroits les plus abrités aux milieux les plus exposés, vraisemblablement sous l'influence de l'augmentation du déficit hygrométrique. En raison de la présence d'une strate de végétation inférieure dense, les effets des traitements appliqués à l'étage dominant sur les semis d'épinette blanche plantés ne se faisaient que faiblement sentir. L'élimination de la végétation indésirable dans les bandes déboisées a entraîné un bien meilleur accroissement en hauteur et en diamètre des plants d'épinette blanche au cours de la deuxième saison de végétation. Dans le centre des bandes où la végétation indésirable avait été éliminée, on a observé un excellent taux de croissance de l'épinette blanche, vraisemblablement sous l'effet d'un microclimat très favorable (éclairage suffisant, température du sol favorable, absence de concurrence à l'égard de l'humidité, déficit hygrométrique modéré et protection contre le gel). La présence d'une strate de végétation inférieure dense a nui à l'établissement de semis naturels d'épinette blanche.

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SMALL OPENINGS IN TREMBLING ASPEN FOREST: MICROCLIMATE AND REGENERATION OF WHITE SPRUCE AND TREMBLING ASPEN

INTRODUCTION

White spruce (*Picea glauca* [Moench] Voss) is often considered difficult to establish following forest harvesting (Stiell 1976). In Ontario, establishment problems have contributed to a decline in the relative importance of white spruce in regeneration programs; while the provincial production of black spruce (*Picea mariana* [Mill.] B.S.P.) seedlings increased from 17 million to 73 million per year during the 1980s, production of white spruce seedlings remained static at about 15 million per year (Ontario Ministry of Natural Resources 1985, 1989).

White spruce establishment difficulties may be attributed to a number of causes. Rapid early growth of broad-leaved species puts white spruce in an unfavorable competitive position on fertile boreal mixedwood sites. Furthermore, white spruce is susceptible to spring frosts and planted seedlings frequently go into "check", a period of slow early growth (Sutton 1968, Stiell 1976, Nienstadt 1982, Nienstadt and Zasada 1990). Establishment from seed is erratic, because of competition and because moist soil is required for germination and for the survival and growth of germinants.

Many of the constraints to white spruce establishment appear to be related to the physical environment. This study focuses on several physical environment factors that influence the establishment of white spruce and its competitors: namely, solar radiation, soil temperature, night air temperature, soil moisture, and atmospheric humidity.

Solar Radiation

White spruce height growth increases with light up to about 50 percent of full light; maximum diameter growth occurs at full light (Logan 1969). Solar radiation is also the predominant influence on soil and air temperature regimes near the soil surface.

Soil Temperature

Rapid initial root growth of planted white spruce, which is necessary to maintain favorable water and nutrient balances (Burdett 1990), is inhibited by cold soils. Cold soils also inhibit suckering of trembling aspen (*Populus tremuloides* Michx.) (Maini and Horton 1966).

Night Air Temperature

Since white spruce is considered highly susceptible to frost damage (Nienstadt and Zasada 1990), treatments

that increase minimum air temperatures are beneficial for establishment. On clear, calm nights when frost risk is greatest, minimum air temperatures near the soil surface are strongly influenced by the long-wave energy balance of the surface. On such nights, the sky is 'colder' than vegetation and emits less long-wave radiation. Surfaces with greater exposure to the night sky become colder than surfaces with less exposure. The fraction of sky 'seen' from a surface is known as the sky view factor (*SVF*). The *SVF* is useful for describing forest openings, and varies from 0 to 1. The soil surface within a small forest opening has a small *SVF*; the surface within an extensive clear-cut has a *SVF* of 1.0.

Soil Moisture

Newly planted seedlings are prone to water stress (Burdett 1990), which is exacerbated by low soil moisture. Even slight deficiencies of soil moisture can reduce initial root growth of white spruce seedlings (Day and MacGillivray 1975).

Atmospheric Humidity

Seedling water stress is also related to atmospheric humidity, which affects the evaporative demand for water from the plant. Although relative humidity (*RH*) is the most familiar measure of humidity, the measure that most closely reflects atmospheric demand for water is the vapor pressure deficit (*VPD*), given by:

$$VPD = e_{sat}(T_a) - e_a \quad [1]$$

where $e_{sat}(T_a)$ is the saturated vapor pressure at air temperature T_a and e_a is the ambient vapor pressure. Note that $RH = 100 e_a / e_{sat}(T_a)$. It should also be noted that because $e_{sat}(T_a)$ increases with T_a , *VPD* increases with T_a . Thus, the difference between two *VPD* values has an air temperature component, $e_{sat}(T_{a2}) - e_{sat}(T_{a1})$.

The approach used in this study was to provide a range of microclimatic conditions by creating openings in a trembling aspen forest. Preliminary analysis indicated that circular and east-west strip openings one-half and one tree height in width would provide a wide range of microclimatic conditions. Fourteen locations within or adjacent to these openings, as well as the center of a clear-cut and the interior of an uncut forest, were chosen to provide a variety of combinations of microclimate. For instance, the *SVF*

varies from 0 in an uncut forest, to 0.43 in a one-tree-height strip, and to nearly 1.0 in a clear-cut. Solar radiation at ground level varies strongly in the north-south direction within small openings.

Stock quality can also influence the success of seedling establishment (Burdett 1983). This study includes an experiment to determine whether severe root pruning can alter stock quality sufficiently enough to affect establishment.

The study comprises a number of related elements: namely, (i) microclimatic measurements, including solar radiation, air temperature, soil temperature, soil moisture, and atmospheric humidity; (ii) an experiment to examine the influence of the 16 selected environments on the establishment of white spruce by planting and seeding; (iii) measurements of the water relations of the planted white spruce seedlings to help interpret microclimate influences; (iv) an experiment to examine the effect of vegetation control within the strips on the establishment of planted white spruce; (v) an experiment to determine the effect of root pruning on planted white spruce seedlings; (vi) an experiment to examine the role of overstory treatment on aspen regeneration; and (vii) an experiment to examine the role of overstory treatment on the development of leaf area index.

METHODS

Site Description

The study site was located in Halsey Township (47°43' N, 83°11' W), 25 km southeast of Chapleau, Ontario. In 1993, the stand at the study site was about 40 years old, with a dominant tree height of 19 m and a basal area of 36 m² ha⁻¹. The stand originated after forest harvesting (presumably of a mixedwood stand) and was dominated by trembling aspen (84 percent of the basal area), with minor components of balsam fir (*Abies balsamea* [L.] Mill.) (7 percent), white birch (*Betula papyrifera* Marsh.) (7 percent), and white spruce (1 percent). The soil is a deep, fresh, well-drained silt, with local concentrations of cobbles and boulders in the top 50 cm. Understory vegetation included herbs (e.g., *Aster macrophyllus* L. and *A. ciliolatus* Lindl.), ferns (e.g., *Pteridium aquilinum* L. Kuhn), shrubs (e.g., *Corylus cornuta* Marsh. and *Diervilla lonicera* Mill.), and balsam fir.

Harvesting in February and March 1993 created five sizes of openings: a 1.5-ha clear-cut measuring 100 m x 150 m; three 18-m x 150-m east-west strips; three 9-m x 150-m east-west strips; six 18-m-diameter circles; and six 9-m-diameter circles (Fig. 1). Deep snow cover at the time of harvest effectively precluded disturbance of the soil surface.

Microclimate Measurements

Air temperature, soil temperature, and short-wave irradiance were measured at the center of the clear-cut, within the forest interior, and at locations across one opening of each size from mid-June to early September 1993, and from early May to early July 1994. Measurement locations were as follows: 2.4, 7.4, 12.5, 17.4, 22.3, and 27.4 m north of the southern edge of the 18-m strip; 1.9, 4.8, 7.9, and 13.2 m north of the southern edge of the 9-m strip; 3.0, 9.5, 16.5, and 22.4 m north of the southern edge of the 18-m circle along the north-south diameter; and 4.5 and 13.9 m north of the southern edge of the 9-m circle along the north-south diameter. Solar radiation was measured at a height of 1.2 m, air temperature at 15 cm above the soil surface, and soil temperature at 5 cm below the soil surface.

During July and August 1994, air (15-cm height) and soil temperatures (5- and 20-cm depths) were measured in the vegetation control and no vegetation control treatments at the center of the strips and in the clear-cut. Data were collected from July 10 to 18, 1994, in the three 18-m strips; from July 20 to August 2, 1994, in the three 9-m strips; and from July 8 to August 31, 1994, in the clear-cut (20-cm depth soil temperature measurements for the clear-cut were unavailable prior to July 20).

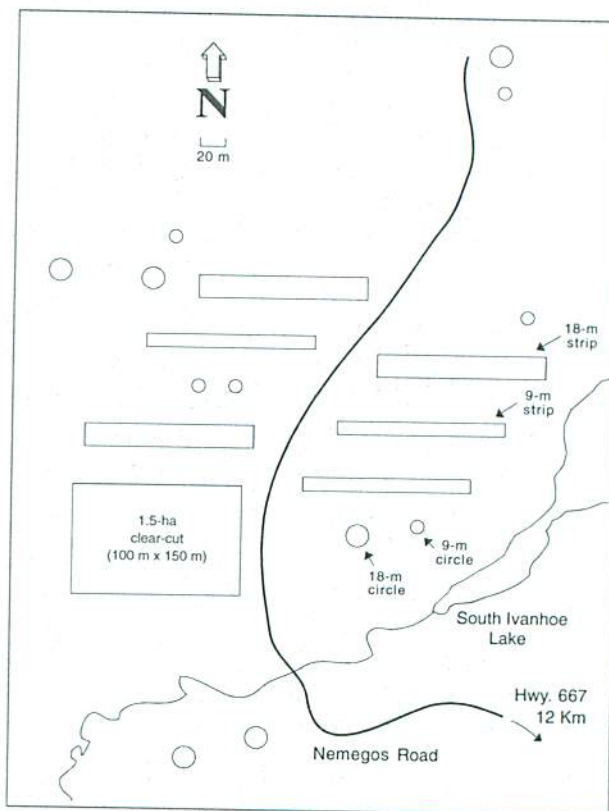


Figure 1. Study location and experimental layout.

Signals were recorded every 5 seconds and averaged half-hourly. The sensors used are those described in Carlson and Groot (1997).

Humidity was measured at a height of 15 cm during July and August 1994 using aspirated thermocouple psychrometers constructed following Lafleur (1988). Measurements were made at 5-second intervals in the forest, in the vegetation control and no vegetation control treatments in the center of the clear-cut, and in the center of the 9-m strip. The vapor pressure deficit (VPD) was computed by subtracting the measured humidity from the saturation vapor pressure (e_{sat}) at the dry bulb temperature (T_d). The e_{sat} (kPa) was computed as $0.61078 \exp(17.269 T_d / (T_d + 237.30))$ (Rosenberg et al. 1983).

Relative values of the air temperature component of the VPD across the width of the 9-m and 18-m strips were determined by computing the e_{sat} from measured air temperatures and then subtracting the e_{sat} based on air temperature in the forest. These relative values represent the difference in VPD between a location and the forest due to air temperature differences. Differences in humidity, which were not measured across the strips, would augment differences in VPD .

During the 1993 and 1994 growing seasons, soil moisture was periodically measured in the clear-cut; in the uncut forest; in the 18-m-wide strips at distances of 2, 4, 9, 14, and 16 m from the south edge; and in the 9-m-wide strips at distances of 2, 5, and 8 m from the south edge. Volumetric soil water content ($m^3 m^{-3}$) was measured at depths of 5 and 10 cm using Time Domain Reflectometry (TDR) probes (Trace Systems, Soilmoisture Equipment Corp., Santa Barbara, CA.), and at depths of 20, 35, 50, 65, and 80 cm using a neutron meter (Campbell Pacific Nuclear Corp., Martinez, CA.). Soil matric potential was measured at depths of 15, 30, 45, 80, and 100 cm using tensiometers constructed following Marthaler et al. (1983), and read with a pressure transducer (Soil Measurement Systems, Tucson, AZ.).

White Spruce Environment Experiment—Planted Seedling Component

White spruce seedlings (seed source 49°30'N 86°00'W, a location 280 km northwest of the study site) were grown in a peat-vermiculite mixture in Ray Leach tubes in a Canadian Forest Service greenhouse at Sault Ste. Marie, Ontario, from mid-April to mid-July 1992, and then moved outdoors. Mean height at the time of planting in the spring of 1993 was 15.1 cm.

Seedlings were planted in late May 1993 in groups of 30 at 16 positions chosen to represent a range of environments (Fig. 2). No mechanical site preparation was used; boot screening was used to remove surface debris and some of the organic layer. No vegetation control treatments were carried out in this experiment.

Seedling shoot length, annual shoot increment, and ground level diameter were measured in October 1994, after the second growing season. One-way analysis of variance was used to examine the influence of planting environment on growth.

White Spruce Seedling Water Relations

Stomatal conductance (g_s), transpiration (T), and mid-morning stem xylem pressure potential (ψ_{xt}) of planted white spruce in the environment experiment were measured periodically during the 1993 growing season. Both g_s and T were measured over a 30-second period with a transient, ventilated porometer (Micromet Systems Inc., Vancouver, BC.; Model CS-102), which covered the entire seedling. Stem ψ_{xt} was measured in the field with a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA.; Plant Water Status Console). Immediately upon excision, the seedling stem was enclosed in a plastic bag, transported to the instrument, and placed in the chamber with only a small section of stem protruding from the bag for determination of ψ_{xt} . Mid-morning measurements of g_s and T were made on 11 days in July and August 1993. On four of these days, measurements of g_s and T were taken every 2 hours from sunrise to sunset. Readings of ψ_{xt} were made on 3 of these 4 days.

Soil-plant liquid flow resistance (R_{sp}), representing the sum of the soil, root, and stem resistances along the flow path, was calculated as (Jones 1983):

$$R_{sp} = (\psi_{sr} - \psi_{xt}) / E \quad [2]$$

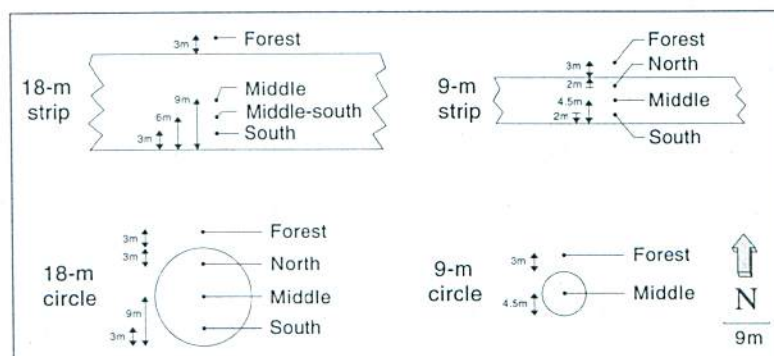


Figure 2. Arrangement of positions in environments experiment for white spruce planting and seeding. Two positions are not shown: the center of the clear-cut and the intact forest.

where ψ_{sr} is the bulk root zone soil water potential (measured with tensiometers) and E , the transpiration flux density (T/A), is considered the steady state water flux through the seedling.

Seedling projected leaf area (A) was measured with a Mk2 Delta-T Area Measurement System (Cambridge, UK), after removing all needles from the stem.

White Spruce Environment Experiment—Seed Spot Component

White spruce seed (Seedlot 42-31-0-00) was surface-sown on scalps about 20 cm in diameter. These scalps were created manually with a hoe to expose the forest floor—mineral soil interface. Six seeds (viability 89 percent) were placed in each scalp during late May 1993.

Groups of 50 seed spots were established at the same 16 positions as were used in the planted seedling component of the white spruce environment experiment (Fig. 2).

The number of seedlings at each spot was assessed in September 1993. In October 1994, the number and heights of seedlings at each spot were assessed. One-way analysis of variance was used to examine the influence of seed spot environment on seedling establishment.

Vegetation Control Experiment

Within each 9-m and 18-m wide strip, white spruce seedlings (same stock as in the white spruce environment experiment) were planted (May 1993) in rows of ten seedlings, oriented parallel to the length of the strip. Two sets of these rows were established at various positions across the strip and in the forest north of the strip (Fig. 3). Two sets of rows of ten seedlings were also planted at the center of the clear-cut. Vegetation was controlled in one set of rows within each strip and in the clear-cut by backpack sprayer application of the herbicide Vision® (glyphosate) in 1 percent solution on August 10–11, 1993 (6.6 l ha^{-1}) and on July 27, 1994 (3.3 l ha^{-1}). White spruce seedlings, covered during the application of herbicide, were not injured. Nonlinear regression was used to relate seedling growth characteristics to planting position relative to the forest edge.

Root Pruning Experiment

The performance of white spruce seedlings with intact and pruned root systems was compared. One-half of the seedling root system was removed by cutting along a vertical plane through the vertical axis of the root plug. No effort was made to preserve any main tap roots that may have existed. The pruning was carried out in the field immediately before planting.

Within both the clear-cut and the intact forest, three replications of 30 seedlings were established for each treatment on May 20, 1993. Results were examined using an unpaired two-tailed t-test with the assumption of unequal variance.

Aspen Regeneration

The density and height of trembling aspen root suckers and stump sprouts were measured on circular plots (5-m^2 area) in October 1993. Three lines of plots were established within each strip and the clear-cut, and one north-south line was established in each circular opening. In the 9-m strips and circles, plots were located at the following positions: within the opening, 2 m from the north (N) and south (S) stand edges; and within the forest 2, 7, and 17 m from the N and S stand edges. The same positions were used in the 18-m strips and circles, but here plots were also established in the centers of the openings. In the clear-cut, plots were located at the following positions: within the clear-cut, 2, 5, 15, and 30 m from the N and S edges; at the center; and within the forests 2, 7, and 17 m from the N and S stand edges. Values for the forest were obtained from the plots 17 m away from the 9-m circles.

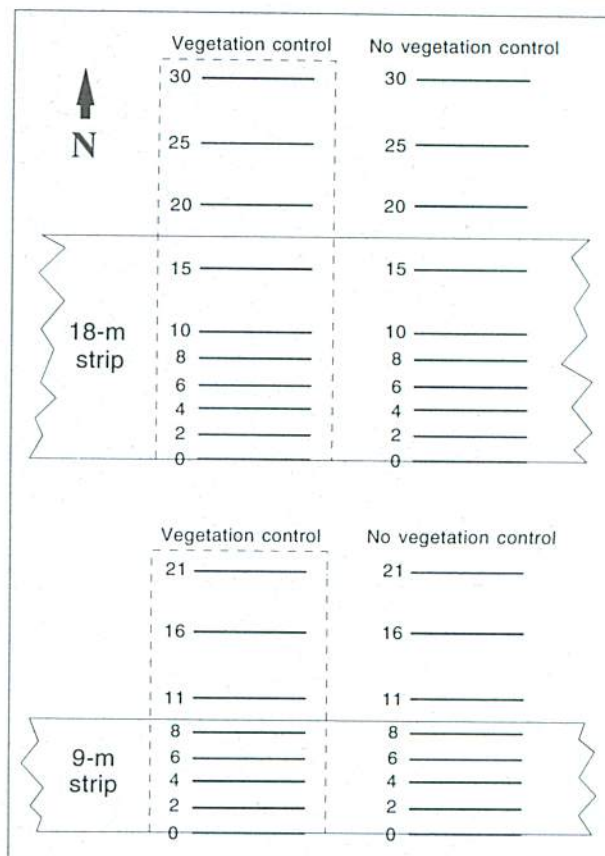


Figure 3. Arrangement of white spruce planting positions (rows of ten seedlings) in the competition control experiment. Distances (m) are from the south edge of the strip.

One-way analysis of variance was used to examine the influence of opening size and shape on aspen density and height at the center of the opening. For the 9-m strip and circular openings, values at the center of the opening were estimated by averaging the values measured within the opening 2 m from the N and S stand edges.

Two-way analysis of variance was used to explore the influence of position within the opening and opening configuration on aspen density and height. Observations from the plots within the strips and circles 2 m from the N and S stand edges were used in this analysis.

Leaf Area Index

Leaf area index (*LAI*) is the one-sided surface area of leaves within a canopy divided by the ground surface area. *LAI* of the aspen-dominated overstory was measured at eight locations before leaf fall in September 1993 using a LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE.). Understory (below 2-m height) *LAI* was measured at five heights (0, 25, 50, 75, and 100 cm) at locations throughout and adjacent to the openings during August and September 1994 using the LAI-2000.

In five 1-m² plots, the lower vegetation *LAI* was measured by the LAI-2000 and then harvested by clipping. The area of the clipped foliage was measured by an optical scanner to provide a comparison with measurements made by the LAI-2000.

Overstory *LAI* measurements were conducted on September 2 and 17, 1993, during overcast conditions. Overstory *LAI* was measured at eight locations by taking an above-canopy reading within the clear-cut, followed by ten below-canopy readings taken underneath the intact canopy at a 2-m height, and then a final above-canopy reading in the clear-cut. Lower vegetation *LAI* measurements were made from August 23 to September 9, 1994, during overcast or late afternoon conditions for understory layers 0 to 200 cm, 25 to 200 cm, 50 to 200 cm, 75 to 200 cm, and 100 to 200 cm. The *LAI* of a layer was measured by taking an above-canopy reading at 200 cm and then three below-canopy readings, each separated horizontally by about 1 m, at the bottom of the layer. Lower vegetation *LAI* measurements were made at the centers of the aspen measurement plots. Similar measurements were taken at the center of the 9-m circles and strips.

Nonlinear regression was used to examine *LAI* relative to distance from the forest edge.

RESULTS

Microclimate

Solar radiation

Solar radiation during the period June 15 to September 6, 1993, varied considerably among openings (Table 1), ranging from 18 percent of the above-canopy values within the uncut forest to 68 percent of the above-canopy values at the center of the 18-m strip.

With the east-west orientation of the 9-m and 18-m strips, solar radiation for the period June 10 to July 16, 1993, showed a pattern of low values (40 percent of the above-canopy radiation) near the south edge of the strip increasing to a maximum (70 to 80 percent of the above-canopy radiation) in the north half of the strip, and then decreasing into the forest (Figs. 4 and 5).

Soil temperature

The mean soil temperature at the 5-cm depth averaged about 2°C greater in the clear-cut than in the forest during the period June 15–September 6, 1993 (Table 1). Mean soil temperatures at the centers of the strips and circles fell between the clear-cut and forest temperatures. Temperature differences between the clear-cut and forest were greatest (about 3°C) in early July and declined to about 1°C by early September (Carlson and Groot 1997).

The daily maximum 5-cm soil temperature averaged for the period June 14 to July 4, 1993, showed strong variations within openings. For example, the difference in daily maximum temperature between a point 6.6 m south of the center of the 18-m strip and a point 3.5 m north of

Table 1. Microclimatic characteristics at the centers of openings for the period June 15 to September 6, 1993.

Opening	View factor	P (percent) ¹	Air temperature (°C)		Soil temperature (°C) 5-cm depth Mean
			Daily maximum	Daily minimum	
Clear-cut	0.92	100	23.9	6.8	16.0
18-m strip	0.43	68	22.4	7.7	15.2
9-m strip	0.23	57	22.0	9.0	15.3
18-m circle	0.18	55	24.2	8.6	14.6
9-m circle	0.05	26	20.6	9.6	14.0
Forest	0.00	18	20.1	10.0	14.2

¹P (percent) is the total solar radiation measured at 1.2 m above soil surface as a percentage of the total above-canopy radiation.

the center was 4.2°C (Fig. 6), almost as great as the difference between the forest and the clear-cut (4.6°C). For both the 9-m and 18-m strips and for the 18-m circle, the greatest daily maximum 5-cm soil temperature occurred in the north half of the opening (Figs. 6–8).

Within the 9-m (July 20 to August 2, 1994) and 18-m strips (July 10 to July 18, 1994), daily mean, maximum, and minimum soil temperatures at the 5-cm depth were significantly warmer in the vegetation control treatment than in the no vegetation control treatment (Table 2). Soil temperatures were also warmer in vegetation control treatment within the strips at the 20-cm depth, but the differences in maximum and minimum temperatures in the 9-m strip were not significant. In the clear-cut, soil temperatures were also greater in the vegetation control treatment (July 21 to August 31, 1994).

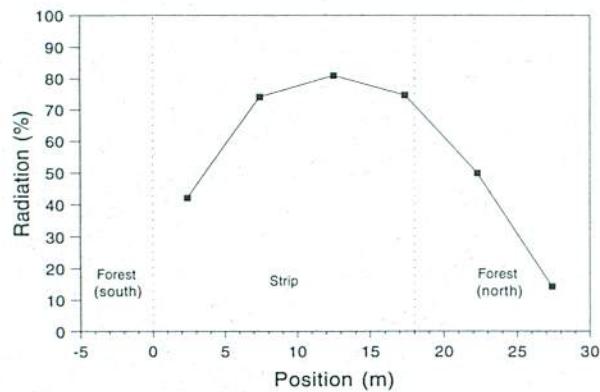


Figure 4. Solar radiation totals (percentage of above-canopy value) across the 18-m strip (June 10–July 6, 1993).

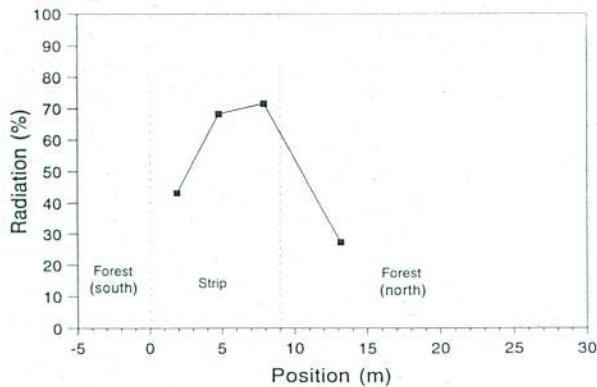


Figure 5. Solar radiation totals (percentage of above-canopy value) across the 9-m strip (June 10–July 6, 1993).

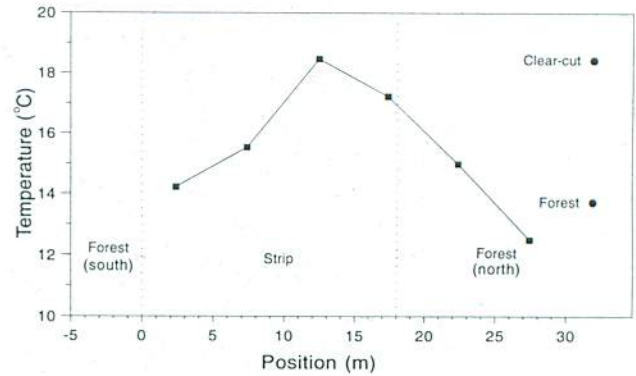


Figure 6. Mean daily maximum soil temperature (5-cm depth) across the 18-m strip (June 14–July 4, 1993).

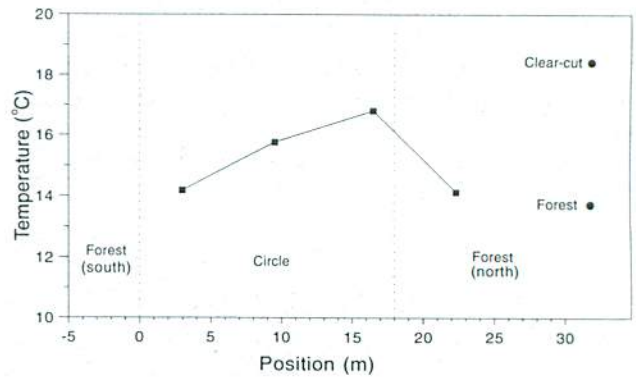


Figure 7. Mean daily maximum soil temperature (5-cm depth) across the 18-m circle (June 14–July 4, 1993).

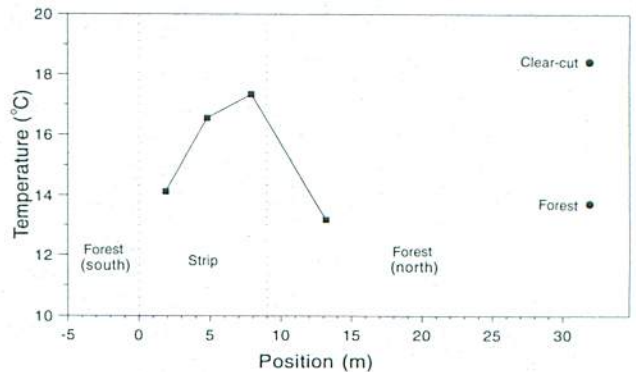


Figure 8. Mean daily maximum soil temperature (5-cm depth) across the 9-m strip (June 14–July 4, 1993).

At the 5-cm depth, mean soil temperatures were about 2–3.6°C warmer in the vegetation control treatment, and maximum temperatures were from 3.6–5.7°C warmer (Table 2). Differences in 5-cm depth soil temperature between the vegetation control and no vegetation control treatments were strongly related to daily solar radiation totals (Fig. 9).

Air temperature

During the growing season, the daily maximum air temperature at a 15-cm height increased and the daily minimum temperature decreased with an increasing size of opening (Table 1). Maxima averaged 3.8°C greater and minima 3.2°C less in the clear-cut than in the forest. On clear, calm nights, minimum temperatures in the clear-cut were nearly 6°C less in the forest (Groot and Carlson 1996).

During 1994, mean and daily maximum air temperatures at 5-cm and 15-cm heights were significantly ($p < 0.05$)

greater in the vegetation control treatment within the 9-m and 18-m strips than in the no vegetation control treatment (Table 3). Similar differences between these treatments were observed in the clear-cut. The largest differences between the vegetation control and no vegetation control treatments (about 4°C) occurred in maximum temperatures at the 5-cm height.

Humidity

On a sunny day (July 30, 1994), daytime humidity at a 15-cm height was least in the vegetation control treatment within the clear-cut, followed by the vegetation control treatment within the 9-m strip (Fig. 10a). Humidity values in the forest and in the no vegetation control treatment within the clear-cut and 9-m strip were similar. The difference in humidity between the forest and the vegetation control treatment within the clear-cut was about 0.5 kPa in mid-afternoon.

Table 2. Soil temperatures in the vegetation control experiment.

	Soil temperature (°C)			$t_{df=4}$	Pooled standard deviation
	Vegetation control	No vegetation control	Difference		
9-m strips (July 20–August 2, 1994)					
Mean at 5-cm depth	17.0	14.6	2.4	5.36*	0.54
Daily maximum at 5-cm depth	19.1	15.5	3.6	4.54*	0.96
Daily minimum at 5-cm depth	15.3	13.8	1.5	4.13*	0.45
Mean at 20-cm depth	15.7	13.4	2.3	3.73*	0.75
Daily maximum at 20-cm depth	17.7	13.7	4.0	2.42	2.04
Daily minimum at 20-cm depth	14.1	13.1	1.0	0.70	1.68
18-m strips (July 10–18, 1994)					
Mean at 5-cm depth	18.3	14.7	3.6	5.99*	0.74
Daily maximum at 5-cm depth	21.8	16.1	5.7	6.85*	1.02
Daily minimum at 5-cm depth	15.2	13.3	1.9	3.78*	0.62
Mean at 20-cm depth	16.8	13.7	3.1	4.94*	0.78
Daily maximum at 20-cm depth	17.6	14.0	3.6	5.36*	0.83
Daily minimum at 20-cm depth	16.2	13.4	2.7	4.45*	0.75
Clear-cut¹ (July 21–August 31, 1994)					
Mean at 5-cm depth	16.5	14.5	2.0		
Daily maximum at 5-cm depth	20.7	16.2	4.5		
Daily minimum at 5-cm depth	12.7	12.7	0.0		
Mean at 20-cm depth	15.4	14.1	1.3		
Daily maximum at 20-cm depth	16.2	14.8	1.4		
Daily minimum at 20-cm depth	14.8	13.6	1.2		

*Significant difference ($\alpha = 0.05$).

¹The clear-cut treatment was not replicated, precluding statistical analysis.

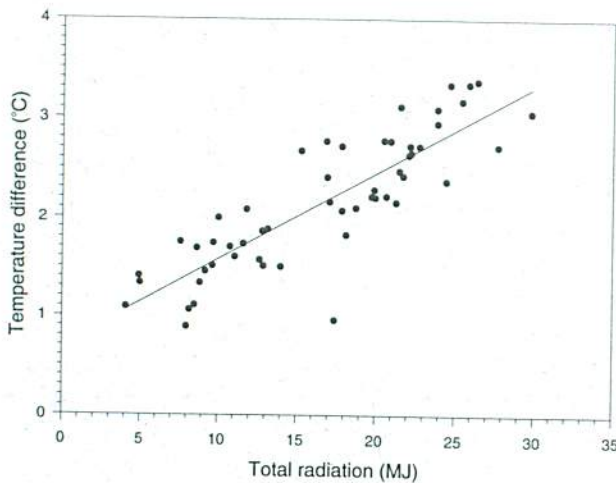


Figure 9. Difference in 5-cm daily mean soil temperature between competition control and no competition control treatments vs. daily above-canopy solar radiation total in the clear-cut (July 8–August 31, 1994). The equation of the least squares fit is $y = 0.71 + 0.087x$, $R^2 = 0.73$.

On the same day, vapor pressure deficits (*VPD*) were greatest in the vegetation control treatment within the clear-cut, again followed by the vegetation control treatment within the 9-m strip (Fig. 10b). *VPDs* were lowest in the forest. At mid-afternoon, the *VPD* in the vegetation control treatment within the clear-cut was 1.25 kPa greater than in the forest and 0.5 kPa greater than in the vegetation control treatment within the 9-m strip.

On August 3, 1994, a cloudy day, daytime humidity was least in the clear-cut, but the range in humidities among all five environments was small (Fig. 11a). Correspondingly, *VPD* was greatest in the clear-cut, but *VPDs* for all environments were generally less than 0.7 kPa for the daytime period (Fig. 11b).

The air temperature component of the *VPD* varied strongly across the 9-m- and 18-m strips on June 2, 1994, a sunny day. This component of the *VPD* was nearly 1 kPa greater near the north edge of the strips than near the south edge (Figs. 12 and 13).

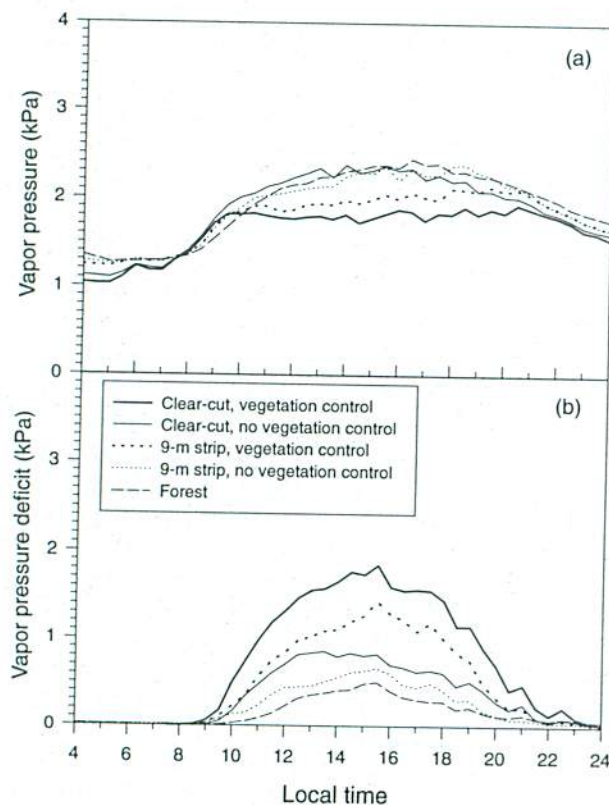


Figure 10a. Daytime pattern of vapor pressure at 15-cm height (July 30, 1994).

Figure 10b. Daytime pattern of vapor pressure deficit at 15-cm height (July 30, 1994).

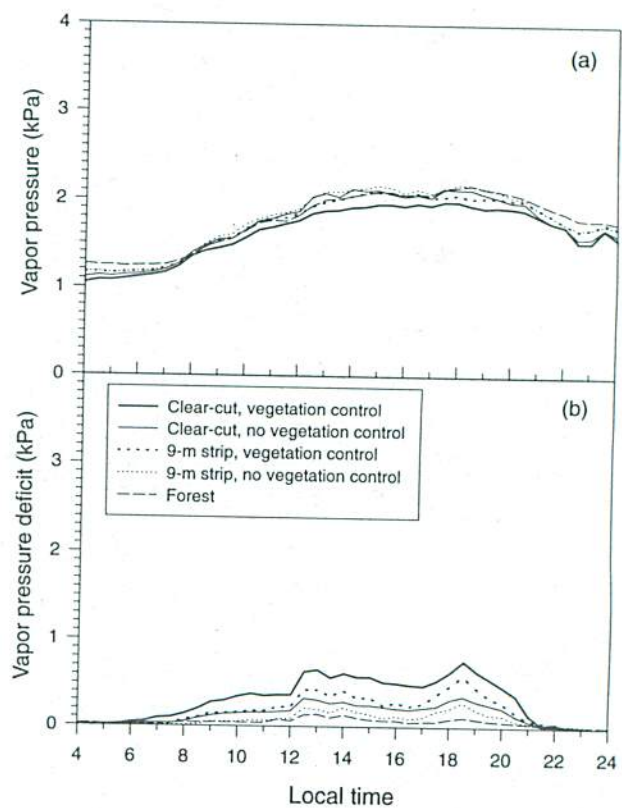


Figure 11a. Daytime pattern of vapor pressure at 15-cm height (August 3, 1994).

Figure 11b. Daytime pattern of vapor pressure deficit at 15-cm height (August 3, 1994).

content was always lower in the adjacent forest than in the clear-cut or the 18-m strip (Figs. 16 and 17).

White Spruce Environment Experiment—Planted Seedling Component

Second growing season annual shoot increments of planted white spruce differed ($p < 0.001$) significantly among the 16 positions. The five positions having the smallest increments were all in the forest (Fig. 18). Second growing season total heights also differed ($p = 0.002$) significantly among positions, although the range from smallest (26.7 cm) to largest (32.7 cm) was only 6 cm (Fig. 19). Second growing season ground level seedling diameter averaged 0.36 cm, and did not vary significantly ($p = 0.24$) among positions. Second growing season survival averaged 95.9 percent, and also did not vary significantly among positions ($p = 0.25$).

A severe frost, which occurred 2 weeks after planting in 1993, damaged many of the new shoots of the planted seedlings. The incidence of frost damage increased with opening size (Fig. 20; Groot and Carlson 1996). Seedlings in the forest and 9-m circle were virtually undamaged, whereas nearly 75 percent of the seedlings in the clear-cut had medium or heavy frost damage. Incidence of medium (one-third to two-thirds of the new shoots injured) to heavy frost damage (more than two-thirds of new shoots injured) in the 9-m and 18-m strips and in the 18-m circle ranged from 47 to 56 percent. No frost damage occurred in 1994.

White Spruce Seedling Water Relations

Stomatal conductance and transpiration

Diurnal trends in white spruce g_s showed a characteristic peak in early to mid-morning, and a gradually but continually descending trend for the rest of the day (Fig. 21). Seedlings in more sheltered environments (the forest and the south sides of the strips) usually had somewhat higher values of g_s throughout the day than did seedlings in more exposed locations (the clear-cut and the northern sides of the strips).

Values of white spruce T usually peaked in early to mid-afternoon. In early summer, values of T in the forest were comparable to those in the openings, but by late summer values were often lower in sheltered locations than in the more exposed locations in the strips (Fig. 22). The highest values of T were usually found on the north sides of the 18-m-wide strips; in contrast, low values were found on the south sides of the strips.

Stem xylem pressure potential

Mean values of midmorning ψ_{xt} ranged from -0.25 to -1.20 MPa among the different treatments on the

3 measurement days (July 23, August 8, and August 22). Values were substantially lower on a day with a high VPD than on a day with a low VPD (e.g., July 23 -3.0 kPa vs. August 22 -0.6 kPa). On August 8 and 22, ψ_{xt} in the forest was similar to that in the clear-cut. Within both the 18-m-wide and 9-m-wide strips there was a distinct gradient in ψ_{xt} across the strip (Fig. 23). Values were highest (least negative) on the south side and lowest just inside the forest bordering the north side. These trends were more evident on a day with a moderate to high VPD (e.g., August 8) than on a day with a low VPD (e.g., August 22).

Liquid flow resistance

Values of R_{sp} were relatively high in the clear-cut and in the forest on both August 8 and August 22 (Fig. 24). In contrast, values of R_{sp} in the strips varied; on August 8 (moderate VPD) R_{sp} was greater on the south side than on the north side of the strips, whereas on August 22 (low VPD) R_{sp} was as low or lower on the south side as on the north side.

White Spruce Environment Experiment—Seed Spot Component

First- and second-year establishment ratios (ratio of established seedlings to viable seeds sown) and second-year seed spot stocking were greatest in the clear-cut and least in the forest (Table 4). When the clear-cut and forest observations were excluded from the analysis of variance, position within openings was not a significant ($p \geq 0.05$) factor in any of the seedling establishment variables. Second-year establishment ratios were less than 0.08 at all locations except the clear-cut.

Vegetation Control Experiment

Second growing season diameter of white spruce in the no vegetation control treatment showed only a slight increase with distance from the forest edge (Fig. 25). However, seedling diameter in the vegetation control treatment was strongly related to distance from the forest edge. Diameters within the openings at 8 m from the forest edge were more than twice as great as diameters within the stand at 12 m from the forest edge (6.6 vs. 3.1 cm, respectively). Seedling diameters in the clear-cut were similar to seedling diameters in corresponding treatments at the 8-m position in the strip.

In both the vegetation control and no vegetation control treatments, white spruce height growth during the second growing season increased in a sigmoidal pattern with distance from the forest edge (Fig. 26), but the increase was greater in the vegetation control treatment. The curve fitted to the data had a value of 18.8 cm at 8 m from the forest edge in the vegetation control treatment and 11.7 cm in the no vegetation control treatment. Within the forest,

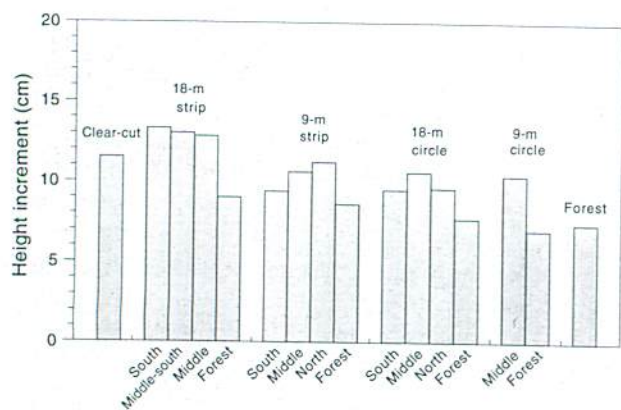


Figure 18. Second growing season height increment of planted white spruce in the environments experiment.

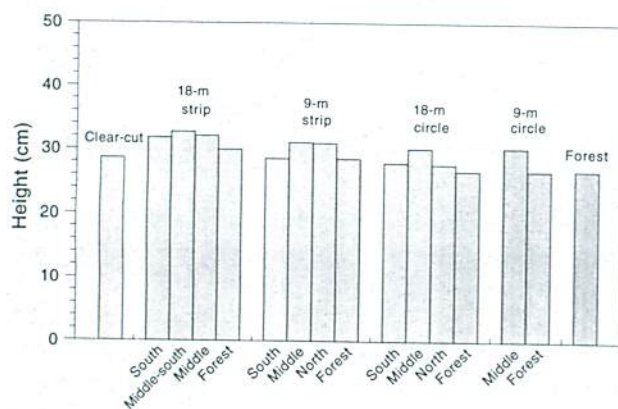


Figure 19. Second growing season total height of planted white spruce in the environments experiment.

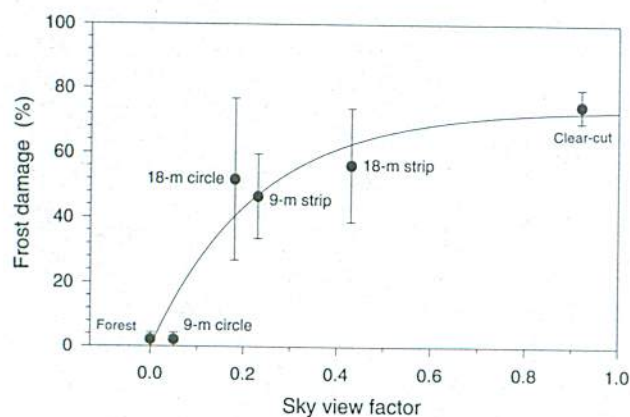


Figure 20. Percentage of seedlings with moderate or severe damage resulting from a frost event in late May 1993 in relation to the sky view factor (after Groot and Carlson 1996). Vertical lines indicate standard errors of the estimates.

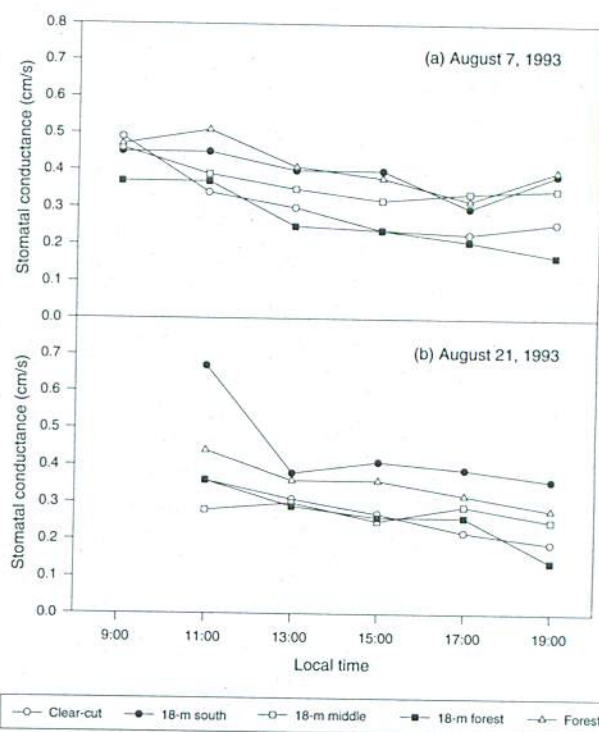


Figure 21. Daytime patterns in white spruce stomatal conductance by seedling location and opening size for: (a) August 7, and (b) August 21. Standard errors of the estimate typically range from 0.01 to 0.04.

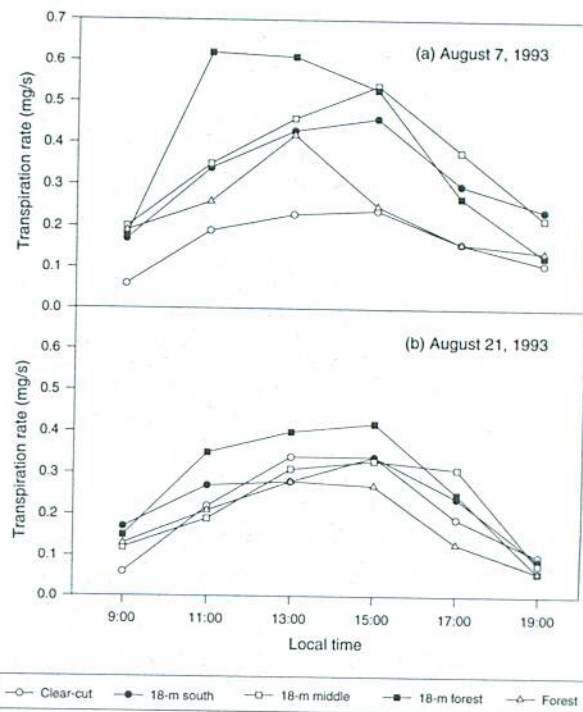


Figure 22. Daytime patterns in white spruce transpiration by seedling location and opening size for: (a) August 7, and (b) August 21. Standard errors of the estimate typically range from 0.005 to 0.05.

Soil moisture

Soil water potential at a 15-cm depth remained greater than -100 kPa at all measurement locations during the 1994 growing season (Figs. 14 and 15). Lowest potentials were observed in the forest. In both the clear-cut and the 18-m strip, water potentials were slightly greater in the vegetation control treatment than in the no vegetation control treatment (Figs. 14 and 15).

Water potentials were lower in the north half of the strip than in the south half, for both vegetation control and no vegetation control treatments (Fig. 15).

At a 5-cm depth, soil water content was often greater in the no vegetation control treatment within the clear-cut than in the vegetation control treatment (Fig. 16). Soil water content at this depth was also greater in the south half of the 18-m strip than in the north half (Fig. 17). Soil water

Table 3. Air temperatures in the vegetation control experiment.

	Air temperature (°C)			$t_{df=4}$	Pooled standard deviation
	Vegetation control	No vegetation control	Difference		
9-m strips (July 20–August 2, 1994)					
Mean at 5-cm height	16.6	15.7	0.9	4.99*	0.21
Daily maximum at 5-cm height	24.2	20.6	3.6	6.05*	0.74
Daily minimum at 5-cm height	11.0	11.4	-0.4	1.61	0.33
Mean at 15-cm height	16.3	15.7	0.6	4.25*	0.17
Daily maximum at 15-cm height	22.9	20.9	2.0	4.14*	0.59
Daily minimum at 15-cm height	11.1	11.2	-0.1	0.49	0.30
Mean at 75-cm height	16.1	15.9	0.2	1.91	0.16
Daily maximum at 75-cm height	21.8	21.8	0.0	0.03	0.44
Daily minimum at 75-cm height	11.4	11.1	0.3	1.35	0.29
18-m strips (July 10–18, 1994)					
Mean at 5-cm height	16.3	15.2	1.2	3.81*	0.38
Daily maximum at 5-cm height	27.8	23.4	4.4	9.70*	0.56
Daily minimum at 5-cm height	6.8	7.5	-0.7	1.21	0.69
Mean at 15-cm height	15.7	15.0	0.7	3.50*	0.24
Daily maximum at 15-cm height	25.3	23.7	1.6	2.94*	0.68
Daily minimum at 15-cm height	7.0	7.0	0.0	0.05	0.56
Mean at 75-cm height	15.3	15.0	0.4	1.32	0.36
Daily maximum at 75-cm height	23.1	23.2	-0.1	0.19	0.52
Daily minimum at 75-cm height	7.5	6.8	0.7	1.91	0.47
Clear-cut¹ (July 21–August 31, 1994)					
Mean at 5-cm height	14.4	13.8	0.6		
Daily maximum at 5-cm height	23.4	19.2	4.2		
Daily minimum at 5-cm height	5.8	8.1	-2.3		
Mean at 15-cm height	14.1	13.7	0.4		
Daily maximum at 15-cm height	22.2	21.0	1.2		
Daily minimum at 15-cm height	6.0	7.3	-1.3		
Mean at 75-cm height	14.1	14.0	0.1		
Daily maximum at 75-cm height	20.6	20.0	0.6		
Daily minimum at 75-cm height	7.2	7.9	-0.7		

*Significant difference ($\alpha = 0.05$).

¹The clear-cut treatment was not replicated, precluding statistical analysis.

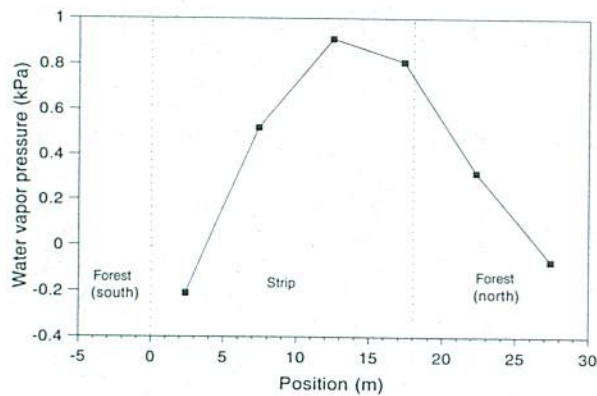


Figure 12. Air temperature component of the vapor pressure deficit in the 18-m strip relative to the forest values (1 200–1 600, June 2, 1994).

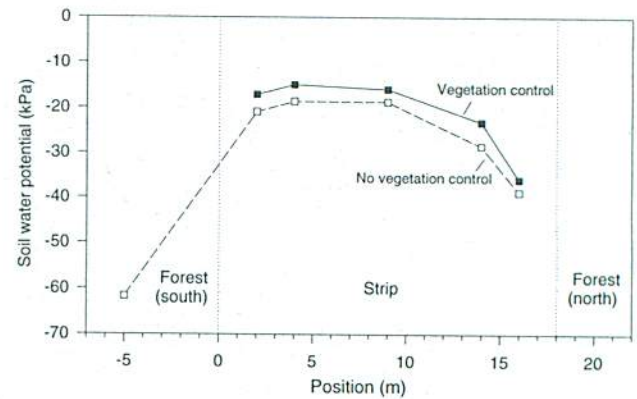


Figure 15. Soil water potential (15-cm depth) across the 18-m strip on August 25, 1994.

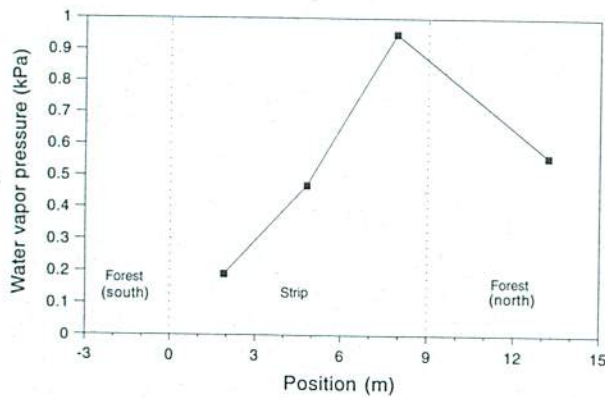


Figure 13. Air temperature component of the vapor pressure deficit in the 9-m strip relative to the forest values (1 200–1 600, June 2, 1994).

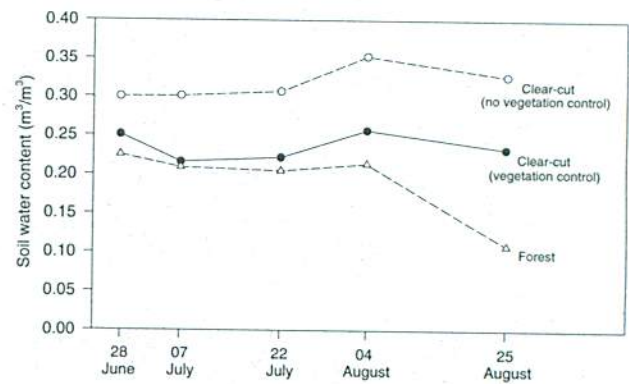


Figure 16. Soil water content (5-cm depth) during 1994 in the clear-cut and in the forest.

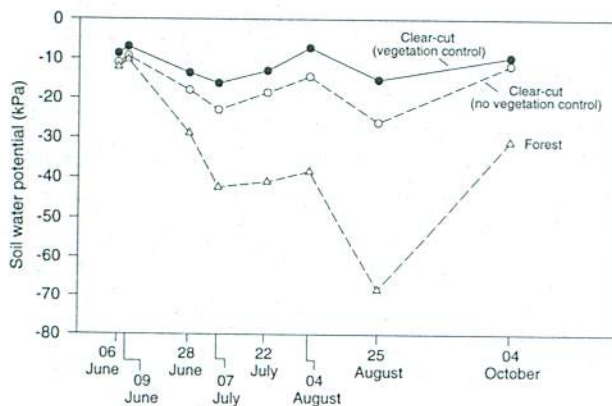


Figure 14. Soil water potential (15-cm depth) during 1994 in the clear-cut and in the forest.

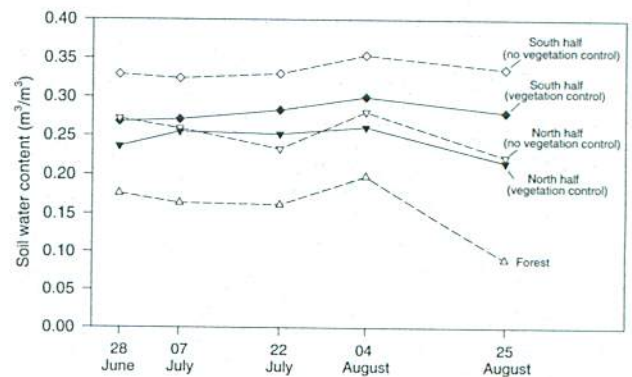


Figure 17. Soil water content (5-cm depth) during 1994 in the 18-m strip.

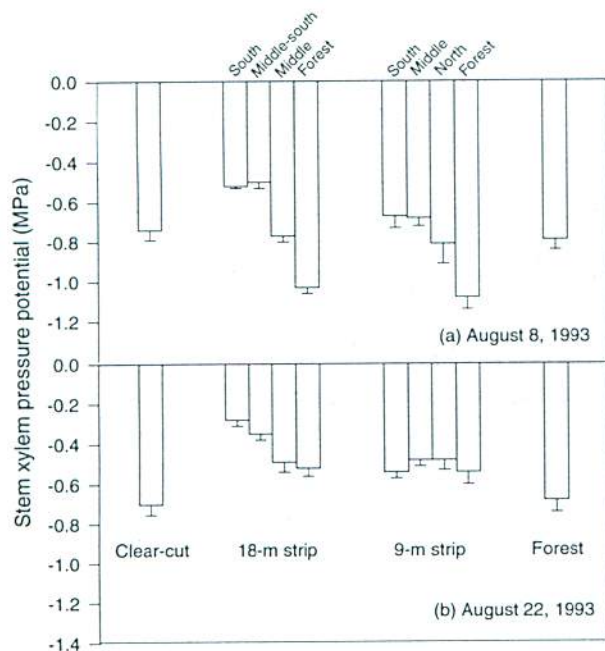


Figure 23. White spruce mid-morning stem xylem pressure potential by seedling location and opening size for: (a) August 8, and (b) August 22. Vertical lines at the top of the bars indicate standard errors of the estimates.

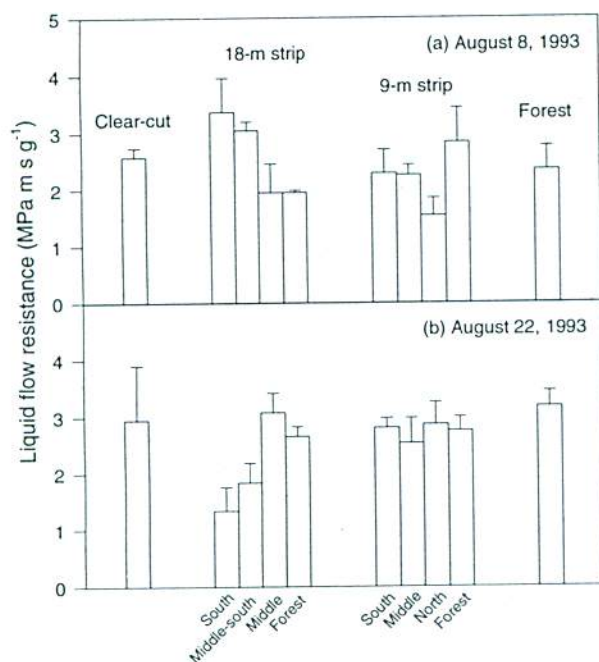


Figure 24. White spruce mid-morning liquid flow resistance by seedling location and opening size for: (a) August 8, and (b) August 22. Vertical lines at the top of the bars indicate standard errors of the estimates.

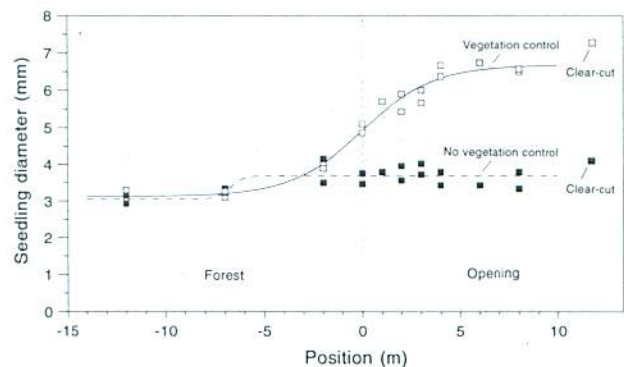


Figure 25. Second growing season diameter of planted white spruce in the vegetation control experiment. Negative distances are within the stand and positive distances are within 9-m and 18-m strips. Least squares fit for the vegetation control treatment: $y = 3.12 + 3.54/(1 + e^{-(x + 0.053)/1.83})$; $R^2 = 0.97$. Least squares fit for the no vegetation control treatment: $y = 3.05 + 0.65/(1 + e^{-(x + 6.71)/0.36})$; $R^2 = 0.40$.

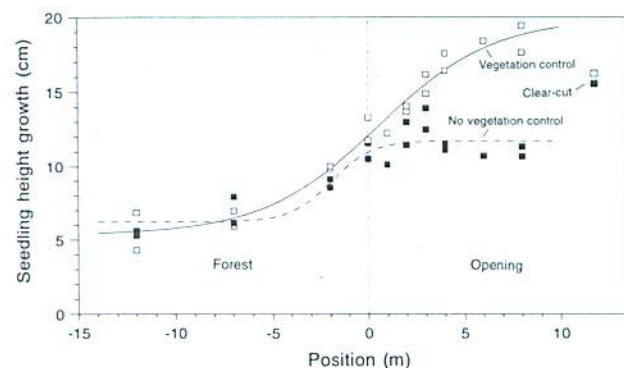


Figure 26. Second growing season height growth of planted white spruce in the vegetation control experiment. Negative distances are within the stand and positive distances are within 9-m and 18-m strips. Least squares fit for the vegetation control treatment: $y = 5.34 + 14.59/(1 + e^{-(x - 0.46)/3.03})$; $R^2 = 0.96$. Least squares fit for the no vegetation control treatment: $y = 6.22 + 5.53/(1 + e^{-(x + 1.92)/1.07})$; $R^2 = 0.81$.

at a distance of 12 m from the forest edge, the value of the fitted curve was near 6 cm for both treatments. Height growth in the clear-cut vegetation control treatment (16.2 cm) was less than the maximum observed in the strip vegetation control treatment. However, in the no vegetation control treatment within the clear-cut, height growth (15.6 cm) was greater than in the corresponding treatment in the strip.

Second growing season total height of white spruce also increased with distance from the forest edge for both treatments, and again the increase was greater for the vegetation control than for the no vegetation control treatment (Fig. 27). The value from the fitted curve at a position within the stand 12 m from the forest edge for both treatments was 26 cm; at a position within the opening 8 m from the forest edge values were 38.8 cm and

31.7 cm for the vegetation control and no vegetation control treatments, respectively. Seedling heights for the corresponding treatments in the clear-cut were less than these values, particularly for the vegetation control treatment (27.0 cm).

The strong relationship between growth of seedlings in the vegetation control treatment and distance from the forest edge produced a pattern of maximum diameter and greatest height growth near the center of the 9-m- and 18-m-wide strips (Figs. 28 and 29).

Root Pruning Experiment

In the clear-cut, 1992, 1993, and 1994 total height of trees with unpruned root systems was greater than that of trees with pruned root systems (Table 5), but the treatments did not differ in 1993 or 1994 height growth or in 1994

Table 4. White spruce establishment in seed spots after one and two growing seasons in the environments experiment.

Location	1st year stocking (proportion of seed spots with one or more seedlings)	1st year establishment ratio (number of seedlings per viable seed sown)	2nd year stocking (proportion of seed spots with one or more seedlings)	2nd year establishment ratio (number of seedlings per viable seed sown)	1st winter survival	2nd year height (cm)
Clear-cut	0.77	0.363	0.51	0.244	0.555	3.3
18-m strip S*	0.57	0.235	0.09	0.031	0.121	2.6
18-m strip M	0.46	0.185	0.01	0.001	0.005	2.0
18-m strip N	0.45	0.184	0.16	0.079	0.245	3.3
18-m strip F	0.41	0.145	0.09	0.048	0.275	2.2
9-m strip S	0.39	0.169	0.07	0.030	0.174	2.8
9-m strip M	0.44	0.202	0.09	0.033	0.144	3.3
9-m strip N	0.39	0.152	0.08	0.042	0.261	2.5
9-m strip F	0.38	0.117	0.05	0.013	0.084	2.8
18-m circle S	0.77	0.360	0.17	0.048	0.141	3.4
18-m circle M	0.63	0.262	0.17	0.064	0.162	2.6
18-m circle N	0.50	0.206	0.11	0.037	0.123	2.5
18-m circle F	0.43	0.170	0.22	0.063	0.338	2.3
9-m circle M	0.44	0.176	0.01	0.003	0.017	3.0
9-m circle F	0.42	0.150	0.06	0.016	0.102	2.2
Forest	0.45	0.130	0.03	0.007	0.045	2.3

Analysis of variance including clear-cut and forest

MSE**	0.026	0.007	0.015	0.002	0.034	0.355
F-ratio	1.81	2.35	2.99	3.57	1.70	1.24
p > F	0.077	0.021	0.005	0.001	0.103	0.319

Analysis of variance excluding clear-cut and forest

MSE	0.030	0.008	0.016	0.002	0.036	0.393
F-ratio	1.22	1.46	0.74	0.68	0.76	1.08
p > F	0.319	0.196	0.798	0.770	0.693	0.429

* S = south, MS = middle-south, M = middle, N = north, F = forest (see Fig. 2).

** MSE = mean square error in analysis of variance.

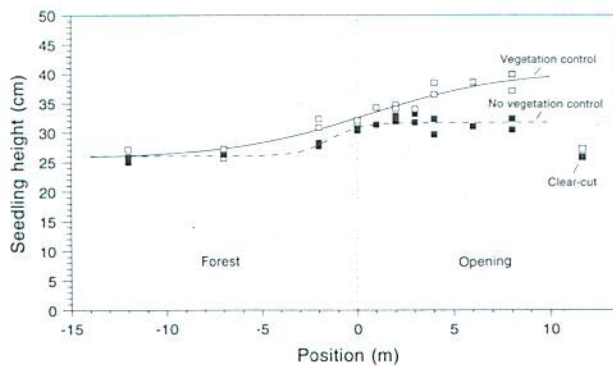


Figure 27. Second growing season total height of planted white spruce in the vegetation control experiment. Negative distances are within the stand and positive distances are within 9-m and 18-m strips. Least squares fit for the vegetation control treatment: $y = 25.7 + 14.8 / (1 + e^{-(x - 0.62)/3.58})$; $R^2 = 0.92$. Least squares fit for the no vegetation control treatment: $y = 26.0 + 5.65 / (1 + e^{-(x + 1.41)/0.89})$; $R^2 = 0.86$.

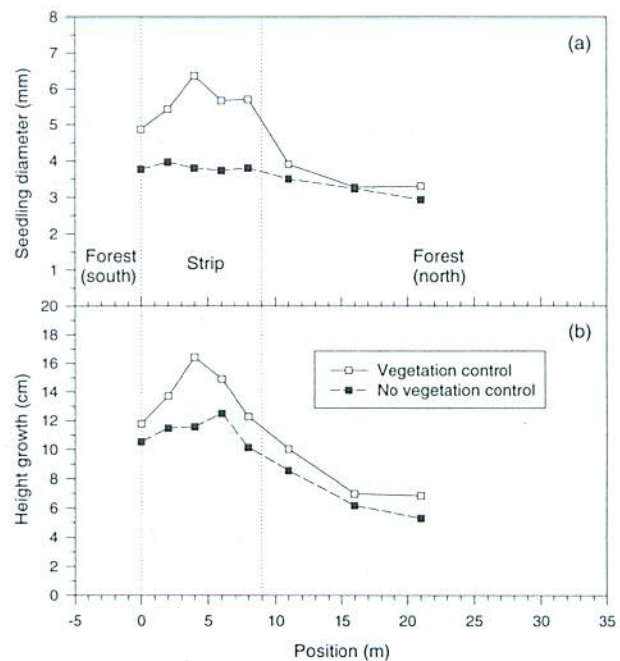


Figure 29. Second growing season (a) diameter and (b) height growth of planted white spruce across 9-m-wide strips in the vegetation control experiment.

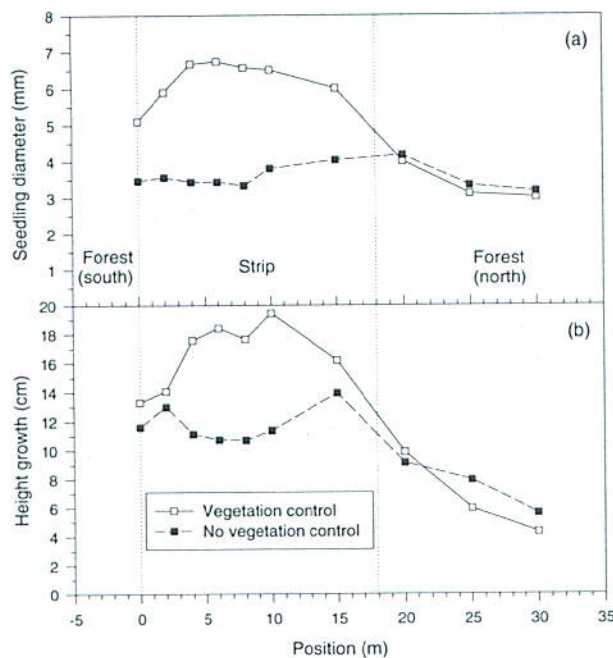


Figure 28. Second growing season (a) diameter and (b) height growth of planted white spruce across 18-m-wide strips in the vegetation control experiment.

Table 5. Height, height growth, diameter, and survival of white spruce seedlings with intact and pruned root systems.

	Pruned	Unpruned	t*	p**
Clear-cut				
1994 height (cm)	24.0	28.5	3.53	0.039
1993 height (cm)	14.7	17.4	4.88	0.005
1992 height (cm)	12.9	14.9	9.70	<0.001
1994 height growth (cm)	9.3	11.1	1.91	0.289
1993 height growth (cm)	1.8	2.5	1.24	0.262
1994 diameter (mm)	3.0	3.6	1.87	0.159
1994 survival (percent)	96.7	100.0	—	—
Forest				
1994 height (cm)	24.3	27.5	6.86	<0.001
1993 height (cm)	18.8	20.9	2.88	0.035
1992 height (cm)	14.6	15.8	1.32	0.258
1994 height growth (cm)	5.5	6.5	1.71	0.148
1993 height growth (cm)	4.2	5.2	4.24	0.005
1994 diameter (mm)	2.7	3.1	7.07	<0.001
1994 survival (percent)	97.8	98.9	0.71	0.506

* t = t-statistic from paired t-test.

** p = probability of exceeding t.

diameter. Survival was high (> 95 percent) in both treatments.

At the forest location, trees with pruned and unpruned root systems did not differ in 1992 total height, but the unpruned trees showed significantly ($p < 0.05$) greater 1993 and 1994 total height. The height growth of unpruned trees was significantly greater than the height growth of unpruned trees in 1993, but not in 1994. The 1994 diameter of unpruned trees was also significantly greater than that of pruned trees.

Aspen Regeneration

Opening configuration was a significant influence on first year aspen density and height at the center of the openings ($p < 0.01$ for each variable). Pairwise comparisons (Student-Newman-Keuls) indicated that means were not significantly different among the clear-cut, 18-m strips, and 18-m circles, all of which had first-year densities exceeding 100 000 stems ha^{-1} (Table 6). Densities were substantial in the 9-m strip (about 60 000 stems ha^{-1}), much lower in the 9-m circle (12 000 stems ha^{-1}), and very low under an intact canopy (< 1 000 stems ha^{-1}). Mean height of aspen stems was more than 50 cm in the clear-cut and 18-m-wide openings, but decreased in the smaller openings and under an intact canopy (Table 6).

Table 6. First-year trembling aspen densities and heights at opening centers.

Opening	Density (stems ha^{-1})	Height (cm)
Clear-cut	173 333 a ¹	57.2 ab
18-m strip	140 889 a	65.1 a
18-m circle	126 667 a	51.9 ab
9-m strip	59 777 b	41.8 b
9-m circle	12 000 c	28.0 c
Forest	800 d	4.9 d
MSE ³	3415.22 ²	80.7
F ⁴	32.5	25.9
p ⁵	<0.0001	<0.0001

¹ Within a column, values followed by the same letter are not significantly different (Student-Newman-Keuls Method).

² A square-root transformation was applied to density values prior to analysis of variance to normalize the data. MSE is in transformed units; density values are in original units.

³ MSE = mean square error in ANOVA.

⁴ F = F-ratio.

⁵ p = probability of exceeding F.

Aspen density and height were significantly ($p = 0.004$ and 0.001, respectively) greater 2 m from the northern edge of strips and circles than 2 m from the southern edge.

Leaf Area Index

In September 1993, overstory *LAI* (mainly trembling aspen) averaged 2.4 (SE = 0.17). This value is more appropriately termed Plant Area Index, since measurements by the LAI-2000 do not distinguish stems and branches from foliage. At the end of the 1994 growing season, lower vegetation *LAI* under an intact overstory averaged 2.1 (SE = 0.18), whereas in the clear-cut, lower-vegetation *LAI* averaged 4.1 (SE = 0.31 for nine measurements within the clear-cut). Lower vegetation included *Aster macrophyllus*, *A. ciliolatus*, *Corylus cornuta*, *Diervilla lonicera*, *Pteridium aquilinum*, *Clintonia borealis* (Ait.) Raf., *Aralia nudicaulis* L., *Lonicera hirsuta*, and trembling aspen. Lower-vegetation *LAI* measured by the Plant Canopy Analyzer averaged 14 percent more than when measured by clipping for the 0–200-cm layer and 42 percent more for the 25–200-cm layer (Fig. 30).

Size of opening had a significant effect on lower-vegetation *LAI* at the center of openings (Table 7). Increases in *LAI* within openings relative to *LAI* within adjacent forests were strongly evident for the 18-m and 9-m strips and for the 18-m circle (Figs. 31 to 33), but less so for the 9-m circle (not shown). Changes in lower-vegetation *LAI* occurred almost entirely within a zone of 10 m on either side of the forest edge (Fig. 34).

DISCUSSION

Microclimate

For solar radiation, air temperature, and soil temperature, the range of microclimate observed within the strip and

Table 7. Lower vegetation leaf area index at the centers of openings.

Opening	<i>LAI</i> at center	n*
Clear-cut**	4.11	1
18-m strip	4.45	3
9-m strip	2.94	3
18-m circle	3.38	6
9-m circle	3.07	5
Intact forest	2.08	6
MSE in ANOVA	0.324	
F ratio	9.50	
probability of exceeding F	<0.01	

* n = sample size.

** Not included in analysis of variance.

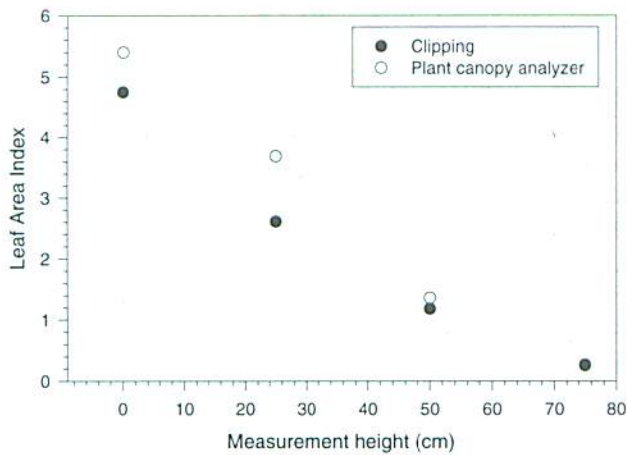


Figure 30. Lower vegetation leaf area index measured by clipping foliage and by a LAI-2000 Plant Canopy Analyzer for layers bounded by the measurement height and 200 cm.

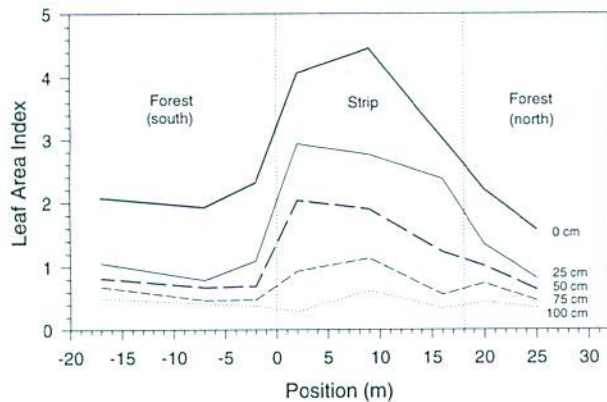


Figure 31. Lower vegetation (< 2-m height) leaf area index at five measurement heights across the 18-m strips, 23 August–9 September, 1994.

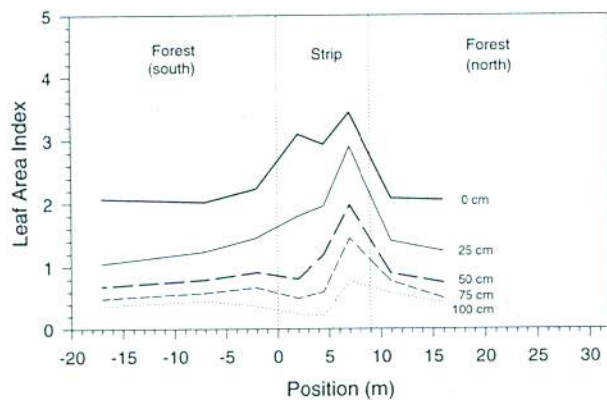


Figure 32. Lower vegetation (< 2-m height) leaf area index at five measurement heights across the 9-m strips, 23 August–9 September, 1994.

circular openings spanned much of the range in microclimate between forest and clear-cut. For these microclimatic variables, clear-cut conditions are approached in rather small openings. Solar radiation at the center of the 9-m circle was only slightly greater than solar radiation under the forest, whereas radiation in the north half of both the 9-m and 18-m strips during mid-summer was almost as great as above-canopy radiation. Similarly, air and soil temperatures at the center of the 18-m strip were generally closer to those observed in the clear-cut than to those observed in the forest. The opposite was true at the center of the 9-m circle.

During the day, solar radiation typically dominates the energy balance of the soil surface, and is a major influence on near-surface air and soil temperature regimes.

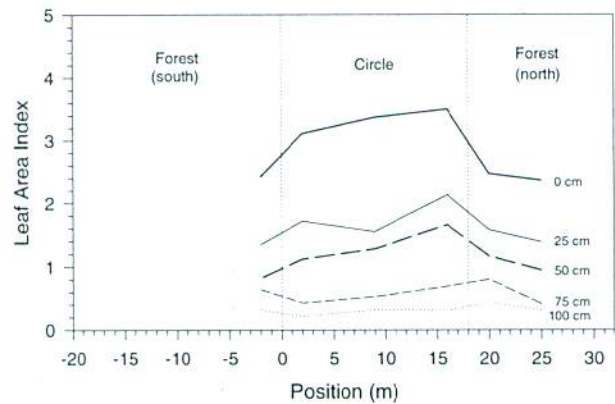


Figure 33. Lower vegetation (< 2-m height) leaf area index at five measurement heights across the 18-m circles, 23 August–9 September, 1994.

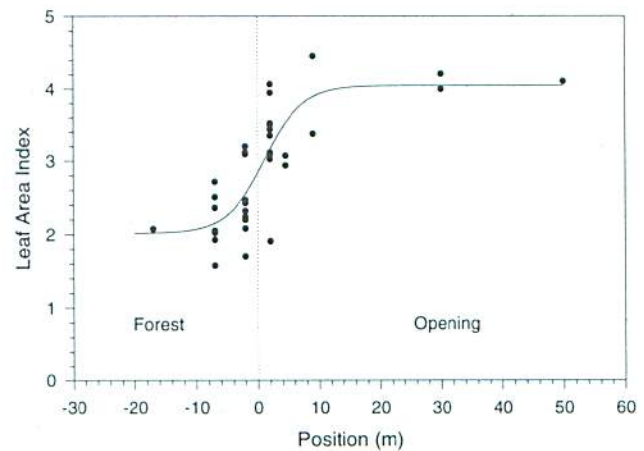


Figure 34. Lower vegetation (< 2-m height) leaf area index in relation to distance from the stand edge, 23 August–9 September, 1994.

This is why the air temperature and soil temperature increase together with radiation as opening size increases, and why the pattern of soil temperature across strips is similar to the pattern of solar radiation.

A lower layer of vegetation intercepts radiation, however, preventing it from reaching the soil surface. As a result, vegetation removal produced an average soil warming of about 2 to 4 °C at a 5-cm depth. At a similar latitude, Wood and von Althen (1993) observed slightly greater temperature differences between vegetated and unvegetated treatments.

At night, the net loss of long-wave radiation from the soil surface increases with the size of opening, and results in lower minimum air temperatures. The average difference in minimum temperature between the clear-cut and forest interior (3°C) is similar to differences observed in *Eucalyptus delegatensis* R.T. Baker (Nunez and Bowman 1986) and *Pinus contorta* Loud. (Cochran 1969) forests. On calm, clear nights, differences in minimum temperature of nearly 6°C were observed between the clear-cut and forest interior (Groot and Carlson 1996). The risk of damage to newly flushed white spruce by late spring frosts increases with the size of opening.

Daytime *VPD* generally increased as the shelter provided by vegetation decreased; the lowest values occurred in the forest and the greatest values occurred in the vegetation control treatment within the clear-cut. A decrease in water vapor pressure from sheltered to exposed environments contributed to this increase in *VPD*, but the increase in air temperature played a greater role. Given this dominant role of air temperature in determining the *VPD*, it is likely that the pattern of *VPD* across the strips paralleled the pattern of the air temperature component of *VPD* across the strips.

Soil moisture levels during 1994 were generally high, with the lowest observed values above -100 kPa. Evapotranspiration and interception by vegetation resulted in consistently drier soil within the forest than within the openings. Within the openings, soil was also drier at a 15-cm depth in the no vegetation control treatment than in the vegetation control treatment because of evapotranspiration. Near the surface (5-cm depth), however, the soil was drier in the vegetation control treatment in the clear-cut and in the 18-m strip than in the no vegetation control treatment, thereby suggesting that high irradiance was causing surface drying. High irradiance likely also caused lower soil moisture in the north half of the 18-m strip than in the south half through effects on both surface evaporation and plant transpiration.

Leaf Area Index

A likely cause of the discrepancy between *LAI* measurements at the 25-cm level by clipping and by the *LAI-2000* is that the instrument sensor is too close to large foliage (particularly *Aster macrophyllus* L.) at this level. This is a violation of the assumption that foliage elements are small relative to the sensor area of view (LICOR 1992). *LAI-2000* measurements for the 25- to 200-cm layer, and to a lesser extent for the 0- to 200-cm layer, probably overestimate *LAI*.

The overstory *LAI* observed in this study (2.4) is similar to values observed for trembling aspen stands in Ontario (Pollard 1970), and at the lower end of the range of values observed for aspen in Alberta (Johnstone and Peterson 1980). The *LAI* of the undisturbed lower vegetation under an intact canopy (2.1) was nearly equal to that of the overstory.

After two growing seasons, the lower-vegetation *LAI* in the clear-cut and in the center of the 18-m strip was nearly the same as the total *LAI* (overstory and lower vegetation) in the intact forest. This demonstrates that on fertile sites the lower vegetation responds very rapidly to increased light. The transition from intact forest values to clear-cut values in lower-vegetation *LAI* occurred almost entirely within 10 m of the forest edge. Lower vegetation at the center of the 18-m strip was not suppressed by the adjacent overstory, whereas suppression did occur at the centers of smaller openings.

Physiology of Planted White Spruce Seedlings

The decreasing trend in white spruce seedling g_s from more sheltered environments to more exposed environments appears best correlated with a concomitant increase in *VPD*. The stomata of most conifers, including white spruce, are highly sensitive to *VPD*, and substantial decreases in g_s accompany increases in *VPD* (Grossnickle and Blake 1986, Sandford and Jarvis 1986, Livingston and Black 1987). On most days, *VPD* increased from more sheltered locations (i.e., the forest and the southern sides of openings) to more exposed locations (the clear-cut and the northern sides of openings). Variations in other factors influencing g_s , including solar irradiance, ψ_{sr} , and soil temperature, appeared to have less influence on g_s than did *VPD*.

Despite their location beneath the aspen canopy, white spruce seedlings planted in the forest had g_s values as great as in any other location, and comparable to those reported for healthy seedlings in other studies (Grossnickle 1988, Grossnickle and Heikurinen 1989). Evidently, on the days investigated (which were, for the most part, sunny) seedling g_s was not strongly light limited below the aspen

canopy. Response curves of g_s to solar irradiance for most conifers show light saturation occurring at 15–25 percent full sunlight (Livingston and Black 1987, Fleming et al. 1996). Thus, on sunny days, it is quite conceivable that g_s of sheltered seedlings (i.e., in the forest and on the south sides of strips) would not be markedly light limited. On cloudy days, however, this may not be the case (cf. Lieffers et al. 1993). There was little indication that soil temperatures or ψ_{sr} had much influence on g_s on the days sampled.

Patterns of T reflected seasonal changes in A, as well as changes in VPD and g_s . By mid-summer seedlings in the clear-cut and in more exposed strip locations had developed larger A than those in more sheltered locations (Fig. 35). This, together with the higher VPDs found in the more exposed locations, resulted in higher T. The effect of VPD on T is readily evident from comparisons of g_s with E (Fig. 36). Despite comparatively low values of g_s , seedlings on the northern border of the strips had similar values of E as did seedlings from more sheltered locations with higher g_s . High values of T have been associated with higher dry matter production in conifers (Spittlehouse 1985, Livingston and Black 1988), and this appears to be the case here as well (Fig. 37).

For the measurement periods, ψ_{xt} never fell below commonly reported turgor loss points for white spruce (Grossnickle 1989, Colombo and Teng 1992). Severe seedling water stress was not apparent in any of the opening positions at this time. Since $T = g_s VDD A$, where VDD is the vapor density deficit (analogous to VPD, but expressed in density units), it can be shown from Equation 2 that ψ_{xt} is a function of g_s , VPD, A, ψ_{sr} , and R_{sp} . In the forest, the relatively low values of ψ_{xt} likely reflected lower values of ψ_{sr} ; VPD and A were generally both smaller in the forest than in the openings. Higher values of ψ_{xt} on the south sides than on the north sides of the strips

likely reflected lower VPD and A. The lowest values of ψ_{xt} were found just within the north edge of the forest, where VPD was high and ψ_{sr} was low.

Trends in R_{sp} were variable. The relatively high values found in the forest likely reflected low ψ_{sr} . It is not clear why R_{sp} was higher in sheltered locations on one day (August 8—moderate VPD), and lower on another day (August 22—low VPD) in the 18-m-wide strip.

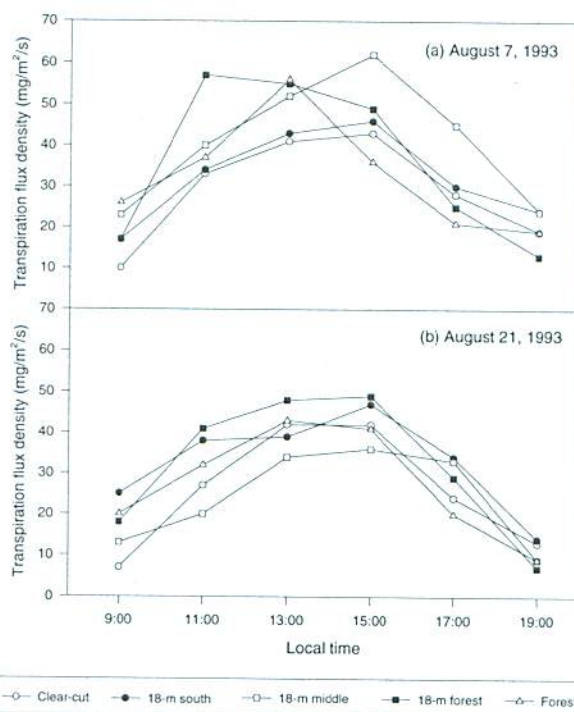


Figure 36. Daytime patterns in white spruce transpiration flux density by seedling location and opening size for: (a) August 7, and (b) August 21. Standard errors of the estimate typically range from 1.0 to 6.0.

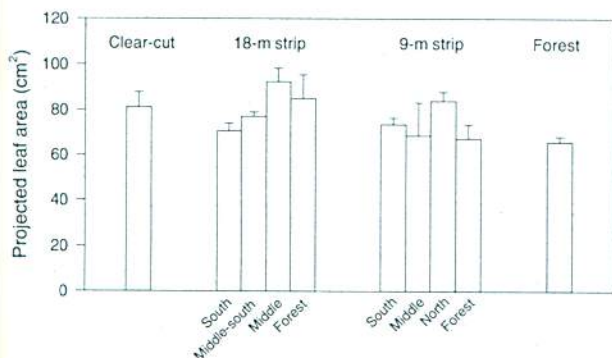


Figure 35. White spruce projected seedling leaf area, August 22, 1993, by seedling location. Vertical lines at the top of the bars indicate standard errors of the estimates.

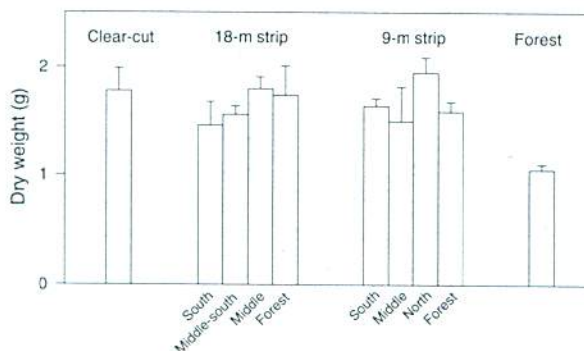


Figure 37. White spruce shoot dry weight, August 22, 1993, by seedling location. Vertical lines at the top of the bars indicate standard errors of the estimates.

The rapid growth of lesser vegetation following harvesting resulted in the seedlings being overtopped during the first growing season. This likely diminished physiological differences related to position in openings before the end of the first growing season. Physiological measurements were not taken on seedlings in the vegetation control treatments, where larger differences among positions probably occurred.

Growth of Planted White Spruce Seedlings

Without vegetation control, position within openings did not have a strong effect on the growth of planted seedlings. Seedling diameters were similar among all environments, and height growth increased only weakly in environments with more light (at a 1.2-m height).

The weak response of planted white spruce to the overstory treatments in treatments with no vegetation control was a consequence of the rapid development of understory vegetation. By the end of the second growing season, white spruce seedlings were enveloped within the lower vegetation layer, isolating them from the microclimatic effects of the overstory treatments.

The strong height and diameter growth response to the herbicide treatment in the vegetation control experiment is consistent with previous findings that white spruce seedling growth is promoted by early and repeated weed control (Wood and von Althen 1993). Growth increases are likely a result of greater light, soil moisture, and soil temperature in the vegetation control treatment.

Controlling the lower vegetation also resulted in a stronger expression of the overstory effects on planted white spruce. In the vegetation control treatment within the strips, white spruce diameter and height growth were greatest in the center of the strips, and not in the north side where there was more light. It is generally considered that white spruce diameter growth increases with light up to full sunlight (Logan 1969, Klinka et al. 1992), so environmental conditions other than light must have been suboptimal in the north half of the strips. Because VPDs were greater and surface water contents were lower at this location, increased seedling water stress is a strong possibility. The first-year measurements of ψ_{xt} and g_s also implicate water stress as a factor in reducing growth in the north half of the strips.

At first glance, the soil moisture measurements do not seem to suggest any serious moisture deficiencies; except for the forest, all 15-cm depth observations were close to or above field capacity

(-33 kPa). According to Day and MacGillivray (1975), however, root growth of white spruce seedlings is highly sensitive to soil moisture; these authors observed little root growth of fall-lifted stock at a soil water potential of -150 kPa, and root growth at -10 kPa substantially exceeded that at -60 kPa. Soil moisture deficiencies were likely greater nearer the soil surface, and placed greater constraints on root growth there.

Growth of white spruce planted in the vegetation control treatment within the strips was also reduced within 5 m of the south edge of the strip compared with the center of the strip. The main limitation to growth here was probably reduced light availability, but lower soil temperature and withdrawal of soil moisture by the adjacent stand may also have played a role.

Second year height growth was greatest in the vegetation control treatment at the center of the 18-m strip, where average growth of 18 to 20 cm yr⁻¹ was attained. This growth rate is substantially greater than most published second year height growth rates for white spruce, and greater than many third-year rates as well (Table 8). Only

Table 8. Early height growth of planted white spruce.

Reference	Stock type	Year	Growth of best treatment (cm/yr)
McMinn (1974)	2+0	2	12
Sutton (1975)	1+2	2	9.8
Mullin and Forcier (1976)	3+0	2	10.8
Mullin and Parker (1976)	3+0	2	9.7
Vyse (1981)	plug	2	5
Vyse (1981)	2+0 and 2+1	2	6
Sutton (1982)		2	~6.0
Burdett et al. (1984)	plug	2	~13
Burdett et al. (1984)	bareroot	2	~5
Wood and Dominy (1985)	3+0	2	~8
Wood and Dominy (1985)	container	2	~10
Brand (1990)	3+0	2	18
Sutton (1975)	1+2	3	24.8
Dobbs (1976)	large 2+1	3	24.0
Dobbs (1976)	plug	3	21.6
Vyse (1981)	plug	3	10
Vyse (1981)	2+0 and 2+1	3	11
Sutton (1982)		3	~17.5
Burdett et al. (1984)	plug	3	~17
Burdett et al. (1984)	bareroot	3	~11
Wood and Dominy (1985)	3+0	3	~12
Wood and Dominy (1985)	container	3	~12
Lautenschlager (1995)	2+2	3	22
Lautenschlager (1995)	paperpot	2	16

one instance of second year height growth rates approaching the 18 to 20 cm yr⁻¹ range appears in the literature (Brand 1990), and this was observed at a site to the south of the boreal forest.

The excellent growth observed in the vegetation control treatment at the center of the 9-m and 18-m strips was the result of the near ideal environment for white spruce: sufficient light, favorable soil temperature, lack of competition for moisture, moderate VPD, and protection from frost. This environment was a product of the shelter provided by stand edges and freedom from competition provided by the vegetation control.

Since white spruce is mid-tolerant of shade, it has been suggested that acceptable height growth of white spruce seedlings can be maintained under partial cover, while the growth of competitors is inhibited. (Lieffers and Stadt 1994). There seems to be little potential for this for aspen-dominated stands on fertile sites. The substantial quantity of light that is transmitted through aspen canopies allows the development of a thriving lower vegetation layer, usually dominated by tall shrubs such as *Corylus cornuta* and *Acer spicatum* Lam. (Rowe 1956). Any increase in light brought about by removal of the overstory results in further development of the lower vegetation. Although this layer can be suppressed somewhat by using very small openings, the total amount of competing vegetation (overstory and understory) likely remains nearly the same. This premise is supported by the similar growth of white spruce seedlings throughout the environments experiment; competition in large openings was similar to that in smaller openings because of the greater development of the lower vegetation. On fertile, aspen-dominated sites, mechanical or chemical treatments are required to control the lower vegetation layer (Lieffers 1995).

Root Pruning

Root pruned trees generally had lesser height growth and smaller diameter than unpruned trees, but these differences were significant only in the forest. The differences in total height in the clear-cut were due largely to the persistence of an initial (1992) difference in total height.

Other workers have obtained similar results, with root pruning having only minor effects on seedling water relations and growth (Sutton 1967, Blake 1983, Simpson 1992). Similarly, although seedling survival in the field decreases at low root growth potential (RGP), growth of surviving seedlings is weakly or not related to RGP (Simpson et al. 1994, Simpson and Vyse 1995).

The failure of a fairly drastic seedling treatment to effect growth reductions suggests that limitations to the early growth of white spruce are less related to seedling condition and more to environmental conditions.

Regeneration of White Spruce from Seed

The low establishment ratios observed in most of the environments indicate that a high effective seeding rate¹ would be required for successful regeneration. This requirement could be satisfied by combining the high rates of natural seedfall occurring in white spruce dominated stands (Kolabinski 1994) with extensive exposure of mineral soil seedbed by site preparation. The median second year establishment ratio of 0.035 seedlings/seed observed in this study, coupled with a natural seedfall of 1 000 000 ha⁻¹ (cf. Waldron 1965, Kolabinski 1994), would yield a second-year density of 35 000 seedling ha⁻¹ on a mineral soil seedbed. Even with further attrition of seedlings, such initial densities should provide for successful regeneration. The summer blade-scarification required for successful natural regeneration of white spruce in strips and shelterwoods in western Canada (Waldron 1966, Kolabinski 1994) would be necessary at this site as well to ensure success. In addition to providing large areas of seedbed, this type of site preparation helps to control competition (Waldron 1966).

The small scalps used in this experiment would not provide sufficient seedbed for satisfactory natural regeneration of white spruce, unless they were spaced very closely. Also, the small scalps, by acting as collectors, may have exacerbated the smothering of seedlings by broad-leaved litter (cf. Waldron 1966).

In this study, establishment of white spruce from seed was best in the clear-cut and poorest in the forest, with no differences apparent among the rest of the openings. Seedling establishment in the clear-cut may have been favored because of less broad-leaved litter and more light. With more intensive site preparation, which removes the lower layer of broad-leaved competition, initial white spruce establishment is better under a canopy, but subsequent growth and survival of seedlings decreases with increasing canopy cover (Waldron 1966).

Given sufficient white spruce seed trees and appropriate site preparation, natural regeneration of white spruce is feasible using clear-cut strips, uniform shelterwood, or single seed trees, but slow early growth should be expected. Average heights ranging from 0.8 to 2.8 m at 22 to 25 years of age have been attained with these systems (Kolabinski 1994, Waldron and Kolabinski 1994).

¹ Effective seeding rate = actual seeding rate x receptive seedbed fraction (Groot and Adams 1994).

Aspen Regeneration

First year aspen densities of more than 100 000 stems ha^{-1} were observed in this study, corresponding with the high initial densities after clear-cutting noted in other studies (Bella 1986, Doucet 1989, Peterson and Peterson 1992). Considerable aspen regeneration occurred even in relatively small openings (9-m-wide strip and 18-m circle). This agrees with observations of substantial aspen regeneration obtained under relatively dense residual stands (Hittenrauch 1976, Walters et al. 1982, Doucet 1989), but contradicts the more generally held view that even small amounts of residual aspen strongly reduce aspen regeneration (Jones 1976, Perala 1977).

Greater aspen regeneration occurred in the north half of openings than in the south half. Higher soil temperatures in these positions was likely a factor in inducing more suckering (Maini and Horton 1966).

SUMMARY

The variation in solar radiation, air temperature, and soil temperature among and within 9-m- and 18-m-wide strips and circular openings was almost as great as the variation between a clear-cut and an intact forest.

The soil was consistently drier under the intact forest than within the openings, and control of the lower vegetation layer generally resulted in moister soil.

The lower vegetation layer developed rapidly following harvesting, and after two growing seasons the *LAI* of the lower vegetation in the clear-cut and in the center of the 18-m strip was similar to the combined *LAI* of the overstory and lower vegetation in the forest.

Without vegetation control, white spruce seedling growth did not vary greatly among environments, suggesting that the combined competition of the overstory and lower vegetation layer was similar among all overstory treatments.

Within 9-m- and 18-m-wide strips, vegetation control strongly increased the early growth of planted white spruce.

Growth of planted white spruce was greatest in the vegetation control treatment near the center of the 18-m-wide strip, where radiation, air and soil temperature, and soil moisture conditions were most beneficial.

Establishment of white spruce from seed was low because of competition from broad-leaved vegetation, but not so low as to preclude the possibility of successful natural regeneration given adequate quantities of seed and seedbed.

MANAGEMENT IMPLICATIONS

Using an aspen overstory to suppress understory vegetation and to favor the growth of planted white spruce growth does not appear to be feasible on fertile sites. The combined competition provided by the overstory and lower vegetation layer is relatively independent of overstory cover on such sites. Significant suppression of trembling aspen suckering can be achieved only with very small openings (e.g., 9-m-diameter circular openings).

On fertile sites, early vegetation control and provision of shelter should generally result in rapid early growth of planted white spruce. This combination provides protection from frost; abundant soil moisture; and favorable light, humidity, and soil temperature regimes. Further work is required to delineate the optimum sizes and shapes of openings. It is evident, however, that shelter effects are associated with rather small openings (roughly one tree height across), since the microclimate rapidly approaches that of a clear-cut as openings increase in size.

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