

Microclimatic and spruce growth gradients adjacent to young aspen stands

Mihai F. Voicu, Philip G. Comeau *

Centre for Enhanced Forest Management, Department of Renewable Resources, University of Alberta,
442 Earth Sciences Building, Edmonton, Alta., Canada T6G 2E3

Received 13 May 2005; received in revised form 22 September 2005; accepted 26 September 2005

Abstract

Effective utilization of a patch or cluster approach to growing aspen-white spruce mixtures in the boreal forest requires an understanding of how the faster growing aspen patches influence microclimate and spruce growth in adjacent spruce patches. In this paper we examine, how young (11–13 year old) aspen (*Populus tremuloides* Michx) patches influence microclimatic conditions in adjacent openings and how these are reflected in the growth of white spruce (*Picea glauca* [Moench] Voss) on three boreal mixedwood sites in west-central Alberta, Canada. Light levels increased continuously across the aspen stand boundary and reached maximum levels within the opening, while soil moisture was highest near the edge of the opening and then decreased with distance into the aspen stand or into the adjacent opening north of the aspen stand. Light levels were reduced over a greater distance when moving north from aspen stand edges compared to openings located south of the young aspen. These young aspen stands provided growing season frost protection within one tree length from the edge. The growth of white spruce was positively related to initial crown size and either light levels or distance from the edge. Stem volume growth was best predicted by initial tree size and the light levels at the midcrown of seedlings.

© 2005 Elsevier B.V. All rights reserved.

Keywords: White spruce; *Picea glauca*; Aspen; *Populus tremuloides*; Mixedwoods; Microclimate; Stand edges; Light; Air temperature; Soil moisture

1. Introduction

Establishment and tending of white spruce in patches, or cluster planting (Sutton, 1974), is a potentially cost-effective option for growing white spruce in mixture with trembling aspen in boreal forests. However, there is concern that the faster growing aspen surrounding spruce patches may cast sufficient shade to reduce spruce growth. In addition, there is interest in the degree to which such an arrangement can provide for beneficial nurse crop effects from the aspen. Gradients in light, soil moisture, soil temperature and air temperature have been observed adjacent to stand edges in other areas.

Several studies (Emmingham and Waring, 1975; Geiger, 1980; Kapos, 1989; Matlack, 1993) show dramatic changes in light levels as one moves from inside a stand into adjacent openings. Light in forest openings varies with opening size, height of boundary trees, and height and density of the

vegetation in the patch (Belsky and Canham, 1994). Light levels in an Engelmann spruce (*Picea engelmannii* Parry ex Engelm) dominated stand increased linearly with distance into an opening, reaching a maximum at one tree length (Huggard and Vyse, 2002). In mature forests of the northeastern U.S., light gradients extended into adjacent fields for 15–20 m (Cadenasso et al., 1997).

Within openings, Matlack (1993) found that north-facing edges of a mature oak–beech forest in eastern U.S. had lower light levels than south-facing edges. In boreal forests the south edge of an opening receives diffuse light from the northern hemisphere of the sky, as well as some light transmitted through the stand, while the northern edge of an opening (if the opening is of sufficient size) will receive both diffuse and direct radiation (Canham et al., 1990).

For a north facing Engelmann spruce stand, the highest levels of soil moisture were found within one-half tree length of the forest edge on both sides of the border (Huggard and Vyse, 2002). Matlack (1993) found that north-facing edges had higher soil moisture than south-facing edges in a mature oak–beech forest in eastern U.S. Soil moisture was also three times greater

* Corresponding author. Tel.: +780 492 1879; fax: +780 492 1767.

E-mail address: phil.comeau@ualberta.ca (P.G. Comeau).

at northwest-facing edges than within the interior of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest (Chen et al., 1993).

Low air temperatures during the growing season can cause frost damage to conifer seedlings (Spittlehouse and Stathers, 1990; Orcutt and Nilsen, 1996; Grossnickle, 2000). Residual aspen and taller young aspen can alleviate the risk of frost damage to planted white spruce seedlings within openings and increase seedling survival (Orlander, 1993; Groot and Carlson, 1996; DeLong, 2000; Langvall and Orlander, 2001; Pritchard and Comeau, 2004). By shading and reducing the exposure of seedlings to high intensity radiation during the day following a cold night, shelter trees reduce frost damage (Lundmark and Hallgren, 1987). Frost damage frequency has also been observed to increase as the density of the sheltering stand decreases (Orlander and Karlson, 2000; Pritchard and Comeau, 2004).

A small number of studies provide information on tree growth adjacent to stand edges. Hansen et al. (1993) showed that significant differences in natural regeneration, seedling establishment and growth of Douglas-fir seedlings were related to distance into the opening from a forest edge. They found reduced growth of Douglas-fir seedlings 20 m north of a 45 m tall mature stand. Similarly, Burton (2002) found that the density of conifer natural regeneration decreased with distance from the forest edge, and was higher on the north-facing than south-facing edges. Emmingham and Waring (1975) showed that Douglas-fir leader length reached a maximum between 4 and 21 m from the edge of a 20–25 m tall stand. Groot et al. (1997) found that growth of white spruce was reduced within 5 m of the north facing edge of a 19 m tall mixedwood stand when compared to the center of the 9 and 18 m wide strips. In another study, maximum conifer heights were found at the center of the opening (York et al., 2003). However, Burton (2002) showed no difference in spruce seedling growth due to proximity to the stand edge. Similarly, Coates (2000) found little to no difference between spruce seedlings grown at south- and north-facing edges but reports that conifer seedling growth 5 years after planting was related to gap size. Growth rapidly increased from small gaps to 1000–2000 m² gaps, but from this threshold to 5000 m², growth leveled-off (Coates, 2000). York et al. (2003) found greater conifer seedling height on south-facing than on north-facing edges for openings smaller than 1 ha.

A number of studies also indicate that the size of the tree or the tree crown influences growth rates (Hatch et al., 1975; Givnish, 1988; Cole and Lorimer, 1994; Biging and Dobbertin, 1995; Choi et al., 2001; Claveau et al., 2002; Comeau et al., 2003; Webster and Lorimer, 2003; Pritchard, 2003) since size reflects the leaf area of the tree.

Despite a broad general knowledge of edge influences in older stands our knowledge of the effects of young aspen on light, soil moisture, soil temperature and air temperature in adjacent openings and their effect on growth of white spruce within the tended patches in boreal forest communities is limited. A knowledge of the distance over which young aspen influences microclimatic conditions is of potential value in the development of management practices designed to provide optimal conditions for the growth of white spruce. This paper

presents results from a study designed to examine gradients of light, air temperature and soil moisture adjacent to the edges of young aspen stands in Alberta and their effect on the growth of white spruce. This study was designed to examine the effects of distance and direction from adjacent aspen stand edges on: (1) light levels (in terms of transmittance); (2) soil moisture; (3) frequency of summer frost events; (4) air temperature; (5) soil temperature. In addition we examine how, growth of white spruce (in terms of diameter, height, stem volume increment, and height allocation ratio) is related to light levels (or distance from the adjacent aspen stand, and initial tree size (in terms of initial crown surface area or initial crown volume)).

2. Materials and methods

2.1. Study area and experimental design

Field studies were conducted at selected Long-Term Study (LTS) field installations established by the Western Boreal Growth and Yield (WESBOGY) Association (Titus and Wang, 2000). The study was carried out during 2003 at three installations located: (a) south of Grande Prairie, Alberta (54°55'N, 118°55'W); (b) east of Peace River, Alberta (Hines Creek, 56°20'N, 118°30'W); (c) north of Peace River, Alberta (Manning, 56°41'N, 117°72'W). At each of these three locations we used four 30 m × 30 m plots where all aspen had been removed 5 or 6 years after planting of white spruce. These plots were located adjacent to natural or spaced aspen (1500, 4000 sph). Spaced aspen plots measured 30 m × 30 m and natural stands extended at least 30 m from the white spruce plots. For the purposes of our study, the two planting densities at which white spruce had been established (500 or 1000 sph) are assumed to respond in a similar manner and are considered here as replications, providing a total of four plots at each location. In 2003 aspen and white spruce saplings were 11–13 years old at each of the three WESBOGY locations, with white spruce maximum height between 1.8 and 3.7 m [white spruce height ranged between 0.3 and 1.8 m (Grande Prairie) and 0.8–3.7 m (Hines Creek and Manning)]. Aspen top height was between 5.0 and 7.0 m.

Study sites were all located in the Central Mixedwoods Ecological Subregion and occur on mesic low-bush cranberry (BM-d) ecosites (Beckingham and Archibald, 1996). Precipitation normals and 2003 monthly averages (rainfall from June to September) for the Hines Creek installation are detailed in Table 1. Soils at all installations were orthic gray luvisols, on morainal parental materials, generally with less than 10% coarse fragments, and clay to clay-loam texture. Slopes at all installations were less than 5%.

2.2. Seedling measurements

For this study, two transects were established in each plot: one going north to south, and the other going east to west through the center of each plot. All spruce seedlings located within 2.5 m on both sides of the transect were selected for measurement of root collar diameter, height, height to crown

Table 1
Precipitation data for Hines Creek installation

Precipitation (rainfall)	Monthly total			
	June	July	August	September
Normals (mm)	76.6	78.8	60.4	35.9
2003 (mm)	42.1	27.5	66.4	17.7

Data are shown for the Fairview weather station (latitude 56°4'N; longitude 118°22'W).

base, and crown radius in each of four cardinal directions. Spruce seedlings located near plot center were counted twice, once for each transect, and they were analyzed separately for each transect. A numbered metal tag was attached to each measured spruce seedling, and the location of each seedling relative to the center of the plot mapped. Distance from the center of the plot to the edge of adjacent aspen (stem line) was measured. Transects were oriented to run perpendicular to plot boundaries. Consequently, transect orientation ranges from 355° to 27° and was another factor used in determining the position of the spruce seedlings in relation to the aspen edge.

2.3. Light measurements

To estimate growing season light (diffuse noninterceptance), LAI-2000 (LI-COR Inc., Lincoln, NB) measurements were taken at the top of the white spruce seedlings and at midcrown height. A view restrictor (180°) was used to block direct radiation from the sun at the time of each measurement. Measurements were taken with the sensor pointing west early in the morning (8–10 a.m.) and east late in the afternoon (5–7 p.m.) with sensors leveled for each reading using bubble levels attached to the optical sensor support. Sensors were positioned just outside of the canopy of the subject tree to avoid having the subject tree influence measurements. From July 7 to July 27, 2003 two LAI-2000 units were used simultaneously (remote mode) (LI-COR Inc., 1992): one mounted on a tripod in the open automatically logging readings every 30 s, and the other used to take measurements at each white spruce seedling within the plots. The two sensors were cross calibrated and paired readings were taken at the tripod to ensure consistency.

Diffuse noninterceptance (DIFN), which is an unbiased estimate of average growing season transmittance (Comeau et al., 1998; Gendron et al., 1998; Lieffers et al., 1999; Comeau, 2000), was determined for each spruce tree using C2000 software (Licor Inc., Lincoln, NEB), with the average of the east and west-facing values used for analysis. A previous study (Comeau et al., 1998) indicated that the outer ring (i.e. ring 5 equivalent to a sky view of 62.3–74.1° from vertical) may give poor estimates of growing season transmittance. Therefore, ring 5 was masked and DIFN values were determined using only rings 1–4 (equivalent to a sky view of 58.1° from vertical).

Between July 7 and 27, 2003, light levels were also measured under the adjacent aspen stand using LAI-2000 plant canopy analyzers. Measurements were taken at points located on a 3 m × 3 m grid starting at the edge of the aspen stand. The grid was established as a continuation of the north-south and

east-west transects along which the spruce was measured. The measurements were taken above the herbaceous and shrubby vegetation at 1.0 m height.

2.4. Soil moisture

Soil moisture was measured at one study site (Hines Creek) using CS616 water content reflectometers [Campbell Scientific (Canada) Corp., Edmonton]. The soil moisture sensors were located at –2, –1, 1, 2, 3, 5, and 7 m north from the south edge (i.e. north-facing edge of the adjacent aspen stand) of the plot (with the stand boundary defined by the location of aspen stems). Sensors were inserted vertically to give an indication of the water content in the upper 30 cm of soil. They were connected to a CR-10X [Campbell Scientific (Canada) Corp., Edmonton] datalogger. Soil volumetric water content (m^3/m^3) was measured hourly and recorded during the period between June 19 and October 7, 2003. The number of hours with VWC below 25% in 2003 was used as an indicator of the duration of soil moisture stress for white spruce. A threshold of 25% was chosen because in 2003 soil moisture rarely reached values below the 15% value (300 kPa) suggested as the threshold at which white spruce growth is seriously impeded (Grossnickle, 2000). However, growth reductions are expected to begin to occur when values are below 25% (or approximately 100 kPa) (Grossnickle, 2000).

To account for possible influences of variation in the leaf area index (LAI) of understory vegetation on soil moisture, LAI-2000 measurements were taken on July 10, 2003 directly above each soil moisture sensor at ground level and above the herbaceous vegetation. Herbaceous (grass, forb and shrub), aspen, and total vegetation LAI were calculated using C2000 software (LI-COR Inc., Lincoln, NEB). Total LAI was estimated using the ground level LAI-2000 measurements, aspen LAI was estimated using the measurements taken above the herbaceous layer, and herbaceous LAI was calculated as the difference between the two. For these LAI measurements rings 4 and 5 were masked and LAI was determined for rings 1–3 only (equivalent to a sky view of 43.4° from vertical). This was done in order to best characterize values at the sample point by minimizing the potential influence of the adjacent stand on the LAI measurements (especially those at ground level).

2.5. Air and soil temperature

To measure air temperature, custom built unshielded fine-wire chromel-constantan thermocouples were installed in the spring of 2003 at 1.0 m height at 13 locations (–25, –17.5, –15, –12.5, –10, –7.5, 0, 7.5, 10, 12.5, 15, 17.5, and 25 m north of the: plot center) along the north-south transect in one plot at each of two locations (Grande Prairie and Hines Creek). To measure soil temperature, custom built shielded fire-wire chromel-constantan thermocouples were installed at 20 cm depth at nine of the above 13 locations (–25, –17.5, –15, –7.5, 0, 7.5, 15, 17.5, and 25 m north of the plot center). Temperature sensors were connected to two AM 16/32-XT multiplexers [Campbell Scientific (Canada) Corp., Edmonton] which were connected to a CR-10X [Campbell Scientific

(Canada) Corp., Edmonton] datalogger. Measurements ($^{\circ}\text{C}$) were taken every 10 min, and hourly averages were recorded. Air temperature was measured continuously from May 9 to October 4, 2003.

2.6. Data preparation

The following variables were calculated in preparation for analysis:

- Number of hours with temperature under 0°C was calculated as sum of hours with temperatures under the 0°C threshold from June 1 to August 31, 2003.
- Number of hours with soil moisture under 25% volumetric water content ($\text{VWC} < 25\%$) was calculated as the sum of hours with soil moisture under the 25% threshold from June 19 to September 30, 2003.
- Air (GDH) and soil (GDH S20) growing degree hours calculated as: $\text{GDH}/\text{GDH S20} = \sum_{\text{May}}^{\text{Sept}} (\text{Havg} - 5^{\circ})$, where Havg is the hourly average air/soil temperature, 5° represents the base air temperature at which the GDH/GDH S20 was calculated. When $(\text{Havg} - 5^{\circ}) < 0$, it was forced to 0. Calculations were based on the period between May 9 and September 30, 2003.
- To standardize GDH for the two sites (Grande Prairie and Hines Creek) delta growing degree hours (ΔGDH) were calculated as: $\Delta\text{GDH} = \text{GDHi} - \text{GDHo}$, where GDHi is the growing degree hours calculated for each air temperature sensor, GDHo the minimum value calculated along each transect (for Grande Prairie GDHo = 11 500; for Hines Creek GDHo = 14 300).
- To standardize GDH S20 for the two sites (Grande Prairie and Hines Creek) delta growing degree hours ($\Delta\text{GDH S20}$) were calculated as: $\Delta\text{GDH S20} = \text{GDH S20i} - \text{GDH S20o}$, where GDH S20i is the growing degree hours calculated for each soil temperature sensor at 20 cm depth. GDH S20o the minimum value calculated along each transect (for Grande Prairie: GDH S20o = 14 700 for south-facing and GDH S20o = 15 000 for north facing; for Hines Creek: GDH S20o = 13 300 for south-facing and GDH S20 = 10 300 for north-facing).
- Stem volume (SV), assuming the volume of a cylinder, as: $\text{SV} = \pi R^2 h$, where R is the root collar radius (i.e. 1/2 of root collar diameter), h the white spruce height.
- Stem volume increment (SVI) as difference between stem volume at the end of the 2003 growing season (SV_{Oct}) and stem volume at the beginning of the 2003 growing season (SV_{May}).
- Initial crown surface area (ICSA), assuming the lateral surface of a cone as: $\text{ICSA} = \pi R \sqrt{R^2 + (h_t - h_c)^2}$, where R is the average crown radius, h_t the white spruce height, h_c the height to crown base.
- Initial crown volume (ICV), assuming the volume of a cone as: $\text{ICV} = \pi R^2 (h_t - h_c)/3$, where R is the average crown radius, h_t the white spruce height, h_c the height to crown base.
- Diameter increment as: $\text{DI} = D_{\text{Oct}} - D_{\text{May}}$, where D_{Oct} is the root collar diameter at the end of the 2003 growing season,

D_{May} the root collar diameter at the beginning of the 2003 growing season.

- Height increment as $\text{HI} = H_{\text{Oct}} - H_{\text{May}}$, where H_{Oct} is the height at the end of the 2003 growing season, H_{May} the height at the beginning of the 2003 growing season.
- Height allocation ratio as: $\text{HAR} = \text{HI}/\text{SVI}$ (Comeau et al., 2003).
- Light levels at the top/midcrown of the white spruce seedlings (DFN-T, DFN-M) as an average of the east and west-facing values using C2000 software (LI-COR Inc., Lincoln, NEB).
- Proportional distance (PD) as distance from the aspen stand edge divided by the difference between adjacent stand height and height of the light measurement (i.e. the number of tree lengths from the edge of aspen stands).

2.7. Data analysis

Regression analysis was used to evaluate the relationships between DFN and PD. Based on the distribution of the data points and previous studies (Comeau and Bedord, 2005), we selected the Gompertz model to describe the relationship between transmittance and PD for each of the four cardinal directions. The equation takes the form:

$$Y = a e^{-e^{-((X-c)/b)}}, \quad (1)$$

where Y is the transmittance, X the proportional distance, a the asymptote or the potential maximum of the transmittance, and b and c are the parameters governing how transmittance approaches its potential maximum.

Based on data point distribution, a modified version of the Gompertz function was used to describe the relationship between air/soil temperature and distance from the adjacent stand. The second equation takes the form:

$$Y = Y_0 + a e^{-e^{-((X-e)/b)}}, \quad (2)$$

where Y is the air/soil temperature (in terms of number of days with temperatures below 0°C or delta growing degree hours), X the proportional distance, Y_0 the minimum air temperature, a the asymptote or the potential maximum of air temperature, and b and c are the parameters governing how air/soil temperature approaches its potential maximum.

Several other sigmoidal models were initially tested, including Weibull, Hill, and Chapman. However, based on these analyses and resulting R^2_{adj} , RMSE, parameter significance, and residual distribution, the Gompertz equation was considered to provide a better fit to these data. A polynomial model was used to evaluate the relationship between soil moisture and distance from the adjacent stand and a multiple linear regression equation was used to examine effects of aspen LAI and herbaceous LAI on soil moisture. Selection of these models was based on a comparison of the fit of these and other models to the data.

Multiple nonlinear regression was used to evaluate the relationships between growth of white spruce seedlings (SVI, DI, HI, and HAR) and light levels (DFN-T, DFN-M) or

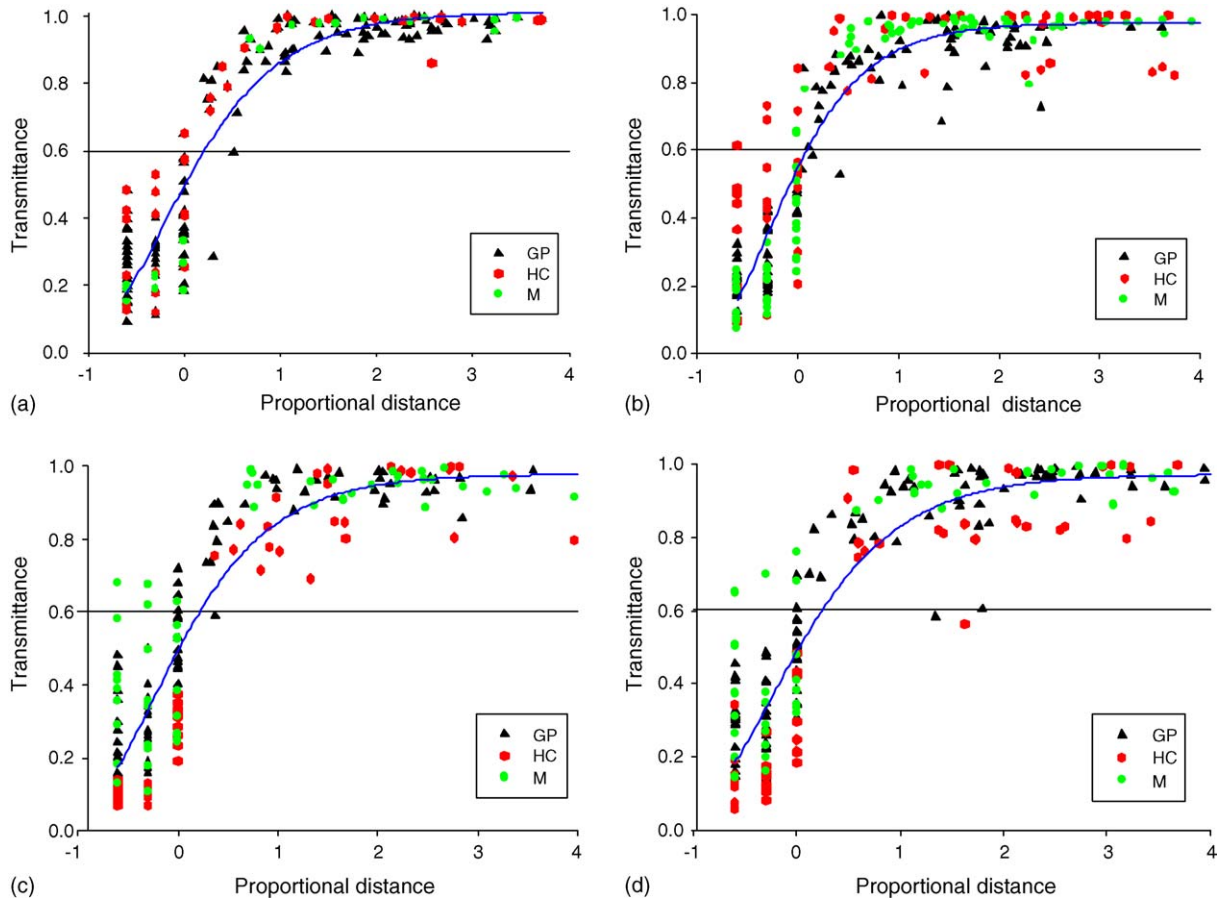


Fig. 1. Relationship between transmittance and proportional distance for north (a), south (b), east (c), and west-facing (d) edges. The lines are described by the equation: $Y = a e^{-e^{-(X-c)/b}}$, with Y = transmittance, X = proportional distance, GP = Grande Prairie, HC = Hires Creek, M = Manning. Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand. Statistical information for these models is provided in Table 2.

distance from the stand edge (PD) and initial size of white spruce seedlings (ICSA, ICV). Various models were tested using SVI, DI HI, and HAR as dependent variables and combinations of initial crown size (ICSA or ICV) with DFN-T, DIFN-M or PD as independent variables. Scatterplots of residuals were examined visually to assess the fit for each equation in combination with evaluation of RMSE and coefficient of determination.

Initial analysis used the indicator (dummy) variable approach (Draper and Smith, 1981; Ott, 1997) to compare coefficients for regressions fitted to data from the different sites or to data from the different cardinal directions. This technique was used to determine whether the sites or the cardinal directions could be pooled and analyzed as a single relationship. Analyses were completed using Version 8.2 of SAS Statistical Software (SAS Institute, Cary, NC). Graphs were prepared using SigmaPlot, Version 8.0 (SPSS Inc.).

3. Results and discussion

3.1. Light levels

Relationships between growing season transmittance (DIFN) and proportional distance and edge orientation were examined. For each direction (i.e. N, S, E, and W-facing) the

indicator variable approach indicated there was no difference among data from the three different locations ($p > 0.05$). Therefore, data were pooled together and analyzed as a single relationship for each direction. However, the indicator variable tests showed there were differences among directions ($p < 0.05$). Therefore the results are presented separately for each cardinal direction (Fig. 1, Table 2).

Light is crucial for photosynthesis and is one of the most important factors influencing the growth of understory plants (Canham et al., 1990; Pacala et al., 1994; Chen and Klinka, 1997; Lieffers et al., 1999; Greene et al., 2002; MacDonald and Thompson, 2003). Competition for light within young hardwood-conifer stands is also recognized as being of decisive

Table 2

Summary of the coefficients from least square fitting of the Gompertz equation (1) for the relationship between light levels and distance from the stand edge

Orientation	a	b	c	n	R^2_{adj}	p -values model
N-facing	0.9987	0.6488	-0.2334	162	0.88	<0.0001
S-facing	0.9768	0.5226	-0.2848	245	0.86	<0.0001
E-facing	0.9792	0.6457	-0.2438	194	0.83	<0.0001
W-facing	0.9731	0.6789	-0.2537	214	0.84	<0.0001

Y = transmittance; X = proportional distance; a – c = equation coefficients.

significance for growth and survival of conifer seedlings (Coates and Burton, 1999). Maximum photosynthesis of white spruce shoots occurs at between 40 and 60% of full light levels (Man and Lieffers, 1997). However, Lieffers and Stadt (1994) found that white spruce require 8% of full sunlight or higher in order to survive.

Light transmittance was strongly related to distance from the adjacent young aspen stand for each of the four cardinal directions. Light increased rapidly across the aspen edge into the opening reaching a maximum at 1.5 tree lengths (Fig. 1). This is consistent with the findings of Emmingham and Waring (1975) that light levels increased rapidly moving across a Douglas-fir edge into the adjacent opening, reaching maximum levels at 1 tree length. Similarly, light levels in an Engelmann spruce dominated stand were shown to increase smoothly into the opening, reaching a maximum at one tree length (Huggard and Vyse, 2002).

Our results also show that the influence of north-facing aspen edges extends over a greater distance into adjacent openings compared to the south-facing edges. Transmittance reached 60% of full sunlight closer to the edge for the aspen stand facing south than for the aspen stand facing north (Fig. 1a and b). This is consistent with previous studies that have shown the shade cast by stand edges is influenced by stand height and orientation of the edge, with more shading near north-facing edges and less shading near south-facing edges (Berry, 1964; Groot and Carlson, 1996). However, the potential negative impact of shade cast by the faster growing aspen into adjacent patches of spruce does not extend very far from the aspen edge (i.e. under 0.3 tree lengths from the edge). As indicated by the reference line for difference of 0.6 (Fig. 1), almost all measurement points within the openings have light levels above this value.

3.2. Soil moisture

The number of hours with volumetric water content under 25% decreased starting 0.4 tree lengths into the aspen stand and reached minimum levels at approximately 0.4 tree lengths into the opening. The number of hours with volumetric water content (VWC) under 25% then increased again with greater distance from the aspen edge (Fig. 2). While having results from only a single transect limits the extent to which general inferences can be made, the results provide useful information on soil moisture gradients adjacent to the stand edge at this one site.

High moisture stress recorded inside the aspen stand is probably due to greater evapotranspiration and rainfall interception resulting in drier soil inside the forest than within the opening (Chen et al., 1993; Groot et al., 1997). The area right at the edge, but inside the forest, receives more light from the side, which in combination with increased wind penetration, may result in increased evapotranspiration and consequently reductions in soil moisture (Ranney et al., 1981; Canham et al., 1990; Giambelluca et al., 2003). The influence of tree crowns extends further than their vertically projected margins, resulting in reduced cover and LAI of understory vegetation adjacent to the edge due to shade, litterfall, and

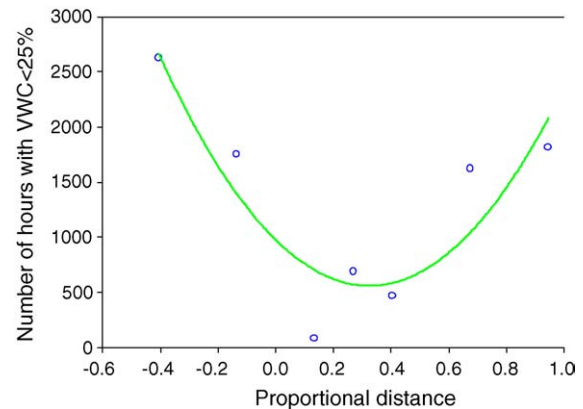


Fig. 2. Observed relationship between number of hours with volumetric water content under 25% (VWC < 25) over the growing season (June 19–September 30) of 2003 and proportional distance, at Hines Creek. The curve is described by the equation: $Y = 975.93 - 2558.08X - 3939.42X^2$, with $R^2_{adj} = 0.71$, $p = 9.9375$, $n = 7$, $Y = \text{VWC} < 25\%$, $X = \text{proportional distance}$. Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand. The height of the adjacent aspen stand is 7 m.

belowground competition (Runkle, 1984; Canham et al., 1990; Williams-Linera, 1990; Matlack, 1994; Oliver and Larson, 1996).

Soil moisture stress was lowest within the opening at the edge of the adjacent aspen stand (Fig. 2). One possibility is that the north-facing edge cast shade for longer periods of time, resulting in increased snow accumulation and extended persistence of the snowpack during the spring close to the stand (Huggard and Vyse, 2002). Water use by vegetation is another factor which may contribute to the observed variation in soil moisture. As leaf area index increases with changes in vegetation type and abundance, an increase in water use is expected (Johns and Lazenby, 1973). Total leaf area index (LAI-T) and aspen leaf area index (LAI-As) decreased moving from the aspen stand into the opening, while the herbaceous vegetation leaf area index (LAI-H) showed a steady increase with distance from the edge (Fig. 3). Our results show that soil moisture stress increases as either herbaceous LAI or aspen LAI increases (Fig. 4). Results from this study also suggest that the herbaceous layer may contribute more per unit LAI (i.e. the slope is larger) to the soil moisture stress than aspen. In addition, differences in root densities inside the forest and in clearings could contribute to differences in soil moisture.

Differences in soil moisture are often reflected in vegetation changes. Soil moisture is an important factor affecting vegetation growth (Rowe, 1956). Root growth of white spruce seedlings is highly sensitive to soil moisture (Day and MacGillivray, 1975), which influences white spruce seedling establishment. Therefore, when soil moisture levels are below threshold levels (25% in this case) they may have a negative influence on white spruce seedling growth. The duration of the soil water stress (defined here as the number of days with soil moisture below 25%) appears to be reduced within openings up to approximately 0.4 tree lengths (based on current height of surrounding aspen) from a north-facing edge. At distances

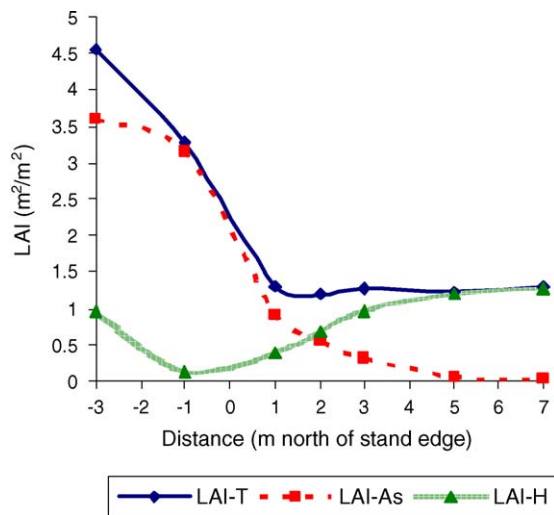


Fig. 3. Patterns of aspen and understory leaf area index (LAI) measured along a transect across the boundary between the young aspen and the adjacent opening. LAI-T = total LAI, LAI-As = aspen LAI, LAI-H = herbaceous vegetation LAI. Negative numbers on x-axis indicate measurement locations inside the aspen stand.

greater than 0.4 tree lengths, increasing leaf area index of the understory vegetation, together with other factors, may result in increased moisture stress. These results suggest that control of understory vegetation may be necessary to reduce competition for water in large openings when reductions in soil moisture are sufficient to limit tree growth.

Further studies with additional replication and test for effects of orientation of the edge are needed. These should be designed to isolate the influence of understory vegetation (by including both a removal treatment and a control) and other factors on soil moisture levels and associated stress to seedlings.

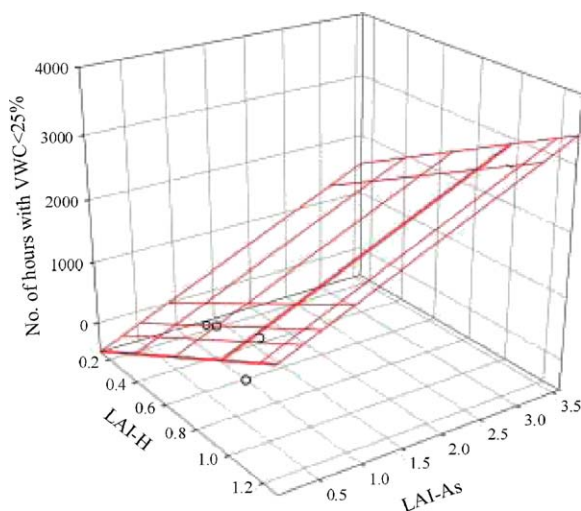


Fig. 4. Relationship between number of hours with volumetric water content under 25% (VWC < 25%) and aspen leaf area index (LAI-As), and herbaceous vegetation leaf area index (LAI-H) for the growing season of 2003, at Hines Creek. The surface is described by the equation: $VWC < 25 = -728.4 + 563.38 \text{ LAI-As} + 1664.05 \text{ LAI-H}$, with $R^2_{\text{adj}} = 0.67$, $p = 0.049$, $n = 7$.

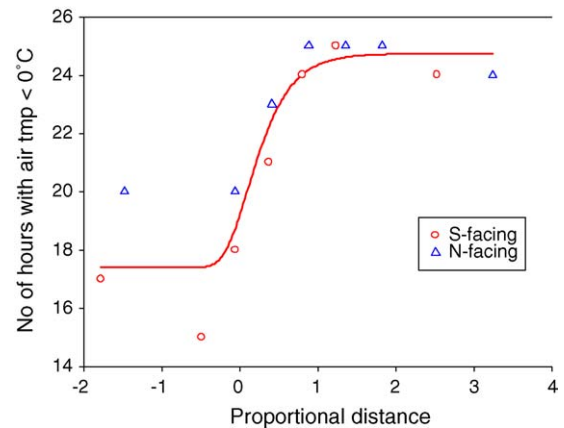


Fig. 5. Relationship between number of hours with temperatures below 0 °C and proportional distance for the growing season (June 1–August 31) of 2003 at Grande Prairie. The line is described by the equation: $Y = 17.41 + 7.33 e^{-e^{((X-0.11)/-0.31)}}$. Y = number of hours with temperatures under 0 °C, X = proportional distance, $R^2_{\text{adj}} = 0.83$, $p < 0.0001$, $n = 14$. Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand.

3.3. Air and soil temperature

The relationship between number of hours with air temperature below 0 °C between June 1 and August 31 of 2003, and proportional distance is presented in Fig. 5. The relationship is presented for one site (Grande Prairie) where both south and north-facing adjacent aspen edges consisted of natural aspen. There was no difference between data from north and south-facing edges ($p > 0.05$). Therefore data were analyzed after being pooled together in a single relationship. The frequency of summer frost increased rapidly with distance from the edge of an aspen stand into the adjacent opening. These results suggest that some degree of frost protection occurs within one tree length from the edge of the 5–7 m tall aspen stands. However, these effects may change with stand age since frost protection increases with height (which will increase with age) and stand density (which will decline with age) (Groot and Carlson, 1996; Groot et al., 1997; Pritchard, 2003). For the other site where air temperature was monitored (Hines Creek) (data not shown) there were no air temperatures below 0 °C between June 1 and August 31 of 2003.

To illustrate the dynamics of temperature changes, hourly data (i.e. hourly average temperatures) for the temperature transect are presented in Fig. 6 for the morning of August 24, 2003. The same temporal trends can be observed for all sensors regardless of their position within the aspen or opening (i.e. temperatures decrease from 2 to 7 a.m., and then start to increase) and the amplitude in temperature changes during the night of the frost event is approximately the same for all sensors regardless of their position. For each hour, air temperatures decreases moving from inside the aspen stand into the opening, reaching a minimum between 1.0 and 1.5 tree lengths from the edge. Observed increases in minimum temperature at the center of the opening (2.5 tree lengths from the edge) when compared

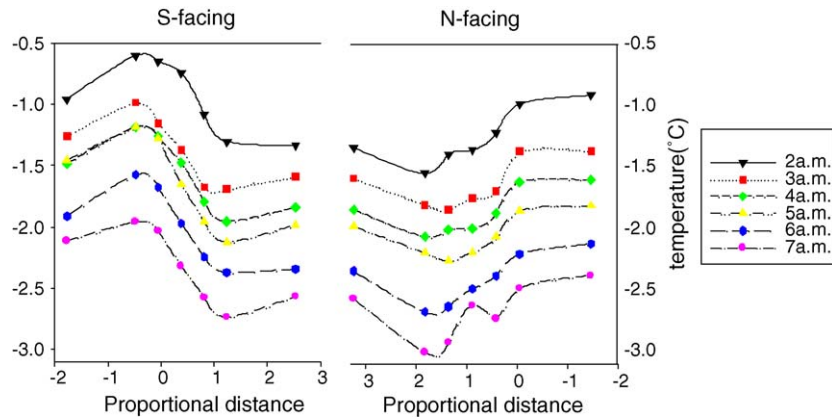


Fig. 6. Air temperature (hourly average) vs. proportional distance for two directions at Grande Prairie, during the night of a frost event (August 24, 2003). Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand.

to values at 1 tree length might be due to higher rates of air movement and mixing at this distance resulting in higher air temperature (Stathers, 1989; Grossnickle, 2000). During the night of a frost event, aspen can provide increased frost protection within 1 tree length of the aspen edge. However, since air temperature inside the aspen stands decreases at almost the same rate as within the opening the aspen stand (at least at this age) may provide only limited reduction in frost damage to spruce when an extreme frost event of extended duration occurs.

The relationship between growing degree hours (hours with mean air temperature over 5 °C) and proportional distance from the adjacent aspen stand is shown in Fig. 7. Testing using the indicator variable principle indicated no difference between data from north-facing and south-facing edges ($p > 0.05$). Therefore, data were pooled together in a single relationship. The amount of accumulated heat increases starting 0.5 tree lengths inside the aspen stand, increasing steadily from the edge of the aspen stand into the adjacent clearing and reaching a maximum at 1.3–1.5 tree lengths. These patterns are similar to those reported for mean air temperatures adjacent to stand edges in a high-elevation coniferous forest (Huggard and Vyse, 2002).

Fig. 8 illustrates the observed pattern for delta growing degree hours at 20 cm in the soil. Due to the small number of data points it was not possible to test for differences between sites or between north- and south-facing edges. For north facing edges, delta GDH increases with distance from the edge, reaching maximum values at proportional distances between 1 and 2 tree lengths. In contrast, for south facing edges soil temperature remains high right up to the edge, then decreases rapidly going into the stand. Huggard and Vyse (2002) and Redding et al. (2003) report similar patterns in soil temperatures in gaps in subalpine coniferous forests in British Columbia.

3.4. Spruce growth

In terms of edge orientation influences on the growth of young conifers, previous studies provide contradictory results. Hansen

et al. (1993) documented reduced growth of coniferous seedlings on north-facing edges, while Coates (2000) and Burton (2002) report little or no difference in seedling growth due to edge orientation. For each of the sites we examined the indicator variable test showed that there was no difference among data from the four different cardinal directions (i.e. N, S, E, and W-facing aspen edges) ($p > 0.05$). Therefore, data were pooled and analyzed as a single relationship for each location. When the indicator variable principle was used to test if the data from all locations could be analyzed together, it showed that a difference existed among sites ($p < 0.05$). Further testing revealed there was no difference among data from two of the locations (i.e. Hines Creek and Manning) ($p > 0.05$), but that these two sites differed significantly ($p < 0.05$) from the Grande Prairie installation. Therefore data were pooled for Hines Creek and

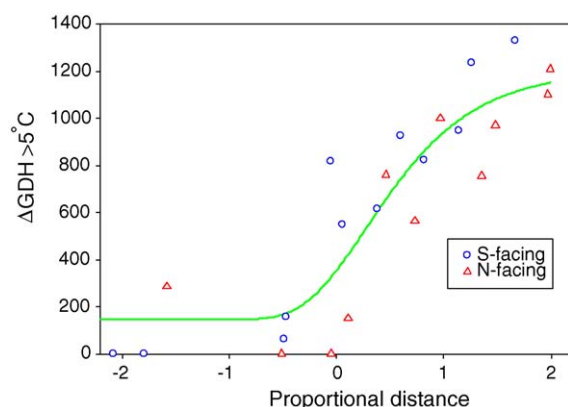


Fig. 7. Relationship between air growing degree hours (Δ GDH) and proportional distance (May 9–September 30, 2003). The line is described by the equation: $Y = 145.5284 + 1057.8694 e^{-(X-0.5754)/-0.2776}$. $Y = \Delta$ GDH, $X =$ proportional distance, $R^2_{adj} = 0.75$, $p < 0.0001$, $n = 24$. Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand. Growing degree hours (Δ GDH) was calculated as: Δ GDH = GDHi – GDHo, where GDHi is the growing degree hours calculated for each air temperature sensor, GDHo the minimum value out of all growing degree hours calculated for each transect.

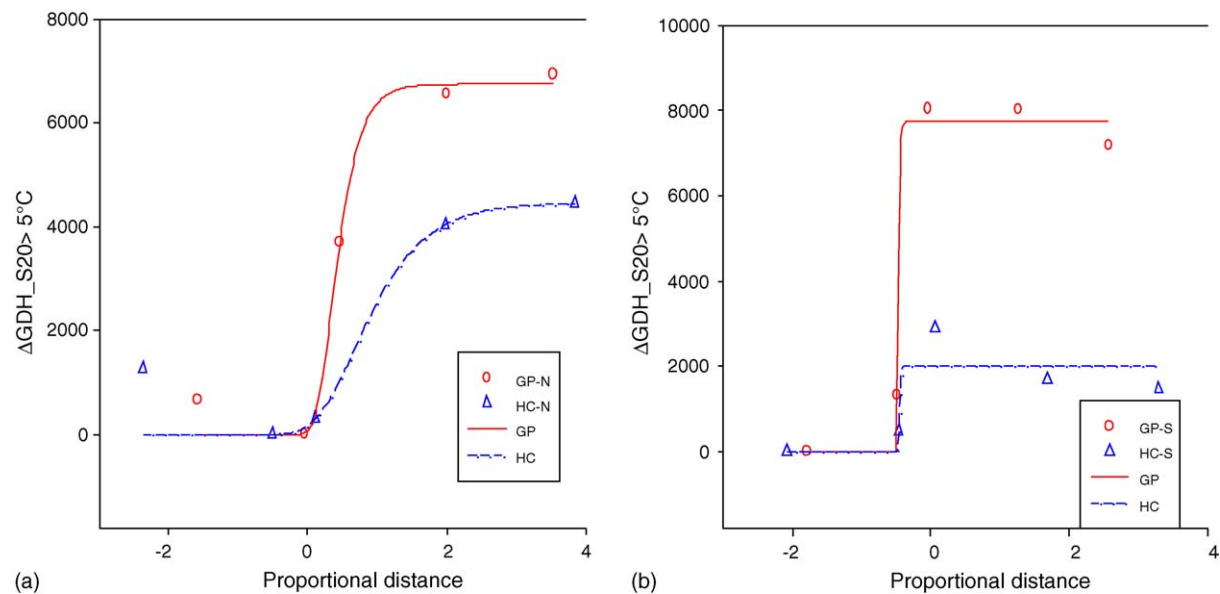


Fig. 8. Relationship between delta soil growing degree hours ($\Delta\text{GDH S20}$) and proportional distance (May 9–September 30, 2003) for north (a) and south (b) facing edges. The lines are described by the equation: $Y = a e^{-e^{-(X-c)/b}}$ with $Y = \Delta\text{GDH S20}$, $X = \text{proportional distance}$, GP = Grande Prairie, HC = Hines Creek, M = Manning. Proportional distance is defined as the number of tree lengths from the edge of the aspen stand, with negative proportional distances indicating points inside of the aspen stand. Statistical information on these models is provided in Table 3.

Manning and analyzed together, while data for the Grande Prairie installation were analyzed separately. However, for the height allocation ratio (HAR) the indicator variable test showed that the data for the Hines Creek and Manning could not be pooled ($p < 0.05$), and therefore all sites were analyzed individually.

Relationships between free growth (height allocation ratio, stem volume growth, diameter or height growth) and transmittance (DIFN at either the top or midcrown or proportional distance) and between free growth and crown size (initial crown surface area or initial crown volume) were significant ($p > 0.0001$) for all three locations included in this study (Table 4).

At all three locations, the highest R^2_{adj} values are found for the relationship between stem volume increment and light (DIFN) levels at either the top or midcrown, combined with initial crown surface area (ICSA) (Table 4). When initial crown surface area was used the R^2_{adj} values were slightly higher (1%) than those found when initial crown volume (ICV) was used (Table 4). Because of the very small differences in R^2_{adj} values

between models using ICSA or ICV, graphic representation and equations are shown only for ICSA.

Differences in DIFN between the midcrown (DIFN-M) and top (DIFN-T) of spruce seedlings were observed. When DIFN-T was used as an independent variable it showed no significance in the selected models and therefore, is not presented here. However, there are a number of possible reasons why midcrown light levels are more strongly correlated with seedling growth rates than tree top measurements. Needles at the top of the seedlings may be spending substantial time under saturated light conditions while needles in the shade near the crown base are probably light limited and rely on brief periods with adequate light to support photosynthetic production (Cannell and Grace, 1993). Since most of the leaf area in young spruce is found near the middle of the crown, and based on low photosynthetic production of the top and base needles it is likely that light levels at midcrown would be better related to tree growth.

Increasing volume growth has been associated with increases in available light levels in a number of studies (Eis, 1967; Logan, 1969; Klinka et al., 1992; Comeau et al., 1993, 2003; Wright et al., 1998; Coates and Burton, 1999; Jobidon, 2000). The present study indicates that only a small proportion of the variation in volume growth could be explained using light (1–14%) or distance from the stand edge (1–18%) by themselves (Table 4, models 1, 2, 11, 12, 21, 22, 31, and 32). However, numerous studies show that seedling growth prediction is dependant on both light levels and the initial size of the tree (where initial size varies) (Hatch et al., 1975; Givnish, 1988; Cole and Lorimer, 1994; Biging and Dobbertin, 1995; Choi et al., 2001; Claveau et al., 2002; Comeau et al., 2003; Webster and Lorimer, 2003; Pritchard, 2003). In this

Table 3

Summary of the coefficients from least square fitting of the Gompertz equation (1) for the relationship between soil growing degree hours ($\Delta\text{GDH S20}$) and distance from the stand edge

Orientation	Site	a	b	c	n	R^2_{adj}	p -values model
N-facing	Grande Prairie	6752.05	0.23	0.35	5	0.9754	0.0123
N-facing	Hines Creek	4470.65	0.56	0.67	5	0.817	0.0915
S-facing	Grande Prairie	7742.2	0.02	-0.48	5	0.9844	0.0078
S-facing	Hines Creek	2013.86	0.01	-0.46	5	0.536	0.232

$Y = (\Delta\text{GDH S20})$; $X = \text{proportional distance}$; $a-c = \text{equation coefficients}$.

Table 4

Selected models and parameter estimates for predicting stem volume increment (cm^3/year) of young white spruce^a

Location	Model no.	Model	n	MS res	R^2_{adj}	a		b		c	
						Estimate	±95%CI	Estimate	±95%CI	Estimate	±95%CI
GP	1	$\text{SVI} = a \times \text{DIFN-M}^b$	202	53774.3	0.03	314.1	70.2	0.9618	0.813		0
	2	$\text{SVI} = a \times \text{PD}^b$	202	55321.3	0.01	246.6	33.4	−0.0674	0.146		0
	3	$\text{SVI} = a \times \text{ICSA}^b$	202	27842.6	0.49	0	0.007	1.2337	0.219		0
	4	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	202	24469.8	0.56	0	0.008	1.2538	0.201	1.22	0.483
	5	$\text{SVI} = a \times \text{ICV}^b \times \text{DIFN-M}^c$	202	24351.8	0.56	0.03	0.049	0.8201	0.132	1.12	0.476
	6	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-T}^c$	202	27628.7	0.50	0	0.01	1.2062	0.216	0.7	0.878
	7	$\text{SVI} = a \times \text{ICSA}^b \times \text{PD}^c$	202	27979.9	0.49	0	0.0071	1.2339	0.219	0	0.084
	8	$\text{DI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	202	0.0265	0.13	0.04	0.038	0.247	0.097	0.3	0.355
	9	$\text{HI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	202	89.4409	0.10	0.29	0.483	0.4429	0.184	0.7	0.632
	10	$\text{HAR} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	202	0.00472	0.56	61.3	40.49	−0.802	0.088	−0.5	0.401
HC	11	$\text{SVI} = a \times \text{DIFN-M}^b$	108	1954816	0.14	4152	405.9	1.3428	0.647		0
	12	$\text{SVI} = a \times \text{PD}^b$	108	1880358	0.18	3045	341.2	0.2709	0.124		0
	13	$\text{SVI} = a \times \text{ICSA}^b$	108	1062058	0.53	0.08	0.172	0.987	0.19		0
	14	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	108	1051372	0.54	0.13	0.288	0.9475	0.2	0.3	0.431
	15	$\text{SVI} = a \times \text{ICV}^b \times \text{DIFN-M}^c$	108	1064155	0.53	0.59	1.11	0.6306	0.134	0.3	0.438
	16	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-T}^c$	108	1058122	0.53	0.12	0.258	0.9564	0.198	0.3	0.536
	17	$\text{SVI} = a \times \text{ICSA}^b \times \text{PD}^c$	108	965841	0.58	0.21	0.425	0.8942	0.188	0.1	0.091
	18	$\text{DI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	108	0.1024	0.02	0.15	0.337	0.18	0.21	0	0.479
	19	$\text{HI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	108	104.7	0.05	4.02	7.521	0.2138	0.171	0	0.39
	20	$\text{HAR} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	108	0.000018	0.58	678	1455	−1.019	0.199	−0.5	0.469
M	21	$\text{SVI} = a \times \text{DIFN-M}^b$	117	2377981	0.01	2742	452.9	1.0335	1.913		0
	22	$\text{SVI} = a \times \text{PD}^b$	117	2226610	0.07	2097	391.3	0.2859	0.184		0
	23	$\text{SVI} = a \times \text{ICSA}^b$	117	714472	0.70	0.14	0.167	0.9455	0.115		0
	24	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	117	678982	0.72	0.13	0.156	0.9589	0.113	1.33	1.064
	25	$\text{SVI} = a \times \text{ICV}^b \times \text{DIFN-M}^c$	117	697744	0.71	0.46	0.498	0.6569	0.079	1.4	1.088
	26	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-T}^c$	117	720711	0.69	0.13	0.185	0.9472	0.133	0	1.2
	27	$\text{SVI} = a \times \text{ICSA}^b \times \text{PD}^c$	117	710333	0.70	0.17	0.209	0.9227	0.119	0.1	0.085
	28	$\text{DI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	117	0.0701	0.19	0.15	0.155	0.1931	0.1	1.5	0.903
	29	$\text{HI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	117	160.3	0.16	1.98	2.525	0.2876	0.122	0.2	0.95
	30	$\text{HAR} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	117	0.000041	0.62	15.1	15.75	−0.671	0.105	−2.6	0.62
HC + M	31	$\text{SVI} = a \times \text{DIFN-M}^b$	225	2498533	0.02	3269	300.6	0.8438	0.707		0
	32	$\text{SVI} = a \times \text{PD}^b$	225	2343283	0.08	2607	273.3	0.2401	0.11		0
	33	$\text{SVI} = a \times \text{ICSA}^b$	225	878508	0.65	0.13	0.138	0.9495	0.1		0
	34	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	225	858779	0.66	0.16	0.169	0.9341	0.099	0.4	0.354
	35	$\text{SVI} = a \times \text{ICV}^b \times \text{DIFN-M}^c$	225	878659	0.65	0.62	0.594	0.628	0.068	0.4	0.359
	36	$\text{SVI} = a \times \text{ICSA}^b \times \text{DIFN-T}^c$	225	874671	0.65	0.13	0.144	0.9474	0.1	0.3	0.427
	37	$\text{SVI} = a \times \text{ICSA}^b \times \text{PD}^c$	225	829844	0.68	0.19	0.206	0.9033	0.099	0.1	0.06
	38	$\text{DI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	225	0.0878	0.07	0.19	0.175	0.1585	0.085	0.3	0.362
	39	$\text{HI} = a \times \text{ICSA}^b \times \text{DIFN-M}^c$	225	133.9	0.12	3.36	3.087	0.234	0.086	0.1	0.349

^a Note: All models are significant ($p < 0.0001$). DIFN-M, diffuse noninterceptance at midcrown of the seedlings; DIFN-T, diffuse noninterceptance t top of the seedlings; PD, proportional distance; ICSA, initial crown surface area; ICV, initial crown volume; SVI, stem volume increment; DI, diameter increment; HI, height increment; HAR, height allocation ratio.

respect the present study found that the stem volume growth of white spruce seedlings at Grande Prairie or at Hines Creek-Manning is best described by an equation involving both initial crown surface area and light levels at the tree crown (Table 4, Fig. 9). For trees growing at similar light levels, growth of white spruce seedlings increases with increasing crown surface areas. Growth of white spruce seedlings is also well predicted by an equation involving both initial crown surface area and the proportional distance from the aspen edge (Table 4, Fig. 10). Our results indicate that the regression equations for growth of white spruce are different for the two locations (Table 4, Figs. 9 and 10). These results are consistent with findings of Pritchard (2003) with differences thought to be due to microclimatic

conditions or other factors (e.g. soil moisture, soil temperature, frost, nutrient availability, other vegetation, etc.) influencing growth. In addition, seedlings growing in the open at the Grande Prairie site had a higher incidence of multiple tops, and dead buds, suggesting that frost and insect injury may be reducing the vigor of spruce at this site. As a result of these factors, seedlings at Grande Prairie are smaller and have smaller crowns than those at Hines Creek and Manning.

Several studies show that diameter and height growth of white spruce seedlings increase as light levels increase (Eis, 1967; Logan, 1969; Klinka et al., 1992; Lieffers and Stadt, 1994; Pacala et al., 1994; Wright et al., 1998; Coates and Burton, 1999; Groot, 1999; Jobidon, 2000; Pritchard, 2003).

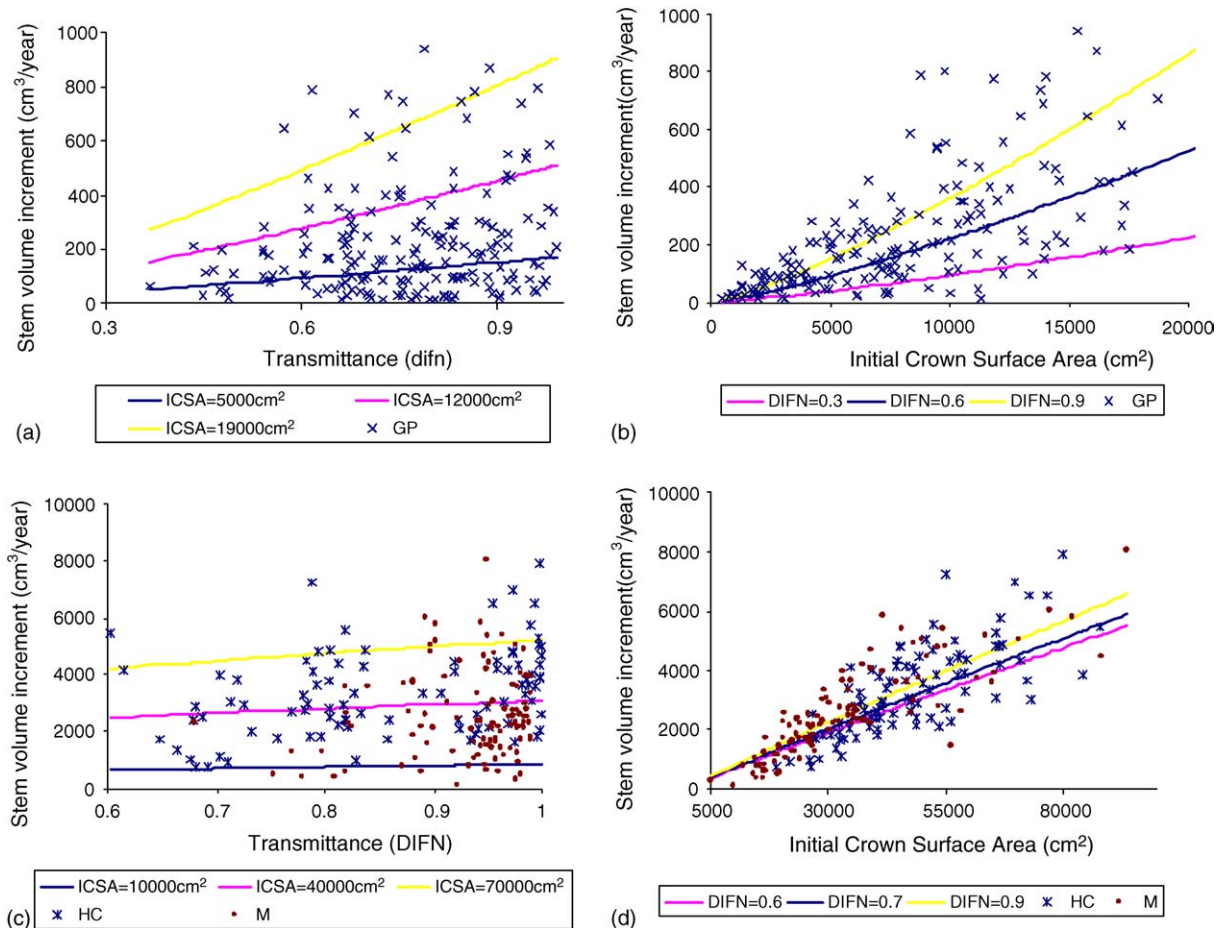


Fig. 9. Relationship between stem volume increment for Grande Prairie (a and b) and Hines Creel–Manning (c and d) and transmittance (a and c), initial crown surface area (b and d). Lines shown are based on regression models described in Table 4 (models 4, and 34), utilizing the indicator variable on x-axis and with values of the second indicator variable as indicated in the legend below each graph (DIFN = diffuse noninterceptance at midcrown; ICSA = initial crown surface area).

However, diameter growth is generally more affected by light availability than height growth (Eis, 1967; Logan, 1969; Wright et al., 1998; Coates and Burton, 1999; Groot, 1999; Jobidon, 2000). Results from our study showed poor relationships between diameter or height growth and the measured independent variables (Table 4). However, as reported by Comeau et al. (2003) for subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) and spruce, we also find that height allocation ratio declines as light levels and initial size increase (Fig. 11).

4. Conclusions

Our study documents relationships between microclimate (light, soil moisture, soil temperature and air temperature) and distance and direction from the adjacent young aspen stand edges. Results indicate that gradient in microclimate occur across boundaries between the taller closed canopy aspen stands and open patches of planted white spruce. While edge orientation did not influence air temperatures, it did influence patterns in light and soil temperature regimes. Results from this study show a strong relationship between stem volume growth and light levels or distance from the edge and initial tree size.

Similarly, height allocation ratio (HAR) is related to both initial tree size and light levels. Orientation of the adjacent young aspen stand does not appear to significantly affect the growth of white spruce.

Results from this study indicate that the negative effects of shading by young aspen on spruce growth are restricted to a narrow band adjacent to the aspen patch equal to 0.3 times the actual height of the aspen while reduction in frost occurrence by the aspen diminishes rapidly with distance from the aspen. In terms of designing patch regimes for spruce-aspen mixedwood stands, these results suggest that provided patches are of sufficient size (likely at least one aspen free length wide), the adjacent aspen will have only limited influence on spruce growth. It may be desirable to keep spruce patches smaller than two aspen free lengths in width to provide for the potential for aspen to reduce frost and suppress growth of understory vegetation. Despite the fact that similar trends in growth response would be anticipated at other similar sites, models presented in this study will need validation before being applied in other cases. In addition, further study is required to determine how these relationships change with stand age.

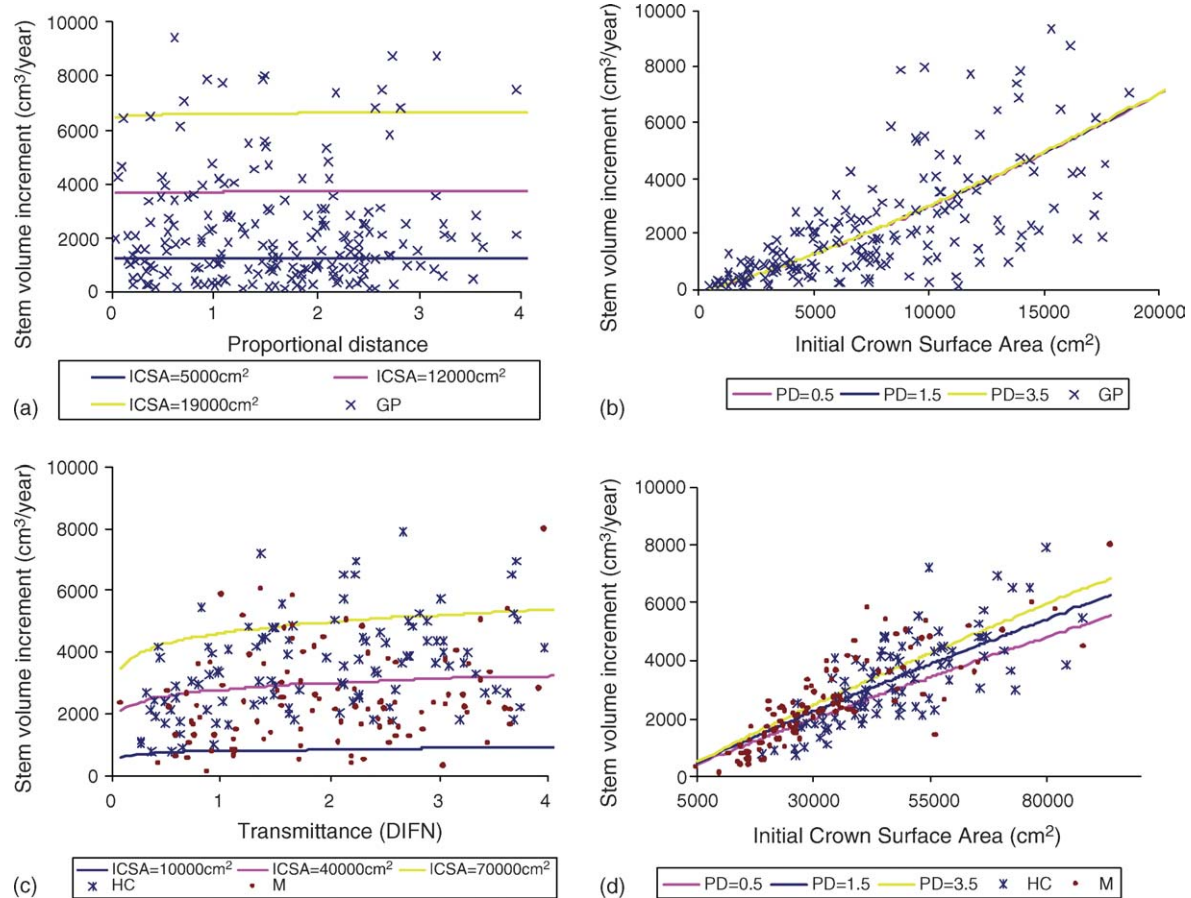


Fig. 10. Relationship between stem volume increment for the Grande Prairie (a and b) and Hines Creek–Manning (c and d) sites and proportional distance (a and c), and initial crown surface area (b and d). Lines shown are based on regression models described in Table 4 (models 7 and 37), utilizing the indicator variable on x -axis and with values of the second; ICSA = initial crown surface area).

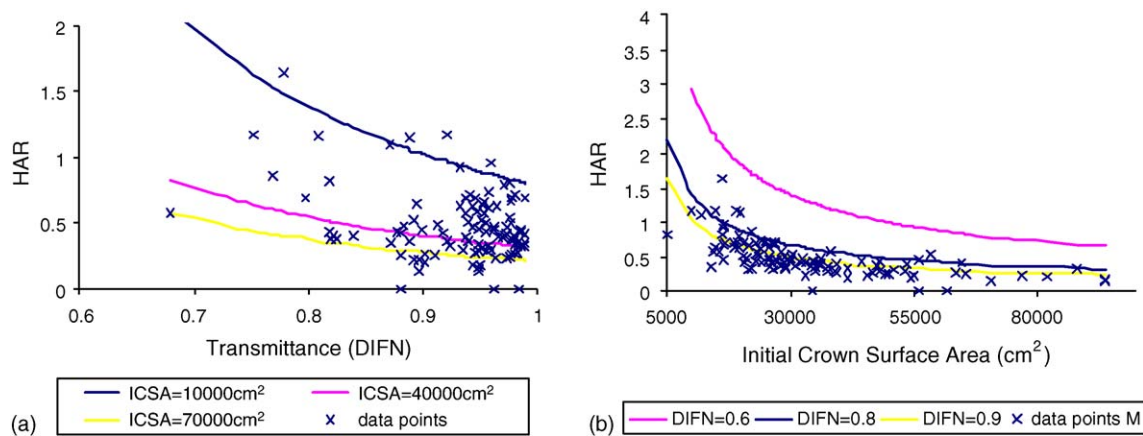


Fig. 11. Relationship between height allocation ratio and transmittance (a) and initial crown surface area (b) at the Manning site. Lines shown are based on regression models described in Table 4 (model 30), utilizing the indicator variable on x -axis and with values of the second indicator variable as indicated in the legend below each graph (HAR = height allocation ratio; DIFN = diffuse noninterceptance at midcrown; ICSA = initial crown surface area).

Acknowledgments

Funding for this project was provided by an NSERC Collaborative Research and Development Grant (Project CRDPJ 247857-01). Personal financial support for Mihai Voicu was provided by an NSERC Industrial Postgraduate Scholarship and the Western Boreal Growth and Yield Association (WESBOGY). We would like to express thanks to Drs. L. Goonewardene and S.J. Titus for assistance with the statistical analysis for this project. Assistance with site location and description as well as permission to use their sites was gratefully received from WESBOGY, Florance Niemi of Daishowa Marubeni International, Peace River and Greg Behuniak of Weyerhaeuser Canada, Grande Prairie. We would like to express our gratitude to Ryan Cheng, Susan Hill, and Cosmin Man for assistance with field data collection. We are grateful to two anonymous reviewers for their constructive suggestions for revisions to this manuscript.

References

- Beckingham, J.D., Archibald, J.H., 1996. Field guide to ecosites of northern Alberta. Can. For. Serv. Special Report 5, 412 pp.
- Belsky, J.A., Canham, C.D., 1994. Forest gaps and isolated savanna trees. *BioScience* 44, 77–84.
- Berry, A.B., 1964. Effect of strip width on proportion of daily light reaching the ground. *For. Chron.* 40, 130–131.
- Biging, G.S., Dobberty, M., 1995. Evaluation of competition indexes in individual tree growth models. *For. Sci.* 41, 360–377.
- Burton, P.J., 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. *Silva Fenn.* 36, 329–352.
- Cadenasso, M.L., Traynor, M.M., Pickett, S.T.A., 1997. Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* 27, 774–782.
- Canham, C.D., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620–631.
- Cannell, M.G.R., Grace, J., 1993. Competition for light: detection, measurement, and quantification. *Can. J. For. Res.* 23, 1969–1979.
- Chen, H.Y.H., Klinka, K., 1997. Light availability and photosynthesis of *Pseudotsuga menziesii* seedlings grown in the open and in the forest understory. *Tree Physiol.* 17, 23–29.
- Chen, J., Franklin, J.F., Spies, T.A., 1993. Contrasting micro-climates among clearcut, edge, and interior of old growth Douglas-fir forest. *Agric. For. Meteorol.* 63, 219–237.
- Choi, J., Lorimer, C.G., Vanderwerker, J., Cole, W.G., Martin, G.L., 2001. A crown model for simulating long-term stand and gap dynamics in northern hardwood forests. *For. Ecol. Manage.* 152, 235–258.
- Claveau, Y., Messier, C., Comeau, P.G., Coates, K.D., 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Can. J. For. Res.* 32, 458–468.
- Coates, K.D., 2000. Conifer seedling response to northern temperate gaps. *For. Ecol. Manage.* 127, 249–269.
- Coates, K.D., Burton, P.J., 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests of British Columbia. *Can. J. For. Res.* 29, 1374–1382.
- Cole, W.G., Lorimer, C.G., 1994. Predicting tree growth from crown variables in managed northern hardwood stands. *For. Ecol. Manage.* 67, 159–175.
- Comeau, P.G., 2000. Measuring light in the forest. B.C. Min. For., Research Branch, Victoria. Extension Note No. 42, 7 pp.
- Comeau, P.G., Bedford, L., 2005. Light under and adjacent to aspen stands and implications for growing spruce, Unpublished.
- Comeau, P.G., Wang, J.R., Letchford, T., 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. *Can. J. For. Res.* 33, 1962–1973.
- Comeau, P.G., Gendron, F., Letchford, T., 1998. A comparison of several methods for estimating light under a paper birch mixedwood stand. *Can. J. For. Res.* 28, 1843–1850.
- Comeau, P.G., Braumand, T.F., Xie, C.-Y., 1993. Effects of overtopping vegetation on light availability and growth of Engelmann spruce (*Picea engelmannii*) seedlings. *Can. J. For. Res.* 23, 2044–2048.
- Day, R.J., MacGillivray, G.R., 1975. Root regeneration of fall lifted white spruce nursery stock in relation to soil moisture content. *For. Chron.* 51, 196–199.
- DeLong, C., 2000. Planting white spruce under trembling aspen: 7-year results of seedling condition and performance. B.C. Min. For., Research Branch, Victoria. Working Paper No. 54, 19 pp.
- Draper, N.R., Smith, H., 1981. *Applied Regression Analysis*. Wiley, New York, p. 709.
- Eis, S., 1967. Establishment and early development of white spruce in the interior of British Columbia. *For. Chron.* 43, 174–177.
- Emmingham, W.H., Waring, R.H., 1975. Conifer growth under different light environments in the Siskiyou Mountains of Southwestern Oregon. *Northwest Sci.* 47, 88–99.
- Geiger, R., 1980. *The Climate Near the Ground*. Harvard University Press, Cambridge, MA, p. 611.
- Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of different methods for estimating light transmittance in forests. *Agric. For. Meteorol.* 92, 55–70.
- Giambelluca, T.W., Ziegler, A.D., Nullet, M.A., Truong, D.M., Tran, L.T., 2003. Transpiration in a small tropical forest patch. *Agric. For. Meteorol.* 117, 1–22.
- Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Physiol.* 15, 63–92.
- Greene, D.F., Kneeshaw, D.D., Messier, C., Lieffers, V.J., Cormier, D., Doucet, R., Coates, K.D., Groot, A., Grover, G., Calogeropoulos, C., 2002. Modeling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). *For. Chron.* 78, 281–295.
- Groot, A., 1999. Effects of shelter and competition on the early growth of planted white spruce (*Picea glauca*). *Can. J. For. Res.* 29, 1002–1014.
- Groot, A., Carlson, D.W., 1996. Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. *Can. J. For. Res.* 26, 1531–1538.
- Groot, A., Carlson, D.W., Fleming, R.L., Wood, J.E., 1997. Small openings in trembling aspen forest: microclimate and regeneration of white spruce and trembling aspen. *Nat. Res. Can. Can. For. Serv. Great Lake Forestry Centre, Sault Ste. Marie, Ont. NODA/NFP Technical Report TR-47*, 25 pp.
- Grossnickle, S.C., 2000. *Ecophysiology of Northern Spruce Species. The Performance of Planted Seedlings*. NRC Research Press, Ottawa, Ont., Canada.
- Hansen, A.J., Garman, S.L., Lee, P., Horvath, E., 1993. Po edge effects influence tree growth rate in Douglas-fir plantations? *Northwest Sci.* 67, 112–116.
- Hatch, C.R., Gerrard, D.J., Tappeiner II, J.C., 1975. Exposed crown surface area: a mathematical index of individual tree growth potential. *Can. J. For. Res.* 5, 224–228.
- Huggard, D.J., Vyse, A., 2002. Edge effect in high-elevation forests at Sicamous Creek. B.C. Min. For., Research Branch, Victoria. Extension Note No. 62, 8 pp.
- Jobidon, R., 2000. Density dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development – a 5-year study. *For. Ecol. Manage.* 130, 77–97.
- Johns, G.G., Lazenby, A., 1973. Defoliation, leaf area index, and the water use of four temperate pasture species under irrigated and dryland conditions. *Aust. J. Agric. Res.* 24, 783–795.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.
- Klinka, K., Wang, Q., Kayahara, G.J., Carter, R.E., Blackwell, B.A., 1992. Light-growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lasiocarpa*). *Can. J. Bot.* 70, 1919–1930.
- Langvall, O., Orlander, G., 2001. Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. *Can. J. For. Res.* 31, 155–164.

- LI-COR Inc., 1992. LAI-2000 Plant Canopy Analyzer Operating Manual. LI-COR Inc., Lincoln, NE, USA.
- Lieffers, V.J., Stadt, K.J., 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. *Can. J. For. Res.* 24, 1193–1198.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* 29, 796–811.
- Logan, K.T., 1969. Growth of tree seedlings as affected by light intensity. IV. Black spruce, white spruce, balsam fir, and eastern white cedar. Dept. Fish. For. Can. For. Serv., Ottawa. Publication No. 1256, 12 pp.
- Lundmark, T., Hallgren, J.-E., 1987. Effects of shade on exposed spruce and pine seedlings planted in the field. *Can. J. For. Res.* 17, 1197–1201.
- MacDonald, G.B., Thompson, D.J., 2003. Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site. *For. Ecol. Manage.* 182, 213–230.
- Man, R., Lieffers, V.J., 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. *Tree Physiol.* 17, 437–444.
- Matlack, G.R., 1993. Microenvironmental variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66, 185–194.
- Matlack, G.R., 1994. Vegetation dynamics of the forest edge-trends in space and successional time. *J. Ecol.* 82, 113–123.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. John Wiley and Sons, Inc., New York, p. 520.
- Orcutt, D.M., Nilsen, E.T., 1996. *The Physiology of Plants Under Stress*, vol. 2. John Wiley and Sons, Inc., New York.
- Orlander, G., 1993. Shading reduces both visible and invisible damage to Norway spruce seedlings in the field. *Forestry* 66, 27–36.
- Orlander, G., Karlson, C., 2000. Influence of shelterwood density on survival and height increment of *Picea abies* advance growth. *Scand. J. For. Res.* 5, 20–29.
- Ott, P., 1997. The use of indicator variables in non-linear regression. Biometric Information Pamphlet No. 56, B.C. Min. For., Victoria, BC, 6 pp.
- Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24, 2172–2183.
- Pritchard, J.M., 2003. The effect of opening size on light, temperature and the growth of white spruce under a trembling aspen canopy. MSc Thesis. University of Alberta, Faculty of Graduate Studies and Research, Edmonton, Alta.
- Pritchard, J.M., Comeau, P.G., 2004. Effects of opening size and stand characteristics on light transmittance and temperature under young aspen stands. *For. Ecol. Manage.* 200, 119–128.
- Ranney, J.W., Brunner, M.C., Levenson, J.B., 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L., Sharpe, M. (Eds.), *Forest Islands in Man Dominated Landscape*, *Ecol. Stud.*, vol. 41. Springer-Verlag, New York, pp. 67–95.
- Redding, T.E., Hope, G.D., Fortin, M.-J., Schmidt, M.G., Bailey, W.G., 2003. Spatial patterns of soil temperature and moisture across subalpine forest-clearcut edges in the southern interior of British Columbia. *Can. J. Soil Sci.* 83, 121–130.
- Rowe, J.S., 1956. Uses of undergrowth plant species in forestry. *Ecology* 37, 461–473.
- Runkle, J.R., 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic. Ecol.* 7, 157–164.
- Spittlehouse, D.L., Stathers, R.J., 1990. Seedling microclimate. B.C. Min. For., Land Manage. Rep. No. 65, 28 pp.
- Stathers, R.J., 1989. Summer frost in young forest plantations. *For. Can., B.C. Min. For., Victoria. FRDA Report No. 152*, 24 pp.
- Sutton, R.F., 1974. White spruce group planting in herbicide treated overmature mixedwood: 11 year results. *For. Chron.* 50, 35–37.
- Titus, S.J., Wang, Z., 2000. WESBOGY long term study. Permanent sample plot data collection manual. <http://www.wesbogy.rr.ualberta.ca/DataCollection-Manual2000.pdf> (visited March 8, 2004).
- Webster, C.R., Lorimer, C.G., 2003. Comparative growing space efficiency of four tree species in mixed conifer-hardwood forests. *For. Ecol. Manage.* 177, 361–377.
- Williams-Linera, G., 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78, 356–373.
- Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth response to light across climatic regions in north-western British Columbia. *Can. J. For. Res.* 28, 871–886.
- York, R.A., Battles, J.A., Heald, R.C., 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. *For. Ecol. Manage.* 179, 107–121.