Aspen competition affects light and white spruce growth across several boreal sites in western Canada

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Abstract: The effectiveness of competition indices for predicting light transmittance and white spruce (*Picea glauca* (Moench) Voss) growth were examined across trembling aspen (*Populus tremuloides* Michx.) density gradients using sites from a long-term study of mixedwood growth and development in Alberta and Saskatchewan. Competition indices based on density (number of trees, basal area, and spacing factor), distance-dependent and -independent size ratio (Hegyi's and Lorimer's), and crown characteristics (crown volume, surface area, and cross-sectional area) were tested. Transmittance was effectively predicted by crown competition indices followed closely by aspen basal area and size ratio indices. Models of spruce growth indicated better results for stem volume compared with diameter or height. Competition alone accounted for less than 60% of stem growth variation, with basal area and transmittance providing some of the best models. The predictive ability of spruce growth was increased up to 93% by adding initial size as a second explanatory variable. In this respect, initial diameter was superior to initial height, crown volume, and surface area. Relationships between competition, transmittance, and spruce growth were found to differ significantly between geographical locations. These results suggest the need for local development of models relating tree growth to competition.

Résumé : L'efficacité d'indices de compétition à prédire la transmittance de la lumière et la croissance de l'épinette blanche (*Picea glauca* (Moench) Voss) a été étudiée le long de gradients de densité de peuplier faux-tremble (*Populus tremuloides* Michx.) en utilisant les stations d'une étude à long terme de la croissance et du développement de peuplements mixtes en Alberta et en Saskatchewan. Parmi les indices de compétition testés, certains étaient basés sur la densité (nombre d'arbres, surface terrière et facteur d'espacement), d'autres étaient dépendants de la distance et indépendants de la taille relative (indices de Hegyi et de Lorimer) et d'autres considéraient les caractéristiques de la cime (volume, surface ou surface projetée de la cime). La transmittance était efficacement prédite par les indices de compétition basés sur la cime, suivis étroitement par les indices basés sur la surface terrière en peuplier et la taille relative. Les modèles de croissance de l'épinette donnaient de meilleurs résultats pour le volume de la tige que pour le diamètre ou la hauteur. Moins de 60 % de la variation de la croissance des arbres était expliquée par la compétition et les meilleurs modèles incluaient la surface terrière et la transmittance. L'efficacité à prédire la croissance de l'épinette a pu être augmentée jusqu'à 93 % en ajoutant la taille initiale comme deuxième variable explicative. À cet égard, le diamètre initial était meilleur que la hauteur initiale, le volume de la cime ou la surface de la cime. Les relations entre la compétition, la transmittance et la croissance de l'épinette étaient significativement différentes selon l'endroit. Ces résultats font ressortir le besoin de mettre au point des modèles locaux qui relient la croissance des arbres à la compétition.

[Traduit par la Rédaction]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is a prominent, widespread, and important competitor with white spruce (*Picea glauca* (Moench) Voss) following disturbance of spruce or mixedwood sites in the boreal forests of North America. Aspen regenerates abundantly, with initial sucker densities over 100 000 stems·ha^{-1}. By age 10, aspen densities drop to about 10 000 stems·ha^{-1} owing to self-thinning (Peterson and Peterson 1992). After fire or clearcutting, aspen grows more rapidly in height than spruce, leading to aspen-dominated stands for the first 40–60 years (Chen and Popadiouk 2002). Meanwhile, spruce may persist in the understory owing to its ability to survive and grow slowly under aspen canopies at light levels as low as 10% of full sunlight (Lieffers and Stadt 1994). However, tending can be used to increase spruce growth and survival (Comeau et al. 2005).

Competition for light has been considered to be the major mechanism by which aspen influences spruce growth in the boreal forest (Burton 1993). Light availability may be improved by manipulating the overstory canopy, and several recent studies have shown that understory light can be predicted by various stand characteristics, especially basal area (Comeau et al. 2003, 2006). Spruce needles and shoots experience photosynthetic saturation at light levels between 40% and 60% of full sunlight (Coates and Burton 1999), and maximum height growth of seedlings may occur at around 40% of full sunlight (Lieffers and Stadt 1994).

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Nevertheless, diameter and stem volume growth of spruce and other conifer saplings typically increase with light levels up to full sunlight (Wright et al. 1998).

Competition indices have been widely used to quantify and interpret the effects of plant competition (Weigelt and Jolliffe 2003). Numerous competition indices have been proposed and tested in studies of forest competition. Indices based on the size ratio between competitors and the subject tree adjusted by distance, initially proposed by Hegyi (1974) and Daniels (1976), have been modified and evaluated in numerous studies (Alemdag 1978; Martin and Ek 1984; Tomé and Burkhart 1989). Since application of distance-dependent indices is limited by the requirement for measurement of intertree distances, distance-independent indices have been more widely applied for evaluating competitive effects (Lorimer 1983; Daniels et al. 1986; Holmes and Reed 1991). Crown-based competition indices have been proposed as alternatives to indices based on more commonly collected height and diameter measurements (Hix and Lorimer 1990; Biging and Dobbertin 1992). Incorporating crown size may include biological information more meaningful to explaining competitive interactions, such as the amount of light intercepted by subject trees and the use of other resources (i.e., water and nutrients). While some indices work better than others under particular sets of conditions, the vast literature on the subject does not indicate any index as being the best under all conditions.

Despite the extensive and successful use of competition indices, there is still criticism of their use. One of the main shortcomings is that competition indices provide a static quantification of competition within a dynamic and changing system (Burton 1993). In addition, most competition studies are limited in space and time (Goldberg and Barton 1992), with little replication across larger geographical areas or across several years, which limits generalization of findings.

Previous studies of aspen competition indicate that simple distance-independent competition indices such as basal area and density can be as effective as more detailed indices in spruce plantations (Steneker and Jarvis 1963; Alemdag 1978; MacIsaac and Navratil 1996). Comeau et al. (2003) reported that basal area and light transmittance provide predictions of white spruce growth similar to those obtained using distance-independent or -dependent size ratio indices of paper birch (*Betula papyrifera* Marsh.) competition, suggesting little benefit from including proximity in a competition index.

Crown-based competition indices have not been tested for their application to the aspen–spruce combination. In addition, there are no published studies designed to examine whether the same relationships between growth and competition apply across a range of sites. This paper evaluates the effectiveness of several competition indices (density, distance-dependent and -independent size ratio, and crown-based indices) for predicting light transmittance and examines the use of these indices together with initial size for describing variation in growth of spruce across a gradient of densities following spacing treatments at four locations. Our objectives were to evaluate the influence of aspen densities on light and growth of spruce and to identify which competition indices provide the most reliable predictions. A second objective was to test for differences in these relationships between four geographical locations (i.e., can a single relationship be applied across a broad range of sites).

Materials and methods

Our study used selected field installations established by the Western Boreal Growth and Yield association (WESBOGY) as part of a Long-Term Study (LTS) of growth and development of tended mixtures of white spruce and trembling aspen. Ten forest companies and government agencies from western Canada are involved, and each member established one block with two installations, one for a superior site and one medium (site quality was determined prior to establishment based on field observations and previous stand information). The LTS consists of plots with different combinations of aspen and spruce densities, randomly assigned in each of the two replicates. Each measurement plot is 20 m × 20 m with a 5 or 10 m treated buffer around the plot. More details on the experimental design and establishment and maintenance of the LTS can be found in WESBOGY (2004).

Our study utilized the four oldest WESBOGY LTS blocks located near Peace River, Grande Prairie, and Edson in Alberta and near Prince Albert in Saskatchewan (Table 1). Both the medium and superior installations for Peace River (abbreviated hereon as PRm and PRs) and Prince Albert (PAm and PAs) have two complete replications. The medium installation for Edson (EDm) includes two complete replications, while at the superior installation (EDs), there is only one replication. At the Grande Prairie (GP) block, the plots have recently been characterized as having very similar site qualities; therefore, GP currently has three replications, as one of the initial four replications was damaged by oil and gas development.

For each installation, plots with five levels of aspen density (0, 500, 1500, and 4000 stems·ha^{-1} and natural unthinned) and two levels of spruce density (500 and 1000 stems·ha^{-1}) were used. Given the current size of spruce (0.7–2.6 m height), intraspecific competition is unlikely to influence growth of individual spruce trees at the present time; therefore, the two levels of spruce density were treated as extra replicates of aspen density. A total of 140 plots were used in our study (5 aspen densities × 2 spruce densities × 2 replicates × 2 site quality levels × 4 locations = 160 plots, less 10 plots lost in Edson and 10 in Grande Prairie).

Sites were generally flat, with slopes less than 5%, with soil drainage ranging from moderate to well drained (Table 1). All sites were characterized as low-bush cranberry ecosites, with mesic moisture regime and medium nutrient regime (Beckingham and Archibald 1996; Beckingham et al. 1996*a*, 1996*b*). Soil parent materials were morainal, glaciolacustrine, and glaciofluvial, with medium to moderately fine texture, and a variety of clay, clay–loam and sandy loam textures, usually with less than 10% coarse fragments. Precipitation during the study period (2002–2003) was below climatic normals (Table 1), resulting in relatively droughty conditions.

In each plot, three spruce seedlings located closest to gridpoints established 5 m north, 5 m southeast, and 5 m southwest of the plot center were selected. Selection of sub-

Table 1. Location and site information for the studied sites.

Location	Latitude and longitude	Elevation (m above sea level)	Natural subregion[a]	Soil subgroup	Year planted	Total annual precipitation (mm)			Growing season precipitation (mm)[b]		
						2002	2003	Normal[c]	2002	2003	Normal
Peace River medium (PRm)	56°55′N, 118°30′W	800	Boreal mixedwood	Orthic Gray Luvisol	1992	256	363	402	170	195	269
Peace River superior (PRs)	56°41′N, 117°72′W	731	Boreal mixedwood	Orthic Gray Luvisol	1992	256	363	402	170	195	269
Grande Prairie (GP)	54°55′N, 118°30′W	762	Boreal mixedwood	Orthic Gray Luvisol	1991	399	392	447	255	175	288
Edson medium (EDm)	53°46′N, 116°41′W	1060	Lower foothills	Brunisolic Gray Luvisol	1992	327	451	562	196	234	415
Edson superior (EDs)	53°48′N, 116°38′W	1120	Lower foothills	Brunisolic Gray Luvisol	1992	327	451	562	196	234	415
Prince Albert medium (PAm)	53°45′N, 105°30′W	552	Midboreal upland	Orthic Gray Luvisol	1990	332	315	424	248	235	295
Prince Albert superior (PAs)	53°40′N, 105°56′W	549	Midboreal upland	Brunisolic Gray Luvisol	1990	332	315	424	248	235	295

[a]From Beckingham and Archibald (1996) and Beckingham et al. (1996*a*, 1996*b*).
[b]Growing season considered to be May–September.
[c]Normal values represent averages for the interval 1971–2000 (source: National Climate Data, Environment Canada).

ject trees aimed to ensure their independence from each other, no edge influences, and no overlap between the aspen competition zones. Root collar diameter, total height, leader length, and crown radii in four cardinal directions were measured for each spruce in May 2002, May 2003, and September 2003. These measurements provided (*i*) growth information on diameter, height, and stem volume (spruce stem volume was calculated using the formula for a cone) during the 2-year measurement period (2002–2003) and (*ii*) data on initial spruce size (diameter, height, and crown size; crown volume and surface area were calculated using the formula for a cone) at the beginning of the growing period (2002).

During the summer of 2002, aspen competition was assessed within a 3.99 m radius plot centered at each selected spruce. While search radius has been shown to impact on the effectiveness of competition measures (Hynynen and Ojansuu 2003), a 3.99 m radius is expected to be optimal for competition quantification based on similar studies conducted in stands of comparable age (Comeau et al. 1998; Simard and Sachs 2004). Diameter at breast height was measured for all aspen in the 3.99 m radius plot. The assessment plot was divided into four quadrants, and in each of them, the closest dominant or codominant aspen was determined and the intertree distance (aspen–spruce) was measured in addition to height, height to crown base, and crown radii (in four cardinal directions). In each competition plot, 10–15 representative aspen were systematically selected across the range of sizes and measured in greater detail (height, height to crown, and crown radii). Regression equations were developed for each treatment plot to estimate height, average crown radius, and crown length as a function of breast height diameter for all aspen. Aspen crown form was assumed to be a prollate ellipsoid (a rotation ellipse around the major axis, crown length, with average crown diameter as the minor axis). Crown surface area, cross-sectional area, and volume were also calculated.

The fraction of full sunlight (transmittance) reaching each subject tree was measured during the summers of 2002 and 2003 using LAI-2000 plant canopy analyzers (Li-COR Inc., Lincoln, Nebraska). Previous studies showed that LAI-2000 sensors provide consistent estimates of light transmittance throughout the growing season (Gendron et al. 1998). In a concurrent study at the GP and PR WESBOGY sites, Voicu (2005) observed that the instantaneous LAI-2000 measurements were highly correlated with photosynthetic photon flux density integrated over the growing season. Light was measured at the top of the spruce seedlings and at midcrown height with the sensor oriented pointing away from the crown of the subject tree and paired subsequently with another simultaneous measurement taken in an adjacent open area at the same height. The sensors were fitted with 180° view restrictors, with one reading taken facing west in the morning and a second reading taken facing east in the afternoon to avoid direct light in the sensor view. For the midcrown measurement, the sensor was located just outside the canopy edge so that it did not include the influence of the subject tree on light levels at this height. The sky portion below 31.9° above the horizon was ignored, and only values from rings 1–4 of the LAI-2000 sensor were used.

Our objectives were to evaluate indices that can be calculated from measurements commonly and readily collected in

Table 2. Formulas used to calculate competition indices (including abbreviations).

Competition index	Formula
Number of trees	N (stems/ha)
Basal area	BA (m^2/ha)
Lorimer's 1	$\mathrm{LOR1} = \sum_{i=1}^{n} \mathrm{DBH}_{\mathrm{AW}i}$ (cm)
Lorimer's 2	$\mathrm{LOR2} = \sum_{i=1}^{n} \mathrm{DBH}_{\mathrm{AW}i}/D_{\mathrm{SW}}$
Crown volume 1	$\mathrm{VCR1} = \sum_{i=1}^{n} \mathrm{VCr}_{\mathrm{AW}i}$ (m^3)
Crown volume 2	$\mathrm{VCR2} = \sum_{i=1}^{n} \mathrm{VCr}_{\mathrm{AW}i}/\mathrm{CrV}_{\mathrm{SW}}$
Crown surface area 1	$\mathrm{SCR1} = \sum_{i=1}^{n} \mathrm{SCr}_{\mathrm{AW}i}$ (m^2)
Crown surface area 2	$\mathrm{SCR2} = \sum_{i=1}^{n} \mathrm{SCr}_{\mathrm{AW}i}/\mathrm{CSA}_{\mathrm{SW}}$
Crown cross-sectional area 1	$\mathrm{SCROS1} = \sum_{i=1}^{n} \mathrm{SCros}_{\mathrm{AW}i}$ (m^2)
Crown cross-sectional area 2	$\mathrm{SCROS2} = \sum_{i=1}^{n} \mathrm{SCros}_{\mathrm{AW}i}/\mathrm{SCros}_{\mathrm{SW}}$
Hegyi's (based on four closest trembling aspen)	$\mathrm{HEG4} = \left(\sum_{i=1}^{4} \mathrm{DBH}_{\mathrm{AW}i}/D_{\mathrm{SW}}\,\mathrm{dist}_i\right)\mathrm{Npl}/4$
Crown volume (based on four closest aspen)	$\mathrm{VCR4} = \left(\sum_{i=1}^{4} \mathrm{VCr}_{\mathrm{AW}i}/\mathrm{CrV}_{\mathrm{SW}}\,\mathrm{dist}_i\right)\mathrm{Npl}/4$
Crown surface area (based on four closest aspen)	$\mathrm{SCR4} = \left(\sum_{i=1}^{4} \mathrm{SCr}_{\mathrm{AW}i}/\mathrm{CSA}_{\mathrm{SW}}\,\mathrm{dist}_i\right)\mathrm{Npl}/4$
Crown sectional area (based on four closest aspen)	$\mathrm{SCROS4} = \left(\sum_{i=1}^{4} \mathrm{SCros}_{\mathrm{AW}i}/\mathrm{SCros}_{\mathrm{SW}}\,\mathrm{dist}_i\right)\mathrm{Npl}/4$
Light transmittance (at white spruce midcrown)	DIFM (%)
Light transmittance (at spruce top)	DIFT (%)
Spacing factor (top of spruce)	$\mathrm{SF}_{\mathrm{T}} = 10\,000/(H_{\mathrm{AW}} - H_{\mathrm{SW}})\sqrt{N}$ (%)
Spacing factor (aspen)	$\mathrm{SF}_{\mathrm{AW}} = 10\,000/H_{\mathrm{AW}}\sqrt{N}$ (%)

Note: $\mathrm{DBH}_{\mathrm{AW}i}$, basal diameter of the ith aspen tree; D_{SW}, root collar diameter of the subject spruce tree; $\mathrm{VCr}_{\mathrm{AW}i}$, crown volume of the ith aspen tree; $\mathrm{CrV}_{\mathrm{SW}}$, crown volume of the subject spruce tree; $\mathrm{SCr}_{\mathrm{AW}i}$, crown surface area of the ith aspen tree; $\mathrm{CSA}_{\mathrm{SW}}$, crown surface area of the subject spruce tree; $\mathrm{SCros}_{\mathrm{AW}i}$, area of the crown horizontal section of the ith aspen tree; $\mathrm{SCros}_{\mathrm{SW}}$, area of the horizontal section at crown base of the subject spruce tree; dist_i, intertree distance between the subject spruce and the ith aspen tree; Npl, number of aspen trees per plot of competition assessment; H_{AW}, dominant height of aspen; H_{SW}, height of subject spruce tree; N, number of aspen trees per hectare; light transmittance was averaged for the 2002 and 2003 growing seasons.

the field. This guided the selection of indices included in our study (Table 2). Competition indices used for predicting understory light incorporated only aspen characteristics and were kept independent of spruce size (i.e., spruce size in Lorimer's and Hegyi's indices was set to 1), except for the spacing factor that was adjusted with the height at which light was measured. Similar indices were used for explaining variation of spruce growth. Indices LOR1, VCR1, SCR1, and SCROS1 included only characteristics of aspen as opposed to LOR2, VCR2, SCR2, and SCROS2, which also included the size of subject spruce. This differentiation was based on concerns that size ratio indices may artificially inflate the coefficient of determination in the regression models by incorporating subject tree size in the competition index. Distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) were based on data collected only from the four closest competitors and adjusted with the number of trees per assessment plot. Spacing factor indices were also used in two forms, one (SF_{T}) adjusted with spruce height, which considers the intertree distance as a ratio of the difference in height between the competitor and subject trees, and another ($\mathrm{SF}_{\mathrm{AW}}$) that uses only aspen height. For plots with aspen densities of zero, values of 0.001 were assigned to competition indices that otherwise would have been zero to allow for different models to be tested.

Simple and multiple nonlinear regression models were developed for each installation (medium and superior) and location to predict (i) understory light as a function of competition indices:

$$[1] \qquad \mathrm{DIFM} = a + \ln(\mathrm{CI}),\ \mathrm{DIFT} = a + \ln(\mathrm{CI})$$

Table 3. Predictive ability of light transmittance (measured at white spruce midcrown) by competition indices (R^2_{adj} values).

Location	Installation	Competition indx N	BA	LOR1	VCR1	SCR1	SCROS1	HEG4	VCR4	SCR4	SCROS4	SF_T
Peace River	Medium	0.80	0.92	0.90	0.89	0.94	0.93	0.85	0.94	0.92	0.92	0.86
	Superior	0.81	0.86	0.86	0.86	0.87	0.88	0.87	0.87	0.88	0.88	0.77
Prince Albert	Medium	0.68	0.80	0.78	0.76	0.78	0.78	0.75	0.73	0.75	0.75	0.73
	Superior	0.65	0.67	0.68	0.64	0.68	0.67	0.70	0.70	0.71	0.70	0.59
Edson	Medium	0.85	0.82	0.86	0.81	0.85	0.85	0.81	0.82	0.83	0.85	0.70
	Superior	0.92	0.94	0.95	0.93	0.96	0.95	0.91	0.92	0.92	0.93	0.74
Grande Prairie		0.46	0.51	0.54	0.52	0.55	0.54	0.51	0.52	0.53	0.51	0.53

Note: All values shown are for statistically significant models ($p < 0.001$) and are based on nonlinear regressions fit to data using the exponential equation DIFM = $a\,e^{(b\mathrm{CI})}$where DIFM is light transmittance in the understory, CI is competition index as defined in Table 2, and a and b are model parameters.

[2] $\mathrm{DIFM} = a(\mathrm{CI})^b,\ \mathrm{DIFT} = a(\mathrm{CI})^b$

[3] $\mathrm{DIFM} = a\,e^{(b\mathrm{CI})},\ \mathrm{DIFT} = a\,e^{(b\mathrm{CI})}$

where transmittance was measured at midcrown (DIFM) and topcrown (DIFT) and CI is competition index as defined in Table 2; (*ii*) spruce growth as a function of competition indices:

[4] $\mathrm{SWgr} = a + \ln(\mathrm{CI})$

[5] $\mathrm{SWgr} = a(\mathrm{CI})^b$

[6] $\mathrm{SWgr} = a\,e^{(b\mathrm{CI})}$

where spruce growth measurements (SWgr) tested were diameter, height, height allocation ratio (the latter as defined in Comeau et al. 2003), and stem volume increment; and (*iii*) spruce growth as a function of competition indices and initial size:

[7] $\mathrm{SWgr} = a(\mathrm{CI})^b(\mathrm{IS})^c$

[8] $\mathrm{SWgr} = a\,e^{(b\mathrm{CI})}\,e^{(c\mathrm{IS})}$

[9] $\mathrm{SWgr} = a(\mathrm{CI})^b\,e^{(c\mathrm{IS})}$

[10] $\mathrm{SWgr} = a\,e^{(b\mathrm{CI})}(\mathrm{IS})^c$

where the initial spruce size (IS) was tested in the form of initial diameter, height, crown volume, and crown surface area.

Model parameters were estimated using least-squares nonlinear regression. Data analysis was completed using the SAS statistical package for Windows (version 8.2) (SAS Institute Inc., Cary, North Carolina). Validity of the underlying assumptions for tested models and evaluation of model fit was based on analysis of residuals plotted against predicted values with the goal of minimizing the residual mean square (Bates and Watts 1988). The adjusted values of the coefficient of determination (R^2_{adj}) were calculated to account for differences in sample size and model complexity (i.e., number of parameters). Despite criticism of using R^2 for nonlinear models (Ratkowsky 1990), R^2 represents a robust tool in deciding on model fit and provides an effective method for comparing the degree to which different independent variables explain variation in a dependent variable (Draper and Smith 1981). The R^2 values also offer additional information on the importance of competition for a particular site (Welden and Slauson 1986). Extra sum of squares testing with indicator variables (Ott 1997) was used to evaluate whether data could be pooled into a single equation for medium and superior sites at each location and for all four geographical locations of our study.

Results

Significant relationships ($p < 0.001$) were found between transmittance and competition indices at all sites (Table 3). Consistently better results were obtained for predicting understory light measured at white spruce midcrown as opposed to light measured at the top of the spruce; therefore, results are shown only for midcrown measurements. Exponential models provided superior prediction and fit the data sets better than other tested models (power and logarithmic). Predictive ability varied with location and competition index, with values of the coefficient of determination (R^2_{adj}) ranging between 0.41 and 0.94. At each site, differences between all of the competition indices except trembling aspen density were small (density was generally one of the poorer indices). The group of indices based on crown size performed better than other indices, and amongst the crown indices, SCR1 was generally superior. Crown indices were followed by a second group of indices comprising basal area, LOR1, and HEG4, of which basal area was marginally better.

Extra sum of squares tests of regression fit to data from different sites and locations showed significant differences for relationships between understory light and aspen basal area or crown surface (Table 4, results shown only for basal area). Since there were no significant differences between medium and superior sites at PR and PA (i.e., no significant differences were detected between PRs and PRm and between PAs and PAm, respectively), data for different site qualities at each location could be pooled. However, significant differences were detected between the medium and superior sites at ED. With the exception of PR with EDm and GP with EDs, all the other combinations indicated significant differences (Fig. 1). Parameter estimates for these relationships are provided in Table 5.

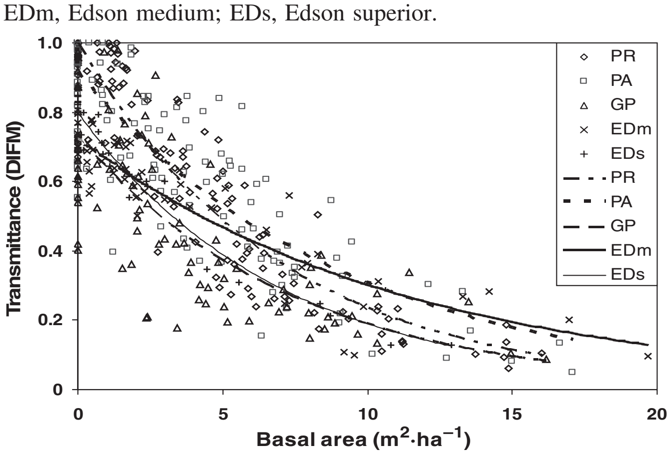
Significant relationships between spruce growth and competition were obtained. Stem volume increment provided

Table 4. Test of difference between locations and installations for models predicting light transmittance as a function of basal area of the overtopping trembling aspen (*p* values).

	Peace River	Prince Albert	Edson medium	Edson superior	Grande Prairie
Peace River		0.042*	0.238	0.0004*	0.0001*
Prince Albert			0.039*	0.00058*	0.0001*
Edson medium				0.008*	0.00056*
Edson superior					0.6208
Grande Prairie					

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model DIFM = $a\,e^{(b\mathrm{BA})}$ where DIFM is light transmittance in the understory, BA is basal area of the overtopping aspen, and *a* and *b* are model parameters; the asterisk associated with the *p* values indicates a significant difference ($p < 0.05$). For Peace River and Prince Albert, there was no significant difference between the medium and superior installations.

Fig. 1. Relationships between light transmittance at midcrown (DIFM) and basal area of overstory trembling aspen (*Populus tremuloides*) for the studied sites. Lines shown are based on nonlinear regressions fit to data using the exponential model DIFM = $a\,e^{(b\mathrm{BA})}$. Parameters values and statistics are provided in Table 5. All models are statistically significant ($p < 0.001$). For the Peace River and Prince Albert locations, data were pooled owing to no significant difference detected between the models for the medium and superior sites. PR, Peace River; PA, Prince Albert; GP, Grande Prairie; EDm, Edson medium; EDs, Edson superior.



consistently better results than diameter and height growth; hence, we focus the presentation of our results on relationships between stem volume growth and competition. As expected, spruce growth increased with available resources (e.g., light) and aspen spacing (Fig. 2). When considered by itself, competition explained less than 60% of the variation of stem growth (Table 6) and the importance of competition (expressed as R^2_{adj} values) was lower for GP ($R^2_{\mathrm{adj}} \leq 0.16$) and ED ($R^2_{\mathrm{adj}} \leq 0.34$) sites and was highest at PR ($R^2_{\mathrm{adj}} \leq 0.60$). The performance of competition indices varied from site to site, with basal area and midcrown light transmittance (DIFM) offering some of the best results. Indices that included spruce tree size (LOR2, VCR2, SCR2, and SCROS2) offered only a small increase of predictive ability as opposed to indices that did not include subject tree size (LOR1, VCR1, SCR1, and SCROS1). Distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) provided slightly inferior results compared with distance-independent indices (LOR2, VCR2, SCR2, and SCR2). Both spacing factor and density consistently ranked low in terms of predictive ability.

Tests for difference between models predicting spruce growth as a function of light transmittance showed significant differences between locations (Table 7). The medium and superior sites for both PA and ED allowed data pooling (no significant difference was detected between PAm and PAs and between EDm and EDs, respectively).

The addition of initial size as a second explanatory variable in multiple nonlinear regression models increased R^2_{adj} values. Several measures of initial spruce size were tested, including initial stem diameter, stem height, volume, and surface area of crown. For example, at PRm, adding spruce crown volume to aspen basal area explained 74% of the variation, crown surface area 74%, height 74%, and diameter 79%, whereas for PRs, crown volume combined with basal area explained 80% of the variation, crown surface area 84%, height 85%, and diameter 86%, respectively; similar trends were observed for the other sites. Thus, results are shown only for the best models obtained when initial spruce diameter was added to competition indices (Table 6). Multiple regression models including competition and initial diameter explained between 63% and 93% of the variation in stem volume increment. Best predictive models across the range of sites included aspen basal area and initial spruce diameter followed by models combining light transmittance and diameter. These relationships are illustrated in Figs. 3 and 4.

Models predicting spruce volume increment as a function of aspen basal area and initial spruce diameter were tested for differences between locations and installations (Table 8). These tests indicated no significant differences between medium and superior installations at each location but indicated that the PR location differed significantly from the other three locations (PA, ED, and GP). Similar differences were obtained when other initial spruce size measures (e.g., height or crown volume) were used in addition to basal area or transmittance (results not shown).

Discussion

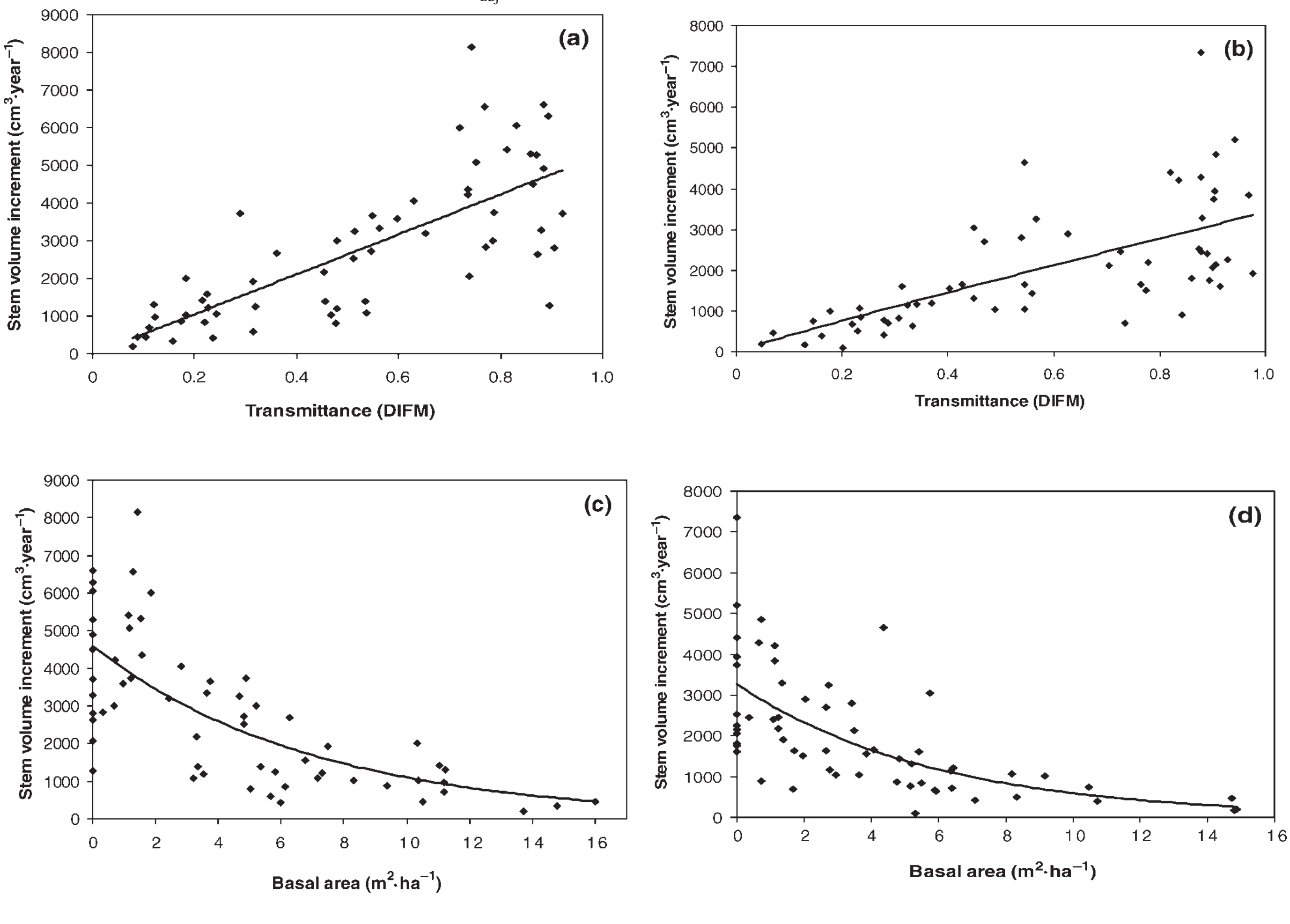
Our results demonstrate the effectiveness of competition indices based on trembling aspen characteristics for predicting understory light in western boreal mixedwoods. While indices based on crown characteristics provided slightly better predictions, other indices, readily obtained from common field measurement such as stem diameter (i.e., Lorimer's index) or basal area, are also effective for predicting light across a broad range of aspen densities and mixedwood sites. Our results are consistent with findings of previous

Table 5. Parameter estimates for models of light transmittance as a function of trembling aspen basal area.

Location	n	MS_{res}	R^2_{adj}	a	b
Peace River medium	60	0.00774	0.92	0.9817 (0.9409 to 1.0225)	–0.1413 (–0.1564 to –0.1262)
Peace River superior	60	0.0134	0.86	1.0237 (0.9705 to 1.0768)	–0.1480 (–0.1691 to –0.1269)
Peace River (data pooled)	120	0.0105	0.89	1.0032 (0.9701 to 1.0363)	–0.1445 (–0.1572 to –0.1318)
Prince Albert medium	55	0.0151	0.80	0.9513 (0.8928 to 1.0098)	–0.1283 (–0.1503 to –0.1064)
Prince Albert superior	54	0.0226	0.67	0.8831 (0.8125 to 0.9536)	–0.0924 (–0.1153 to –0.0694)
Prince Albert (data pooled)	109	0.0194	0.73	0.9155 (0.8695 to 0.9615)	–0.1089 (–0.1250 to –0.0929)
Edson medium	60	0.00545	0.82	0.7266 (0.6991 to 0.7541)	–0.0876 (–0.1014 to –0.0739)
Edson superior	30	0.0029	0.94	0.7989 (0.7708 to 0.8629)	–0.1437 (–0.1652 to –0.1221)
Grande Prairie	86	0.0252	0.51	0.7308 (0.6696 to 0.7921)	–0.1345 (–0.1661 to –0.1030)

Note: Models shown are significant ($p < 0.001$) and are based on nonlinear regressions fit to data based on the exponential equation DIFM = $a\,e^{(b\mathrm{BA})}$ where DIFM is light transmittance in the understory measured at the white spruce midcrown, BA is basal area of the overtopping aspen, and a and b are model parameters reported with 95% confidence limits. For Peace River and Prince Albert, there was no significant difference detected between models for the medium and superior sites, allowing for data pooling.

Fig. 2. Relationships between stem volume increment of white spruce (*Picea glauca*) during the 2-year measurement period (2002–2003) for (*a* and *c*) Peace River medium and (*b* and *d*) Peace River superior and (*a* and *b*) transmittance and (*c* and *d*) trembling aspen basal area. Lines shown on the graphs are based on nonlinear regressions fit to data: (*a*) SVI = 5299.85 DIFM$^{1.0067}$ (n = 60, MS_{res} = 6.623, R^2_{adj} = 0.57); (*b*) SVI = 3424.8 DIFM$^{0.9349}$ (n = 60, MS_{res} = 4.9430, R^2_{adj} = 0.44); (*c*) SVI = 4598.65 $e^{(-0.1433\,\mathrm{BA})}$ (n = 60, MS_{res} = 7.3865, R^2_{adj} = 0.52); (*d*) SVI = 3269.5 $e^{(-0.1704\,\mathrm{BA})}$ (n = 60, MS_{res} = 5.2110, R^2_{adj} = 0.41).



studies (Comeau et al. 2003, 2006). Predictions of transmittance were better at white spruce midcrown than at the top position owing to this location being more consistently located below the base of the live aspen canopy. Observations obtained from examination of vertical light profiles suggest a substantial increase in variability of light conditions and a declining influence of basal area as measurement positions move up through the live aspen canopy (Pritchard and Comeau 2004; Comeau et al. 2006). Equations for estimating transmittance developed in this study should only be applied

Table 6. Predictive ability of white spruce stem volume increment by competition indices and initial diameter (R^2_{adj} values).

Location	Installation	Model type	Competition index *N*	BA	LOR1	LOR2	VCR1	VCR2	SCR1	SCR2	SCROS1
Peace River	Medium	1	0.51	0.52	0.53	0.59	0.47	0.58	0.52	0.60	0.51
		2	0.78	0.79	0.79	0.79	0.78	0.79	0.79	0.79	0.78
	Superior	1	0.36	0.41	0.40	0.45	0.40	0.53	0.40	0.51	0.41
		2	0.85	0.86	0.86	0.85	0.86	0.86	0.86	0.86	0.86
Prince Albert	Medium	1	0.11	0.17	0.14	0.19	0.14	0.30	0.14	0.25	0.13
		2	0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.93
	Superior	1	0.36	0.38	0.38	0.42	0.39	0.53	0.39	0.50	0.39
		2	0.64	0.64	0.64	0.64	0.64	0.66	0.64	0.66	0.64
Edson	Medium	1	0.22	0.23	0.23	0.26	0.23	0.33	0.23	0.31	0.22
		2	0.78	0.79	0.78	0.78	0.80	0.78	0.80	0.78	0.79
	Superior	1	0.20	0.24	0.22	0.27	0.28	0.36	0.26	0.34	0.27
		2	0.89	0.88	0.89	0.89	0.88	0.88	0.89	0.88	0.89
	Grande Prairie	1	0.04	0.05	0.04	0.09	0.04	0.18	0.05	0.15	0.05
		2	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75

Note: All values presented are for statistically significant models ($p < 0.001$). Model 1 is SVI = $a\,\mathrm{e}^{(b\mathrm{CI})}$ for CI = *N* to SCROS4 and SVI = $a(\mathrm{CI})^b$ for $a(\mathrm{CI})^b(\mathrm{Dsw})^c$ for CI = DIFM, DIFT, $\mathrm{SF_T}$, and $\mathrm{SF_{AW}}$. SVI is stem volume increment of spruce, CI is competition index as defined in Table 2, Dsw is initial

Table 7. Test of difference between locations and installations for models predicting stem volume increment of white spruce as a function of transmittance (*p* values).

	Peace River medium	Peace River superior	Prince Albert	Edson	Grande Prairie
Peace River medium		0.003*	0.0001*	0.0001*	0.0001*
Peace River superior			0.043*	0.0001*	0.0001*
Prince Albert				0.069	0.0001*
Edson					0.0001*
Grande Prairie					

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model SVI = $a(\mathrm{DIFM})^b$; where SVI is stem volume increment of spruce, DIFM is light transmittance in the understory measured at the spruce midcrown, and *a* and *b* are model parameters; the asterisk associated with the *p* values indicates a significant difference ($p < 0.05$). For Prince Albert and Edson, there was no significant difference between the medium and superior installations.

to situations where the spruce midcrown point is below the base of the aspen canopy.

Differences in parameter values between locations may be related to the influence of climatic and site factors, particularly soil moisture, on relationships between leaf area index and basal area or crown cover. Messier et al. (1998) suggested this as the reason for differences in understory light levels for stands with similar basal area in Quebec and Alberta. Comeau et al. (2006) also reported regional differences in parameter values for models relating transmittance to aspen basal area that appear to be related to climate. Lower precipitation and soil moisture levels as a result of regional and year to year variation appear to lead to reduced aspen leaf area index and increased light availability in the understory.

Data in our study were collected from a range of aspen densities 5–7 years following spacing, and it is possible that differences in rates of crown and leaf area development between locations and sites influence our results. Temporal and spatial variations in leaf area index attributed to forest management and site factors have been observed in temperate deciduous forests (Le Dantec et al. 2000). Moreover, rates of leaf area index recovery following thinning seem to be site specific owing to differences in productivity (Jokela et al. 2004). Further studies are needed to determine if relationships between transmittance and basal area (or other competition measures) change over time as a reflection of annual growing conditions, time after treatment, and other factors.

Although crown-based indices are expected to perform better than other indices (Biging and Dobbertin 1992), we have found that the performance of stem diameter based indices was only slightly inferior, raising the question of whether the more difficult and expensive field measurements associated with crown indices are justified by the small gain in predictive power. The relatively small difference between indices within individual sites may be explained in part by the strong correlation between aspen measures and leaf area (Pinno et al. 2001). It is somewhat surprising that the number of stems performed reasonably well, with better performance at some sites than at others. Similar results are reported in a study of effects of aspen competition on growth of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in central British Columbia (Newsome et al. 2003). The coefficient of determination for models using number of stems as the competition index was higher for sites with fairly uniform and well-stocked aspen stands than at sites with heterogeneous stands having larger size differentiation. At the same time, basal area appears to serve as a consistently good predictor of both light and spruce growth on a site by site basis. Basal area may be more desirable for general application, since it incorporates both aspen diame-

SCROS2	HEG4	VCR4	SCR4	SCROS4	DIFM	DIFT	SF_T	SF_{AW}
0.57	0.58	0.59	0.59	0.56	0.57	0.48	0.44	0.43
0.79	0.78	0.79	0.79	0.78	0.80	0.77	0.77	0.79
0.50	0.42	0.50	0.47	0.46	0.44	0.46	0.38	0.31
0.86	0.85	0.85	0.85	0.85	0.87	0.86	0.86	0.85
0.25	0.16	0.26	0.21	0.21	0.21	0.16	0.20	0.17
0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.93
0.50	0.38	0.49	0.46	0.46	0.37	0.33	0.44	0.42
0.65	0.63	0.65	0.65	0.64	0.64	0.63	0.64	0.64
0.31	0.26	0.31	0.28	0.30	0.22	0.24	0.21	0.21
0.78	0.77	0.78	0.78	0.78	0.78	0.78	0.79	0.80
0.33	0.27	0.35	0.32	0.33	0.29	0.30	0.22	0.17
0.88	0.88	0.87	0.87	0.87	0.87	0.86	0.86	0.85
0.16	0.06	0.14	0.11	0.11	0.10	0.07	0.03	0.02
0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75

CI = DIFM, DIFT, SF_T, and SF_{AW}; Model 2 is SVI = $a\,e^{(bCI)}(Dsw)^c$ for CI = N to SCROS4 and SVI = stem diameter of spruce, and a, b, and c are model parameters.

Fig. 3. Relationships between stem volume increment of white spruce during the 2-year measurement period (2002–2003) for (*a* and *b*) Peace River medium and (*c* and *d*) Peace River superior and trembling aspen basal area and initial white spruce diameter (2002). Lines shown are based on nonlinear regressions fit to data using the independent variable shown on the *x*-axis and with values of the second independent variable set to three different values selected to illustrate the range of variation in this variable as indicated in the legend below each graph. Regression models: (*a* and *b*) SVI = 271.75 $e^{(-0.0620\,BA)}\,Dsw^{1.9539}$ (n = 60, MS_{res} = 3.2906, R^2_{adj} = 0.79); (*c* and *d*) SVI = 59.5 $e^{(-0.0522\,BA)}\,Dsw^{2.9912}$ (n = 60, MS_{res} = 1.2416, R^2_{adj} = 0.86).

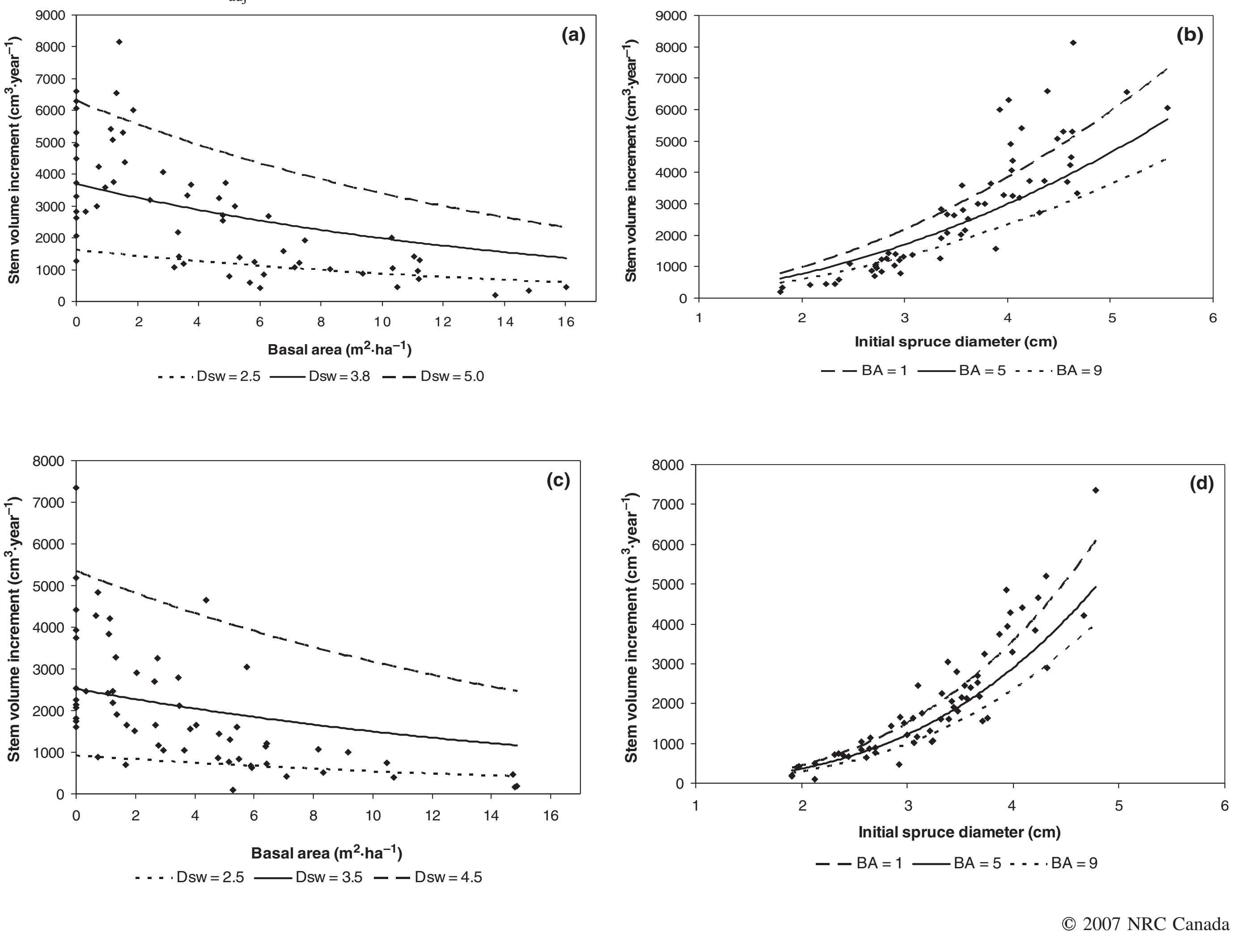


Fig. 4. Relationships between stem volume increment of white spruce during the 2-year measurement period (2002–2003) for (*a* and *b*) Peace River medium and (*c* and *d*) Peace River superior and light transmittance and initial white spruce diameter (2002). Lines shown are based on nonlinear regressions fit to data using the independent variable shown on the *x*-axis and with values of the second independent variable set to three different values selected to illustrate the range of variation in this variable as indicated in the legend below each graph. Regression models: (*a* and *b*) SVI = 312.1 DIFM$^{0.4382}$ Dsw$^{1.8968}$ (n = 60, MS_{res} = 3.1749, R^2_{adj} = 0.80); (*c* and *d*) SVI = 65.5 DIFM$^{0.3205}$ Dsw$^{2.9363}$ (n = 60, MS_{res} = 1.2054, R^2_{adj} = 0.87).

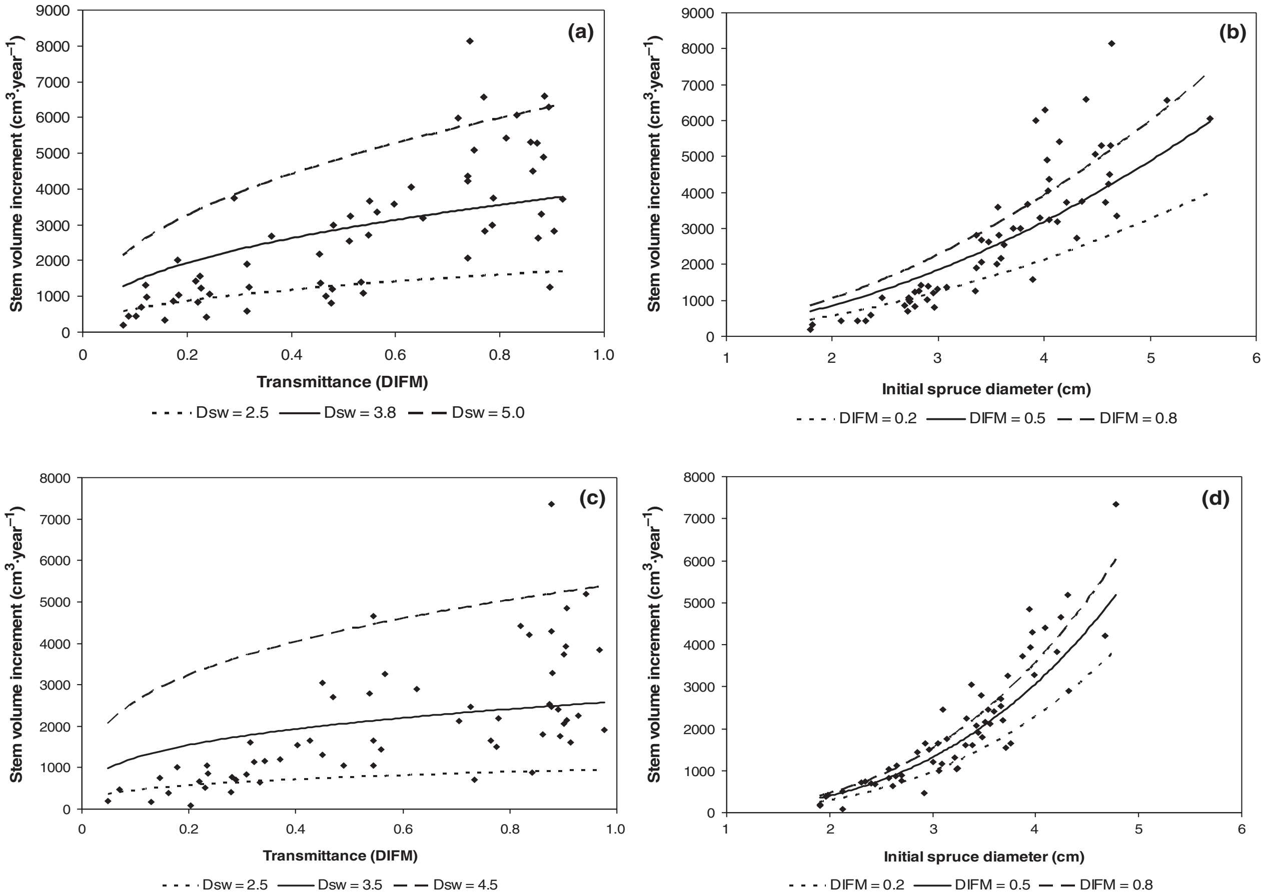


Table 8. Test of difference between locations and installations for models predicting stem volume increment of white spruce as a function of basal area of overtopping trembling aspen and initial stem diameter of spruce (p values).

	Peace River	Prince Albert	Edson	Grande Prairie
Peace River		0.0001*	0.0001*	0.0001*
Prince Albert			0.706	0.283
Edson				0.068
Grande Prairie				

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model SVI = $a\,e^{(b\mathrm{BA})}(\mathrm{Dsw})^c$ where SVI is stem volume increment of spruce, BA is basal area of overtopping aspen, Dsw is initial stem diameter of spruce, and *a*, *b*, and *c* are model parameters; the asterisk associated with the *p* values indicates a significant difference (p < 0.05). For all locations, there was no significant difference between the medium and superior installations.

ter, which is correlated with leaf area of individual trees, and the number of trees; consequently, basal area may be applicable across a range of ages and sites.

The group of indices that included crop tree size (LOR2, VCR2, SCR2, and SCROS2) offered only a slight improvement over indices that did not include crop tree size (LOR1, VCR1, SCR1, and SCROS1); therefore, concerns over artificially inflating predictive power through including crop tree size in size ratio indices were partially alleviated for the particular stand structure in our study (i.e., young mixedwoods with planted spruce under spaced aspen). Another controversial aspect is whether to incorporate distance between crop tree and competitors in competition indices (Daniels et al. 1986; Tomé and Burkhart 1989). In our study, distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) provided inferior predictions to distance-independent indices, confirming previous findings for juvenile mixtures of spruce and aspen or paper birch (Alemdag 1978; Comeau et al. 2003). Our versions of distance-dependent indices were based on spatial information from only the four closest competitors, given practical methodological limitations, while the search radius was 3.99 m (see Materials and methods). However, it is still possible that distance-dependent indices perform better than distance-independent indices in more heterogeneous stands where larger competition plots are used.

Our results are consistent with the expectation (e.g., Wright et al. 1998; Coates and Burton 1999) that increases in available resources are associated with positive spruce growth responses. However, the measures of competition explain less than 60% of the variation in spruce stem increment, suggesting that aspen competition is only one of many factors affecting growth. The fact that R^2_{adj} values are lower for GP, ED, and PA than for PR may reflect the effects of microclimatic extremes (frost), wildlife, and competition from other vegetation (i.e., grasses and shrubs). In addition, our findings show that there are differences in growth–competition relationships between locations. Other studies indicate that competitive effects may vary as a function of climate, availability of resources, and influences of other limiting factors. Both the most effective competition measure and the relationships between lodgepole pine growth and competition were found to vary with study location (Newsome et al. 2003). Pritchard (2003) and Voicu and Comeau (2006) also found significant site differences in relationships between white spruce growth and transmittance. Green and Hawkins (2005) suggested that competitive interactions may differ between north-facing and south-facing slopes in subboreal mixedwood stands owing to changes in environmental conditions.

There are few plant competition studies that examined the influence of environmental factors on competition. An extensive literature search and meta-analysis of results from plant competition studies (Goldberg and Barton 1992) suggest that the magnitude of competition does not depend on site, but authors did not find it conclusive given the very limited number of studies testing site influences. Moreover, the same meta-analysis indicates that outcomes of competition studies are sometimes conflicting; for example, findings from natural density studies are not consistent with results from experimentally created gradients.

Another aspect often neglected when interpreting competition effects is that competition and facilitation usually occur together and can result in very complex interactions (Holmgren et al. 1997). Broadleaf overstory manipulation simultaneously impacts competitive and facilitative interactions (Simard and Vyse 2006). Facilitative effects of aspen in the boreal forest may include reduced photorespiration and photoinhibition of understory spruce (Singsaas et al. 2000; Langvall and Örlander 2001), reduced grass and shrub competition (Lieffers and Stadt 1994), amelioration of frost (Groot and Carlson 1996; Pritchard and Comeau 2004), and reduced incidence of insect damage (Taylor et al. 1996). Separating the influences of competition and facilitation on tree performance is difficult, and facilitation may be overshadowed by the importance of competition for light. Nevertheless, the balance between competition and facilitation may shift from site to site owing to variation in the relative occurrence and importance of each factor (Callaway 1998) and may offer another explanation for variation in relationships between growth and competition. For example, frost occurrence and intensity and the incidence of insect damage were observed to be site specific in boreal mixedwood sites (Voicu and Comeau 2006).

Although competition for light seems to be the driving factor affecting spruce growth, other interactions are also likely to be occurring at the same time, such as competition for other resources (water and nutrients), physical interaction (e.g., leader whipping), microclimatic effects (soil and air temperature), and other interactions (DeLong 1991). The differential availability of resources and their interplay influence sapling growth in the understory (Finzi and Canham 2000). In addition, local site characteristics may affect growth relationships (Kobe 1996).

Adding initial size as a second explanatory variable increased the predictive power of our models of spruce growth. The ability of competition indices to explain growth variation seems to be limited and the use of initial size as an additional variable is recommended by several studies (Morris and MacDonald 1991; MacFarlane and Kobe 2006). While competition indices incorporate present growth conditions, subject tree size at the beginning of the growing period is considered to account for past factors, acting as the "tree memory" of previous external and internal influences (Hatch et al. 1975). Subject tree size may also provide a surrogate measurement of tree leaf area, which will have an important influence on the amount of light being absorbed and utilized by the tree (Pritchard 2003).

In our study, initial diameter performed better for describing variation in spruce growth than other initial size measures. This is consistent with the pipe model theory (Waring et al. 1982; Chiba 1998), suggesting that stem conducting cross-sectional area is strongly correlated with tree leaf area. In some cases, other measures of tree size such as crown surface area have been more closely related to growth than diameter or height (Pritchard 2003; Voicu and Comeau 2006). Variation in the effectiveness of tree measures may be influenced by the ability to represent variation in leaf area, as well as by site, relative position in the canopy, or other characteristics that may influence tree growth.

Our results show that several types of competition indices can be used to predict understory transmittance and spruce growth. Simple indices such as basal area or Lorimer's had very close predictive abilities to those of more complex indices based on crown measurements. Selection of which index to use in certain conditions should be based on desired levels of precision and resources available to collect and process field data. Indices tested in our study can have a direct application in traditional growth and yield models and can facilitate the transition of growth modeling from the juvenile stage to intermediate and mature stands (Vanclay 1994). Moreover, some of the indices tested in our study may provide a link to other types of models. For example, basal area may incorporate light into empirical growth and yield models, whereas crown size may offer a link to other hybrid and process-based models.

Conclusions

Results from our study indicate that distance-independent competition indices (basal area and Lorimer's) work as well or better than distance-dependent indices for characterizing trembling aspen competition with white spruce in young mixedwood boreal stands in western Canada. Crown competition indices provide only a small gain over simpler indices readily obtained from common field measurements. Relationships between aspen competition and either light or spruce growth vary from site to site, making region-specific calibration of these relationships necessary. Further study is needed to understand the factors contributing to this variation.

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References

Alemdag, I.S. 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. Can. For. Serv. For. Manag. Inst. Inf. Rep. FMR-X-108.

Bates, D.M., and Watts, D.G. 1988. Non-linear regression analysis and its applications. Wiley, New York.

Beckingham, J.D., and Archibald, J.H. 1996. Field guide to ecosites of northern Alberta. Can. For. Serv. North. For. Cent. Spec. Rep. 5.

Beckingham, J.D., Corns, I.G.W., and Archibald, J.H. 1996*a*. Field guide to ecosites of west-central Alberta. Can. For. Serv. North. For. Cent. Spec. Rep. 9.

Beckingham, J.D., Nielsen, D.G., and Futoranski, V.A. 1996*b*. Field guide to ecosites of the mid-boreal ecoregions of Saskatchewan. Can. For. Serv. North. For. Cent. Spec. Rep. 6.

Biging, G.S., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**: 695–720.

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can. J. For. Res. **23**: 2141–2152.

Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos, **82**: 561–573. doi:10.2307/3546376.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**: 137–166. doi:10.1139/a02-007.

Chiba, Y. 1998. Architectural analysis of relationships between biomass and basal area based on pipe model theory. Ecol. Model. **108**: 219–225. doi:10.1016/S0304-3800(98)00030-1.

Coates, K.D., and 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. doi:10.1139/cjfr-29-9-1374.

Comeau, P.G., Letchford, T., and Wang, J.R. 1998. An evaluation of indexes for estimating competition for light by paper birch. *In* Third International Conference on Forest Vegetation Management: popular summaries. *Edited by* Robert G. Wagner and Dean G. Thompson. Ont. Minist. Nat. Resour. Ont. For. Inst. For. Res. Inf. Pap. No. 141. pp. 408–410.

Comeau, P.G., Wang, J.R., and 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. doi:10.1139/x03-117.

Comeau, P.G., Kabzems, R., McClarnon, J., and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. For. Chron. **81**: 559–574.

Comeau, P.G., Heineman, J.L., and Newsome, T. 2006. Evaluation of relationships between understory light and aspen basal area in the B.C. central interior. For. Ecol. Manag. **226**: 80–87.

Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. **22**: 454–456.

Daniels, R.F., Burkhart, H.E., and Clason, T.R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. **16**: 1230–1237.

DeLong, S.C. 1991. The light interception index: a potential tool for assisting in vegetation management decisions. Can. J. For. Res. **21**: 1037–1042.

Draper, N.R., and Smith, H. 1981. Applied regression analysis. Wiley, New York.

Finzi, A.C., and Canham, C.D. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. For. Ecol. Manag. **131**: 153–165.

Gendron, F., Messier, C., and Comeau, P.G. 1998. Comparison of different methods for estimating light transmittance in forest. Agric. For. Meteorol. **92**: 55–70. doi:10.1016/S0168-1923(98)00082-3.

Goldberg, D.E., and Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am. Nat. **139**: 771–801. doi:10.1086/285357.

Green, D.S., and Hawkins, C.D.B. 2005. Competitive interactions in sub-boreal birch–spruce forests differ on opposing slope aspects. For. Ecol. Manag. **214**: 1–10.

Groot, A., and 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.

Hatch, C.R., Gerrard, D.J., and Tappeiner, J.C., II. 1975. Exposed crown surface area: a mathematical index of individual tree growth potential. Can. J. For. Res. **5**: 224–228.

Hegyi, F. 1974. A simulation model for managing jack pine stands. *In* Growth models for tree and stand simulation. *Edited by* Jöran Fries. Royal College of Forestry, Stockholm, Sweden. pp. 74–90.

Hix, D.M., and Lorimer, C.G. 1990. Growth–competition relationships in young hardwood stands on two contrasting sites in southwestern Wisconsin. For. Sci. **36**: 1032–1049.

Holmes, M.J., and Reed, D.D. 1991. Competition indices for mixed species northern hardwoods. For. Sci. **37**: 1338–1349.

Holmgren, M., Scheffer, M., and Houston, M.A. 1997. The interplay of facilitation and competition in plant communities. Ecology, **78**: 1966–1975. doi:10.2307/2265937.

Hynynen, J., and Ojansuu, R. 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. Can. J. For. Res. **33**: 455–465. doi:10.1139/x02-173.

Jokela, E.J., Dougherty, P.M., and Martin, T.A. 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. For. Ecol. Manag. **192**: 117–130.

Kobe, R.K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecol. Monogr. **66**: 181–201. doi:10.2307/2963474.

Langvall, O., and Örlander, G. 2001. Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Can. J. For. Res. **31**: 155–164. doi:10.1139/cjfr-31-1-155.

Le Dantec, V., Dufrêne, E., and Saugier, B. 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. For. Ecol. Manag. **134**: 71–81.

Lieffers, V.J., and 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.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. **6**: 343–360.

MacFarlane, D.W., and Kobe, R.K. 2006. Selecting models for capturing tree-size effects on growth–resource relationships. Can. J. For. Res. **36**: 1695–1704. doi:10.1139/X06-054.

MacIsaac, D.A., and Navratil, S. 1996. Competition dynamics in juvenile boreal hardwood–conifer mixtures. *In* Silviculture of temperate and boreal broadleaf–conifer mixtures. *Edited by* Philip G. Comeau and Keith D. Thomas. B.C. Minist. For. Land Manag. Handb. pp. 23–34.

Martin, G.L., and Ek, A.R. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. For. Sci. **30**: 731–743.

Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment of mixed forest. J. Veg. Sci. **9**: 511–520. doi:10.2307/3237266.

Morris, D.M., and MacDonald, G.B. 1991. Development of a competition index for young conifer plantations established on boreal mixedwood sites. For. Chron. **67**: 403–410.

Newsome, T., Heineman, J.L., and Nemec, A. 2003. Competitive effects of trembling aspen on lodgepole pine performance in the SBS and IDF zones of the Cariboo–Chilcotin region of south-central British Columbia. B.C. Minist. For. Res. Branch Tech. Rep. 005.

Ott, P. 1997. The use of indicator variables in non-linear regression. B.C. Minist. For. Biom. Inf. Pamphlet No. 56.

Peterson, E.B., and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Can. For. Serv. North. For. Cent. Spec. Rep. 1.

Pinno, B.D., Lieffers, V.J., and Stadt, K.J. 2001. Measuring and modelling the crown and light transmission characteristics of juvenile aspen. Can. J. For. Res. **31**: 1930–1939. doi:10.1139/cjfr-31-11-1930.

Pritchard, J.M. 2003. The effect of opening size on light, temperature and the growth of white spruce under a trembling aspen canopy. M.Sc. thesis, Faculty of Graduate Studies and Research, University of Alberta, Edmonton, Alta.

Pritchard, J.M., and Comeau, P.G. 2004. Effects of opening size and stand characteristics on light transmittance and temperature under young trembling aspen stands. For. Ecol. Manag. **200**: 119–128.

Ratkowsky, D.A. 1990. Handbook of nonlinear regression models. M. Dekker, New York.

Simard, S.W., and Sachs, D.L. 2004. Assessment of interspecific competition using relative height and distance indices in an age sequence of seral interior cedar–hemlock forest in British Columbia. Can. J. For. Res. **34**: 1228–1240. doi:10.1139/x04-008.

Simard, S.W., and Vyse, A. 2006. Trade-offs between competition and facilitation: a case study of vegetation management in the interior cedar–hemlock forests of southern British Columbia. Can. J. For. Res. **36**: 2486–2496. doi:10.1139/X06-150.

Singsaas, E.L., Ort, D.R., and DeLucia, E.H. 2000. Diurnal regulation of photosynthesis in understory saplings. New Phytol. **145**: 39–49. doi:10.1046/j.1469-8137.2000.00556.x.

Steneker, G.A., and Jarvis, J.M. 1963. A preliminary study to assess competition in a white spruce – trembling aspen stand. For. Chron. **39**: 334–336.

Taylor, S.P., Alfaro, R.I., DeLong, C., and Rankin, L. 1996. The effects of overstory shading on white pine weevil damage to white spruce and its effect on spruce growth rates. Can. J. For. Res. **26**: 306–312.

Tomé, M., and Burkhart, H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. **35**: 816–831.

Vanclay, J.K. 1994. Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, U.K.

Voicu, M.F. 2005. Gradients in microclimate and spruce growth adjacent to young aspen stands. M.Sc. thesis, Faculty of Graduate Studies and Research, University of Alberta, Edmonton, Alta.

Voicu, M.F., and Comeau, P.G. 2006. Microclimatic and spruce growth gradients adjacent to young aspen stands. For. Ecol. Manag. **221**: 13–26.

Waring, R.H., Scroeder, P.E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **12**: 556–560.

Weigelt, A., and Jolliffe, P. 2003. Indices of plant competition. J. Ecol. **91**: 707–720. doi:10.1046/j.1365-2745.2003.00805.x.

Welden, C.W., and Slauson, W.L. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Q. Rev. Biol. **61**: 23–44. PMID:3961095.

WESBOGY. 2004. Long term study of growth and development of mixed stands of spruce and aspen. Experimental Design, Data Collection and Database Maintenance Manual [online]. Available from http://www.wesbogy.rr.ualberta.ca/DataCollectionManual2004.pdf [cited 5 September 2006].

Wright, E.F., Coates, K.D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. **28**: 871–886. doi:10.1139/cjfr-28-6-871.