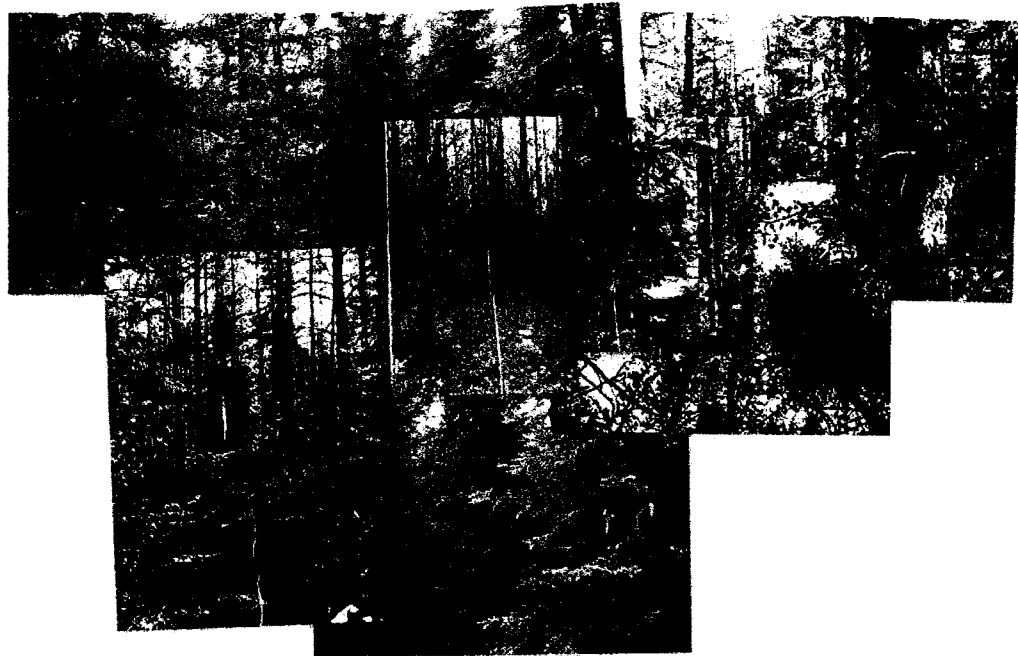


ASSESSING ABOVE- AND BELOWGROUND COMPETITIVE EFFECTS
IN PURE AND MIXED STANDS OF JACK PINE (*Pinus banksiana*)
AND BLACK SPRUCE (*Picea mariana*)

by

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Faculty of Forestry and the Forest Environment
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Lakehead University

September 2009

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ABSTRACT

Cowie, T.L. 2009. Assessing above- and belowground competitive effects in pure and mixed stands of jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*). 118pp.

Keywords: aboveground competition, belowground competition, conifer mixedwood, competition index, competitive reduction, radial growth.

Ecological principles of niche, competition and competitive reduction suggest that competition in mixed stands composed of pine and spruce may experience positive interactions through (1) vertical stratification of canopy and (2) vertical separation of roots.

In order to evaluate above- and belowground competitive interactions of pure and mixed stands composed of jack pine (*Pinus banksiana* (Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) I: (1) reviewed mechanisms of competition and competitive reduction, (2) located even-aged, unmanaged single- and mixed-species stands of pine and spruce on intermediate sites within the boreal forest of Northwestern Ontario, (3) calculated three competition indices to quantify competition in pure and mixed stands of the component species and compared the indices to identify which best describes competition in a mixed stand, and (4) determined if rooting patterns of pine and spruce are affected by a mixture.

Competition indices showed that spruce generally experienced a wider variety of competitive conditions over pine. Values computed from a species-specific index indicated that there is a strong intraspecific effect within both the target tree species. However, while jack pine showed to have a strong interspecific competitive effect on black spruce, black spruce had a weak interspecific competitive on jack pine. The weak relationship between radial growth and competition index suggests that competition may not be strong in these stands, which may reflect the complementary growth patterns and resource requirements of the component species or the stage of stand development.

Jack pine preferred to put its roots in the upper portion of the mineral soil regardless of stand type. However, there was a significantly higher percentage of jack pine roots in the lower mineral soil layers of the mixedwood stand compared to spruce, which indicates jack pine are exploiting more of the soil profile in the mixtures. It was found that black spruce prefer to root in the organic and upper mineral soil layers regardless of site or stand type. In the mixedwood, the spruce had a significantly smaller amount of biomass because it is sharing soil space with pine, causing the spruce to put their roots in the available space.

These results suggest that pine-spruce mixedwood have the potential to be more productive than pure stands of the component species as competition is likely reduced in these stands due to differing growth patterns. Investigation into the productivity of these stands is necessary so that silvicultural prescriptions can be developed for these naturally occurring stands commonly found throughout northwestern Ontario.

CONTENTS

LIBRARY RIGHTS STATEMENT	ii
A CAUTION TO THE READER	iii
ABSTRACT	iv
CONTENTS	v
TABLES	vii
FIGURES	ix
ACKNOWLEDGEMENTS	x
INTRODUCTION	1
LITERATURE REVIEW	3
CANADIAN BOREAL FOREST	3
OVERVIEW OF JACK PINE AND BLACK SPRUCE	4
Jack Pine	4
Black Spruce	6
POTENTIAL FOR INCREASED PRODUCTIVITY IN MIXED STANDS	8
Ecological Theories	9
Reduction of Crown Competition	13
Physiological Separation	13
Physical Separation	14
Temporal Separation	16
Reduction of Root Competition	17
Physiological Separation	18
Physical Separation	18
Temporal Separation	19
SPECIES INTERACTIONS	19
Pure Stands	20
Mixed Stands	20
POTENTIAL OF REDUCED COMPETITION IN JACK PINE- BLACK SPRUCE MIXED STANDS	22
COMPETITION INDICES TO DESCRIBE COMPETITIVE INTERACTIONS	24
MANAGING JACK PINE-BLACK SPRUCE MIXEDWOODS	29

MATERIALS AND METHODS	32
EXPERIMENTAL SITES	32
EXPERIMENTAL DESIGN AND DATA COLLECTION	35
COMPETITION INDICES	41
ROOT CORES	44
DATA ANALYSIS	46
Linear Regression Model	46
Analysis of Variance Model	47
RESULTS AND DISCUSSION	50
COMPETITION INDICES	50
Competition Index as a Predictor of Radial Growth	59
BELOWGROUND COMPETITION	69
Black Spruce	72
Jack Pine	73
CONCLUSION	76
LITERATURE CITED	78
APPENDIX I: SUMMARY OF STAND STATISTICS OF RECONNAISSANCE DATA COLLECTION	92
APPENDIX II: SUMMARY OF INDIVIDUAL TREE CHARACTERISTICS AND COMPETITION INDEX DATA	93
APPENDIX III: SUMMARY OF ANALYSIS OF VARIANCE RESULTS FOR BLACK SPRUCE	116
APPENDIX IV: SUMMARY OF ANALYSIS OF VARIANCE RESULTS FOR JACK PINE	117
APPENDIX V: ROOT BIOMASS STATISTICS BY STAND TYPE	118

TABLES

Table

1. Species' mixture studies.	9
2. Examples of distance-independent and distance-dependent competition indices.	26
3. Maximum likelihood parameter of Canham's model.	28
4. Nomenclature used to describe the results and discuss the results of this study.	33
5. Study site characteristics.	35
6. Summary of stand characteristics for the Gamsby and Greta sites and stand types	40
7. List of competition indices used in this study.	41
8. Expected Mean Square derivation for Equation 4.	49
9. Hypothesis tests for Equation 4.	49
10. Descriptive statistics for each competition index by species.	51
11. The fifteen highest index values by competition index with corresponding stand and individual tree characteristics for black spruce.	55
12. The fifteen highest index values by competition index with corresponding stand and individual tree characteristics for jack pine.	56
13. Linear regression coefficients and statistics for predicting radial growth from competition index.	62
14. Slopes (B) and t-values calculated to test differences between species for competition index versus radial growth shown in Figure 6.	64
15. Summary of F-ratios calculated by ANOVA for black spruce and jack pine root biomass and percentage root biomass.	69
16. Student-Newman-Keuls tests of significant main effects for black spruce root biomass and percentage root biomass.	70

Table

17. Student-Newman-Keuls tests of significant main effects for jack pine root biomass and percentage root biomass.	70
18. Summary stand statistics from reconnaissance data collection. The mean represents the average of five plots per stand and site type.	92
19. Summary table of black spruce individual tree characteristics and competition index data.	93
20. Summary table of jack pine individual tree characteristics and competition index data.	103
21. Summary of ANOVA components for black spruce root biomass.	116
22. Summary of ANOVA components for percentage of black spruce root biomass.	116
23. Summary of ANOVA components for jack pine root biomass.	117
24. Summary of ANOVA components for percentage of jack pine root biomass.	118
25. Summary of root biomass statistics by stand type.	118

FIGURES

Figure

1. Diagrams of jack pine-black spruce plantation designs; (a) fine-grained mixture with a stratified canopy with an equal proportion of each species; (b) fine grained mixture as well, but with unequal species proportions. 31
2. Examples of a) a pure spruce transect, b) a pure jack pine transect and c) a mixedwood transect 37
3. Diagram depicting the methodology used for selecting the position to collect root cores. The subject and competitor trees are denoted by S and C, respectively. 45
4. Frequency distribution of computed competition indices for black spruce (top) and jack pine (bottom) 52
5. Estimated λ and 95% confidence intervals for the per capita effect of each of the four species of competitors on target species of a) jack pine and b) black spruce. 58
6. Scatterplots and fitted regression line of radial growth and competition index (Hegyi, Schütz, and Canham, respectively) for spruce and pine. 61
7. Expected vs. observed radial growth for black spruce (left) and jack pine (right) for Hegyi's, Schütz's, and Canham's competition indices, respectively. Lines are a 1:1 relationship between predicted and observed growth. 66
8. Expected vs. observed radial growth for black spruce (top) and jack pine (bottom) for Canham's adapted maximum likelihood estimation (MLE) model. Lines are a 1:1 relationship between predicted and observed growth. 67
9. Relationship between depth and a) average Sb root biomass, b) average Pj root biomass, c) average percentage Sb root biomass, and d) average percentage of Pj root biomass. 71

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INTRODUCTION

Mixedwoods are forest ecosystems in which no single species comprises more than 80% of the total basal area (MacDonald 1995). Mixed-species stands with a deciduous component have received a lot of attention in the literature (e.g. Wierman and Oliver 1979; Brown 1992; Montagnini 2000; Montagnini *et al.* 1995; Wang *et al.* 1995, 2000; DeBell *et al.* 1997; Man and Lieffers 1999; Valkonen and Valsta 2001, Frivold and Frank 2002, Bauhus *et al.* 2004, Green 2004, Kabzems and Garcia 2004, Green and Hawkins 2005, Légaré *et al.* 2005, and Pitt and Bell 2005). Much less is known about mixed stands composed of two conifer species (OMNR 2003). Under the Crown Forest Sustainability Act (CFSA, 1994), forest managers in Ontario are required to implement silvicultural systems that emulate natural pattern and disturbance regimes and conserve biodiversity (OMNR 2002). Mixed-species stands by definition are more diverse than their pure counterparts (Powers 1989) and comprise nearly half (~45%) of Ontario's productive forest (OMNR 2007). In addition, mixed-species stands have the potential of increased productivity over their pure counterparts.

Due to the forecasted decline in allowable harvest of merchantable volume in the boreal forest, intensive silviculture, including mixedwood management, may enhance forest productivity and provide an alternative means of acquiring wood fibre through shortened rotations. The literature suggests that conifer mixedwoods can be more productive than pure stands through competitive reduction and facilitation (Vandermeer 1989) if the component species differ in growth patterns (Karsh 1986; Kelty 1992; Pukkala *et al.* 1994; Chen *et al.* 2003; Amoroso and Turnblom 2006).

Conifer mixedwoods make up approximately 25% of Ontario's productive forest (OMNR 2007). Stands composed of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) are especially common in Northern Ontario on drier sites (OMNR 2003). These stands tend to have a multi-story structure as these species differ in shade tolerance, and consequently growth rates. Non-stand replacing disturbances such as insect and disease outbreaks may be mimicked in conifer mixedwoods by implementing a two-pass removal silvicultural system allowing for the harvest of merchantable jack pine, while enhancing growth of residual black spruce (Hole 1993). A good understanding of how jack pine and black spruce interact when grown together is essential before silvicultural prescriptions can be developed for their management.

The objectives of this study with respect to stands of jack pine, black spruce and their mixtures are: (1) to review mechanisms of competition and competitive reduction, (2) to compare three competition indices to identify which best describes competition in mixed- and pure stands, and (3) to determine if rooting patterns are affected by a mixture. The results from this study have implications for future conifer mixed-species research in Ontario, particularly forest productivity as it relates to competition. In addition, this research can aid in forming hypotheses to test for potential productivity gains of mixed conifer stands in terms of timber volume.

LITERATURE REVIEW

CANADIAN BOREAL FOREST

In Canada, the boreal forest covers approximately 30% of the landscape and makes up 77% of Canada's total forest (NRCAN 2005). The boreal forest stretches from the Yukon to Newfoundland and is found in all provinces except New Brunswick, Nova Scotia, and Prince Edward Island (Rowe 1972). Boreal tree species include black spruce, white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine, and larch (*Larix laricina* (Du Roi) K. Koch) (Weetman 1995).

Boreal mixedwoods (BMWs) make up 22% of Canada's forests (NRCAN 2005). Boreal mixedwoods are defined in Ontario as stands dominated by shade-intolerant hardwoods in early succession, mid-tolerant conifers in mid-succession, and shade-tolerant conifers in late successional stages (Chen and Popadiuk 2002) and comprise nearly half of Ontario's productive forest (OMNR 2007). This definition applies to productive sites conducive to mixed-species growth and generally refers to mixed-species stands with a trembling aspen or white birch component.

Mixed stands composed of jack pine and black spruce are common in northwestern Ontario (OMNR 2003), yet there is no silvicultural program currently in place that targets their development and management. A good understanding of the species' silvics is needed in order to predict how they may interact when grown together.

OVERVIEW OF JACK PINE AND BLACK SPRUCE

Jack Pine

Jack pine is a small to medium sized tree; average height is between 17- and 20 m, while diameters range between 20- and 25 cm at maturity (Rudolph and Laidly 1990). The crown architecture of jack pine varies depending on the growing conditions. Open-grown trees exhibit tapered trunks, open conical crowns, and ascending branches (Farrar 1995). Forest grown trees display slender, straight trunks, with short crowns. On poor sites, jack pine trees are often short and twisted, with long stout branches, giving them a disorderly appearance (Farrar 1995). In general, jack pine crowns are sparse compared to those of spruce and allow more light to penetrate the canopy.

In Canada, jack pine is an important source of pulpwood, lumber, and round timber, also providing habitat for birds and small mammals (Rudolph and Laidly 1990). Jack pine is found across Canada from the Atlantic Ocean west to the McKenzie River Valley (Karsh 1986), but is most abundant in Ontario (Rudolph and Laidly 1990). Jack pine covers 5.9 million hectares within the Boreal and Great Lake-St. Lawrence forest regions, contributing 17% of species composition in the boreal forest, second only to black spruce (OMNR 2000). In Ontario, the most productive jack pine stands occur in a crescent-shaped area beginning south of Thunder Bay, continuing north of Lake Nipigon and back south to the area east of Lake Superior and north of Sault Ste. Marie (Fowells 1965).

Jack pine is a pioneer species that readily invades sites where the mineral soil has been exposed by major disturbance, such as fire. In its northern (boreal) range, jack pine bears predominantly serotinous cones, an adaptation to frequent wildfire. It usually grows in pure even-aged or mixed stands on less fertile and drier soils than those

required by other boreal species (Rudolph and Laidly 1990). Jack pine reaches optimal growth on moderately moist sandy loam and clay loam soils (Moore 1984). It exhibits high nutrient-use efficiency (NUE) and water-use efficiency (WUE) and as such, is adapted to dry and infertile soils (Robinson *et al.* 2001). Due to its high WUE, jack pine is more resilient under drought stress than black spruce (Karsh 1986; Grossnickle and Blake 1986; Dang *et al.* 1997; Hebert *et al.* 2006). Robinson *et al.* (2001) showed jack pine seedlings' to have NUEs within an approximate range of 0.05 to 0.25 $\mu\text{mol CO}_2\cdot\text{s}^{-1}\cdot\text{gN}^{-1}$ and WUEs between 0.25 and 5.5 $\mu\text{mol CO}_2\cdot\text{mmol H}_2\text{O}^{-1}$. The values for NUE and WUE decreased as competition increased and varied over time and among specific competitors.

Jack pine seedlings grow faster than other boreal conifers and develop relatively deep roots (Rudolph and Laidly 1990). Roots may reach depths of 2.7 m on sites with deep soils, although the bulk of the rooting system consists of laterals restricted to the upper 46 cm of the soil profile (Rudolph and Laidly 1990). Intense competition for soil moisture and nutrients will cause the lateral roots of jack pine to grow downward (Karsh 1986). Jack pine is one of the most shade-intolerant tree species in its native range. It can be outcompeted by faster growing hardwoods such as trembling aspen or white birch (Rudolph and Laidly 1990).

Seedling growth is rapid with individuals reaching breast height within 5 - 8 years of establishment (Fowells 1965). Mature trees are approximately 17 - 20 m in height and have diameters of 20 - 30 cm at breast height (dbh). Jack pine stands begin to deteriorate after 80 years on good sites and 60 years on poor sites (Rudolph and Laidly 1990); individuals may live to be 150 years old (Farrar 1995). Jack pine can grow on a wide variety of soil types including dry and gravelly soils. However, it will reach its

silvicultural rotation age sooner on well-drained loamy sands. Site quality improves with increasing; i) fine sand, silt, and clay content, ii) water holding capacity, and iii) cation exchange capacity in the upper mineral layers (Rudolph and Laidly 1990).

Generally, jack pine is more productive on deep sites compared to shallow sites. This may be attributed to a relatively deep rooting system which can both access and exploit water and nutrient resources efficiently on deep sites.

Black Spruce

The physical traits of black spruce also vary depending on site and growing conditions. On lowland wet sites, trees are small reaching 8-12 m in height and 13 cm in diameter, with narrow spire-like crowns (Viereck and Johnston 1990). On well-drained upland sites, trees are of medium size and may reach 20 m in height and 25 cm in diameter. In general, the crown architecture of black spruce can be described by short principal branches with drooping lower branches with upturned tips. The upper part of the crown is often very dense (Farrar 1995), allowing little light to penetrate the canopy.

Black spruce is Canada's most important pulpwood species (Viereck and Johnston 1990), providing very high quality pulp because of long fibres in the wood. In its old growth stage, black spruce forests also provide critical habitat for many wildlife species, including the endangered pine marten (*Martes martes*) and woodland caribou (*Rangifer tarandus- caribou*). Black spruce grows coast to coast across Canada; northward from Newfoundland to northwestern Alaska (Fowells 1965). In Ontario alone, black spruce accounts for 50% of the coniferous growing stock and a large portion of Ontario's annual allowable cut (OMNR 2008).

Black spruce usually grows on wet organic soils, which are poorly drained and extremely low in nutrient availability, particularly nitrogen (Patterson *et al.* 1997;

Viereck and Johnston 1990). According to Patterson *et al.* (1997), black spruce may possess the following traits as an adaptation to wet environments:

- 1) low maximal relative growth rates,
- 2) high physiological capacity to extract nutrients, and
- 3) high metabolic ability in the use of nutrients to produce new biomass

Upland black spruce stands tend to be of higher quality, producing healthier trees in a shorter rotation than lowland stands (Viereck and Johnston 1990). Black spruce commonly grows in pure stands on organic sites and in mixed stands on mineral sites with jack pine being a common associate on drier sites (Viereck and Johnston 1990).

Compared to jack pine, black spruce has a shallow root system (Fowells 1965). Its roots may reach 60 cm in depth, but most spread laterally at the moss humus interface with the bulk of the roots in the upper 20 cm of the organic horizons (Viereck and Johnston 1990). Black spruce grows more slowly than many trees and shrubs with which it is associated and therefore encounters considerable competition where species are abundant. It is often found in the understory of jack pine (eastern and central Canada) and lodgepole pine [*Pinus contorta* Dougl. ex. Loud.] (western Canada) stands on dry sites and succeeds pine in the absence of fire or harvesting (Viereck and Johnston 1990).

The silvics of these species indicate that differential resource-use may occur in stands composed jack pine and black spruce, which may lead to a reduction in competition and consequently increased growth.

POTENTIAL FOR INCREASED PRODUCTIVITY IN MIXED STANDS

Traditionally, stand composition, species abundance, growth and productivity of plants have been attributed primarily to competition (Connell 1983; Goldberg and Werner 1983; Fowler 1986; Aarssen and Epp 1990). A large body of literature exists to support the role and the mechanisms of competition (e.g. Ford 1975; Bonan 1988, 1991; Lieffers and Titus 1989; Weiner 1990; Newton and Jolliffe 1998; Brooker *et al.* 2005; Lamb and Cahill 2006; Weigelt *et al.* 2007). However, an increasing number of experimental studies over the past 20 years are providing evidence to support alternative ecological theories, particularly competitive reduction and facilitation (e.g. Wang 1997; Chen *et al.* 2003; Légaré *et al.* 2005; Amoroso and Turnblom 2006). It has been reported that positive plant species interactions may play a major role in the reproduction, distribution, diversity, and productivity of plant communities (Hunter and Aarssen 1988; Kelty 1992; Callaway 1995).

Many naturally occurring mixtures have been investigated to determine whether potential gains exist in terms of productivity by growing mixed-species stands (Table 1). Mixtures have been found to be both more and less productive than their pure counterparts, depending on the species, developmental stage, and site in question (Watt 1955; Grubb 1977; Grace 1985; Kelty 1992; Binkley *et al.* 1992; Callaway 1995; DeBell *et al.* 1997).

Table 1. Species' mixture studies.

Species Mixture	Author(s)
<i>Eucalyptus- Albizia</i>	Binkley <i>et al.</i> 1992; DeBell <i>et al.</i> 1997
<i>Eucalyptus – Acacia mearnsii</i>	Khanna 1997; Bauhus <i>et al.</i> 2004; Forrester <i>et al.</i> 2006
<i>Eucalyptus – Acacia peregrine</i>	Bristow <i>et al.</i> 2006
<i>Fagus sylvatica – Picea abies</i>	Schmid and Kazda 2001; Thelin <i>et al.</i> 2002; Pretzsch and Schütze 2005; Reiter <i>et al.</i> 2005; Bolte and Villanueva 2006
<i>Picea abies – Betula pubescens</i>	Thelin <i>et al.</i> 2002; Doležal <i>et al.</i> 2006
<i>Pseudotsuga menziesii – Alnus rugosa</i>	Shainsky and Radosevich 1992; Binkley 2003; D'Amato and Puettmann 2004
<i>Populus balsamea – Populus tremuloides – Picea glauca – Pinus contorta</i>	Stadt <i>et al.</i> 2007
<i>Populus tremuloides – Picea mariana</i>	Légaré <i>et al.</i> 2004, 2005
<i>Betula papyrifera – Abies lasiocarpa</i>	Wang <i>et al.</i> 2000
<i>Thuja plicata – Tsuga heterophylla</i>	Collins 2000; Wang <i>et al.</i> 2002; Chen <i>et al.</i> 2003; Varga <i>et al.</i> 2005
<i>Pinus contorta – Larix occidentalis</i>	Chen <i>et al.</i> 2003
<i>Pinus contorta – Picea mariana</i>	Chen <i>et al.</i> 2003
<i>Pinus contorta – Pinus ponderosa</i>	Garber and Maguire 2004
<i>Abies grandis – Pinus contorta</i>	Garber and Maguire 2004
<i>Tsuga Canadensis – Picea rubens</i>	Seymour and Kenefic 2002
<i>Tsuga heterophylla – Thuja plicata</i>	Canham <i>et al.</i> 2004
<i>Pseudotsuga menziesii – Tsuga heterophylla</i>	Amoroso and Turnblom 2006
<i>Pinus ponderosa – Pseudotsuga menziesii</i>	Fajardo <i>et al.</i> 2006

Ecological Theories

Three main ecological principles need to be considered when reflecting on how different tree species are able to coexist in forest stands; 1) niche, 2) competition, and 3) competitive reduction. A niche refers to the habitat and position an organism fills in its environment (Grinnell 1917); there are more modern, slightly different interpretations of this word. Elton (1927) stated that a species has a genetically controlled fundamental niche. However, due to competition, it generally only occupies a subset of this, which is referred to as its realized niche (Miller 1964).

Competition is defined as a negative interaction between individuals for limited resources (Kimmins 2004). In ecology, competition is often further defined as intra- and interspecific competition occurring between individuals or another species, respectively. Competitive exclusion, or the idea that no two species occupying the same niche can coexist indefinitely, represents the ultimate outcome of competition (Grime 1973) but is rarely found in nature. Unfortunately, after this point, the nomenclature of competition becomes less clear. In the following paragraphs, I will attempt to explain predominant concepts that apply to my study.

Resource preemption and resource depletion are two concepts that have been used to describe the mechanisms of intraspecific competition within pure even-aged stands (e.g. Newton and Jolliffe 1998). Resource preemption is characterized by larger-sized competitors acquiring a relatively greater proportion of limited resources than smaller-sized competitors (Weiner 1990) and is usually invoked to describe competition for aboveground resources. When thinking in terms of how competition is distributed among trees in a stand, preemption processes are described as being asymmetrical in their effect on tree development. To illustrate, dominant trees in the canopy receive full sunlight and owing to their position, shade out sub-canopy trees, so that the latter receive little to no light. Smaller trees do affect larger individuals by shading out lower branches but are not competing to the same extent. Asymmetrical competition has also been used to describe the temporal advantages of species establishment in a stand (Freckleton and Watkinson 2001). Individuals that occupy a stand first become dominant in the canopy and obtain the majority of resources. Individuals that emerge later occupy the subcanopy and have little effect on the pre-existing trees.

Conversely, resource depletion refers to the idea that limited resources are utilized by competitors in direct proportion to their relative sizes (Weiner 1990) and is usually invoked to describe competition for belowground resources (Newton and Jolliffe 1998). In this case, competition is thought to be distributed among trees symmetrically (Forrester *et al.* 2006). This is because all plants regardless of size are able to acquire equal resources per unit root surface area (Weiner 1985, Weiner and Thomas 1986). However, competition for belowground resources can become asymmetrical if variations in root structure, growth rates, or mycorrhizal associations increase the competitive ability of one species over the other (Forrester *et al.* 2006).

Concurrently, resource depletion and preemption affects relative growth rates and the resultant size hierarchy within dense stands (Weiner 1990). It is useful to introduce the terms one- and two-sided competition as they are often used to describe the outcome of resource preemption and resource depletion, respectively. In mixed stands, the intensity of one-sided competition depends on species' differences, particularly that of shade tolerance and growth rates. The intensity of two-sided competition depends not only on the component species' ability to exploit and utilize belowground resources but also on how they respond to resource deficiencies and excesses (Minore 1979; Bravo *et al.* 2001). While the differences in growth rates between species are exaggerated by one-sided competition for light they are diminished by two-sided competition for nutrients, thus closing the gap in tree size (Weiner 1990; Bravo *et al.* 2001).

Newton and Jolliffe (1998) noted that competition by larger sized individuals led to decreases in specific volume increment, relative growth rates, and relative production rates in smaller individuals. They reasoned that the amount of photosynthate available

to sub-canopy trees for growth and maintenance was reduced, most likely due to changes in carbon allocation patterns and/or lower photosynthetic rates. Stands at the establishment phase or those of relatively low stand density did not exhibit this result (Newton and Jolliffe 1998).

Interactions between individual trees are not always competitive in nature, and there are a variety of ways that the negative effects of competition on growth can be reduced. It is possible for two (or more) species to not only coexist but attain greater productivity than their pure counterparts through competitive reduction (Kelty 1992; Callaway 1995; Man and Lieffers 1999). This concept has also been referred to as the “competitive production principle” (Vandermeer 1989) in reference to the advantage of mixed-species stands over single-species stands as a result of reduced competition. Where competitive exclusion is the end result of complete competition, competitive production recognizes that two species with similar yet distinct requirements may coexist as they experience only weak or reduced competition (Vandermeer 1989). Explanatory mechanisms for the reduction of competition experienced by plants in mixed stands may include differential resource allocation or differentiation in resource use (Vandermeer 1989). These mechanisms are discussed in more detail below in terms of physiological, physical, and temporal separation. Competitive reduction is not to be confused with facilitation, commensalism, or mutualism. Competition and beneficent interactions, including facilitation, can occur simultaneously with potential outcomes varying from exclusion to coexistence involving little competition, loss of one competitor, or competitive reduction (Hunter and Aarssen 1988). Facilitation refers to positive interactions between plants leading to an increase in productivity in mixed stands of trees. Facilitative effects are more commonly seen in mixed stands composed

of a deciduous and coniferous component, with the former often being a nitrogen fixing species. This type of interaction would be described as commensalism by community ecologists since one organism indirectly benefits the other with no reciprocation (Kimmins 2004). For a complete review on facilitative interactions see Callaway (1995). Mutualism describes an interaction between two organisms where both benefit from the existence of the other (Kimmins 2004). The ideas behind commensalism and mutualism imply no negative effect to either organism. Competitive reduction does not negate negative effects; rather it describes a reduction in “harm” to either or both species.

Although competition for light, water, and nutrients occur simultaneously, investigations into the interactions in mixed-species stands tend to divide the areas of study into aboveground competition for light and belowground competition for soil resources (Kelty 1992).

Reduction of Crown Competition

The quest for light highly influences competitive interactions in plant communities (Canham 1990). Aboveground space in forests is fixed, which limits the space leaves can occupy to intercept light (Collins 2000). However, competition can be reduced in the canopy if individual trees of different species are able to separate themselves so that they utilize space more efficiently, filling unique niches. This separation can occur physiologically, physically, or temporally (Callaway 1995).

Physiological Separation

Shade tolerance refers to the relative ability of a plant to survive and grow under low light levels (Daniel *et al.* 1979) and plays an important role in forest structure (Valladares and Niinemets 2008). A gradient of shade tolerance exists from very

tolerant to shade to shade-intolerant, in which case a plant cannot survive shaded conditions. Shade tolerance is an important factor when predicting how two species may interact and the resultant stand dynamics (Bugmann 1996). Species with varying shade tolerances differ in a large amount of physiological traits (Valladares and Niinemets 2008), such as leaf area index (LAI), photosynthetic capacity, and light compensation point.

Complementary differences in shade tolerance can lead to reduced competition in a mixed-species stand. Shade intolerant tree species generally have a more open tree crown and consequently, lower LAI and higher photosynthetic capacity (Bassow and Bazzaz 1997). Light saturated photosynthetic rates differ between shade-intolerant and shade-tolerant trees, with the former reaching the light compensation point at higher light levels than the latter (Givnish 1988). Light compensation point refers to the level of illumination at which the rate of photosynthesis equals the respiration rate (Lewis *et al.* 2000). Shade-tolerant species have lower photosynthetic rates than shade-intolerant species and become light-saturated at lower light levels. Therefore, a combination of shade-intolerant overstory and shade-tolerant understory would reduce competition for light as the two species occupy different niches by acquiring light at different intensities (Kelty 1992).

Physical Separation

Physiological adaptations associated with shade tolerance are complemented by physical adaptations of the crown (Collins 2000), which reflect differences in carbon allocation patterns. At the tree level, carbon is allocated to those areas within the tree that are most likely to increase the plant's survival. Large amounts of carbon are required to repair and maintain the functions of living cells located in existing non-

photosynthetic tissues, as well as for the construction of new leaves, roots, and reproductive structures (Barnes *et al.* 1998). Meeting the carbohydrate demand of tree crowns and roots is the first priority of a plant. The storage of carbohydrates in leaves, stem, and coarse roots has a lower priority than the production of new leaves and roots to acquire resources. Allocation of carbohydrates to stem growth follows that of storage, while the production of chemicals to defend against insects and pathogens is of lowest priority (Waring and Schlesinger 1985).

Allocation patterns are affected by not only the environmental conditions and the age of the stand but also by the shade tolerance of the species. Shade-intolerant species will allocate their resources to stem, branches, and foliage differently than shade-tolerant species (Kelty 1992; Man and Lieffers 1999). Intolerant species tend to allocate more resources to height growth than lateral growth, and as a result attain faster juvenile height growth rates than do shade-tolerant species (Kelty 1992). Shade-tolerant species, on the other hand, allocate more resources to lateral growth, in order to aid interception of light and generally have slower juvenile height growth rates (Kelty 1992). Stratified canopies thus tend to develop naturally in mixed stands composed of species with differing shade tolerances (Amoroso and Turnblom 2006). Trees of differing shade tolerance separate their crowns physically and acquire light at different locations in the canopy thereby reducing niche overlap.

Leaf area and orientation of foliage are two other physical adaptations that complement spatial separation of crowns. Shade-intolerant species generally have low leaf area and orient their leaves on an angle allowing more light to penetrate the canopy to their lower branches (Westoby *et al.* 2002). Alternatively, shade-tolerant species support greater leaf areas and position their leaves horizontally, thereby capturing more

available light (Assmann 1970; Kelty 1992). These physical adaptations enable shade tolerant species to capture diffuse light below the canopy of shade-intolerant species (Collins 2000).

Temporal Separation

Interspecific competition can also be reduced through temporal separation. This occurs seasonally, through phenological separation, or over longer time scales, through successional separation (Man and Lieffers 1999). Phenological separation complements the effects of stratification especially if the stand has a deciduous species in the overstory and a conifer understory. Constabel and Lieffers (1996) found light transmission at three heights, ground, 0.5 m, and 1.3 m, in mixed aspen-white spruce stands was higher in the spring and fall when the aspen are leafless. In these stands, the spruce benefit because they can photosynthesize both earlier and later in the growing season when the poplar are without foliage (Constabel and Lieffers 1996). This may aid in reducing competition since the understory conifer can exploit a longer growing season (Man and Lieffers 1999). Productivity values for black spruce in the western boreal forest of Quebec are approximately $1 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, which is very low (Légaré *et al.* 2005). The tendency of black spruce stands to accumulate organic matter, trapping nutrients, has been used to explain their poor productivity. An aspen overstory is thought to enhance productivity in aspen-spruce mixtures, because the chemical properties of the aspen litter tend to increase nutrient cycling by facilitating decomposition of spruce organic matter (Flanagan and Van Cleve 1983). Aspen-spruce stands in the western boreal forest of Quebec have been found to have productivity values of $2\text{-}3 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (Légaré *et al.* 2005). This difference in productivity has

been hypothesized to be attributed to a combination of reduced competition through phenological separation and increased nutrient cycling.

Early successional species tend to be fast-growing and short-lived, while mid-to-late successional species tend to be slower-growing and attain increased longevity. Seral stage is highly related to shade tolerance (Bailey and Poulton 1968). Shade-intolerant early successional species will occupy a site first and then be slowly replaced by more tolerant species. It is expected that a stand occupied by a shade-intolerant species in early succession and then replaced by a shade-tolerant species in later stages should have higher overall volume production than pure stands of either species (Man and Lieffers 1999). Evidence from a case study of jack pine-black spruce mixedwoods by Hole (1993) near Thunder Bay, Ontario, showed that increased merchantable volume production is possible under a two-pass silvicultural system. This type of harvesting system takes advantage of the differing growth rates of species in a mixed stand.

Reduction of Root Competition

Examination of belowground competition and root structure and functions has received a lot less attention than competition for light. Of the limited literature dealing with belowground interactions in mixed-species stands, the majority pertains to mixtures of deciduous and coniferous species. Very few have examined belowground competition in conifer mixedwoods (e.g. Eis 1974; Wang *et al.* 2002). As with aboveground resources, soil resources can be partitioned through physiological, physical, and temporal separation. The degree to which belowground resources are limited depends upon the site, season, and species present. Different tree species have different root structures and root at different depths in the soil profile (Spurr and Barnes 1980).

Physiological Separation

Different tree species may require different nutrients in varying amounts due to physiological adaptations (Kelty 1992). For example, nitrogen is often considered to be the most limited nutrient in the boreal forest and is available in both ammonium and nitrate forms (Waring and Schlesinger 1985). Competition can be reduced in mixed stands if the component species prefer to uptake nitrogen in its different forms and proportions. Collins (2000) studied positive species interactions in western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) stands. He inferred competition for nitrogen may be reduced in mixed stands because redcedar preferentially uptakes nitrate, while hemlock prefers ammonium. Both jack pine and black spruce prefer inorganic nitrogen in its ammonium form (Swan 1960), so it is unlikely that these species physiologically separate themselves for belowground resources in this manner.

Physical Separation

Soil resources may be partitioned between competing species if the roots of those species occupy different areas of the soil profile. Bolte and Villanueva (2006) reported nearly complete separation of beech (lower layers) and spruce (upper layers) roots in mixed stands. Wang *et al.* (2002) examined mixed stands of western hemlock and western redcedar, and found contrasting results; while the density of fine roots was higher in the mixed stands, roots did not stratify. However, the authors acknowledged that these species are known to occupy similar areas of the soil profile and penetrate to similar depths.

Temporal Separation

Species that demonstrated temporal separation reduce above- and belowground competition simultaneously (Collins 2000). Seasonally, conifers take advantage of the time period when deciduous species are not photosynthesizing to uptake additional water and soil nutrients. Successionally, early seral species have greater access to belowground resources in early stand establishment as they grow faster. As trees in stratified stands age, the overstory species begin to die, allowing later successional species in the understory greater access to soil resources. Since both jack pine and black spruce retain their foliage throughout the year, phenological separation of belowground resources is unlikely.

SPECIES INTERACTIONS

Negative and positive interactions occur simultaneously between plant species occurring in mixtures (Collins 2000). The net outcome of one species' on another is the result of multiple interactions (Weldon and Slauson 1986; Callaway 1995) and is further affected by the developmental stage of the involved species, severity of the environment, and the degree to which resources are limited (Callaway 1995). It is therefore, necessary to study the competitive interactions of each mixture relative to a particular site type and life stage.

Interactions in mixed-species stands occur as the component species compete to capture limited light, water, and nutrients (Jose *et al.* 2006). The degree to which two species will interact depends on the overlap of their requirements for growth and survival. The amount of differentiation between species required to utilize resources more completely when occupying the same site is referred to as "limiting similarity"

(Mackenzie *et al.* 1998). Therefore, the more similar the species in their requirements, the more interspecific competition in a mixed stand will resemble intraspecific competition in a pure stand (Kelty 1992; Jose *et al.* 2006).

Pure Stands

Pure even-aged stands occur after a large disturbance such as fire or harvesting has cleared the land (Smith *et al.* 1997). When timber production is the primary management objective, there is a tendency to favour pure stands of the most productive species since it is both cheaper and easier to manage from a silvicultural point of view (Amoroso and Turnblom 2006). Pure stands experience intraspecific competition which can be more intense than interspecific competition experienced in mixed stands (Mackenzie *et al.* 1998). Crown lift occurs earlier in dense stands as a result of increasing tree height and competition (Makala and Vanninen 1998). However, mixed stands may also facilitate crown lift early in stand development if the understory species effectively shades out the lower bole of the dominant tree species. This could have a positive effect on wood quality in forests managed for lumber by ensuring longer boles with smaller or fewer knots and consequently, higher quality wood.

Mixed Stands

Mixed stands are common in nature especially where soil and climate do not restrict growth (Smith *et al.* 1997). Mixed stands are favoured by forest managers when objectives for management include wildlife conservation, biodiversity, aesthetics, resistance to wind damage, and protection from insect and disease outbreaks (Kelty 1992). As discussed previously, photosynthetic efficiency of foliage, height growth patterns, form, phenology, and rooting patterns have been suggested as potential reasons for a mixed-species stand having overall greater productivity than a pure stand (Kelty

1992). The most productive stands are stratified mixtures composed of faster-growing shade-intolerant species growing above slower-starting shade-tolerant species (Smith 1986; Smith *et al.* 1997). As previously stated, due to differences in shade tolerances among the species these stand types may experience less intense inter- than intraspecific light competition (Amoroso and Turnblom 2006). Mixed species stands are most productive when established at high densities (Amoroso and Turnblom 2006) on sites of medium fertility (Chen *et al.* 2003; Pukkala *et al.* 1994) where neither of the two species is clearly superior to the other.

Amoroso and Turnblom (2006) studied pure and 50/50 mixtures of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock plantations at different densities to compare total yield between mixed-species stands as opposed to monocultures. It was found that shade-intolerant Douglas-fir trees experienced increases in diameter, height, and individual tree volume in the mixture compared to in the pure stand. The opposite effect was found for shade-tolerant western hemlock. Amoroso and Turnblom (2006) determined that mixed stands were more productive than pure stands when densities were high. Low density in mixtures does not allow these two species to express differences in their resource-use because the shade-tolerant hemlock (with a slow juvenile growth rate) was able to escape early suppression.

Chen *et al.* (2003) reported on the productivity differences among even-aged stands of unmanaged single- and mixed-species coniferous stands composed of trees with similar and differing shade tolerances; 1) western hemlock – red cedar, 2) lodgepole pine – western larch (*Larix occidentalis* Nutt.), 3) and lodgepole pine – black spruce. They found that compared with single-species stands, the productivity of a mixed-species stands can be: 1) lower (e.g. a mixture composed of two shade-intolerant

species with similar growth patterns), 2) intermediate, (e.g. a mixture of two shade-tolerant species with different growth dynamics), or 3) higher (e.g. a stratified mixture of shade-intolerant and shade-tolerant species with differing growth patterns).

The lodgepole pine – black spruce mixture found in Western Canada is analogous to jack pine – black spruce mixtures native to the boreal forests of Ontario. It is then reasonable to expect productivity gains in jack pine – black spruce mixtures.

Pukkala *et al.* (1994) used both a single-tree growth model and artificial deterministic simulation models to compare yields of different mixtures of Scots pine and Norway spruce (*Picea abies* (L.) H. Karst) under different thinning regimes. Their findings suggest that volume increment can be 10 to 15% higher in a conifer mixture than a pure pine or spruce stand. Their models also indicated that a spruce competitor decreases the growth rate of a neighbouring spruce more than a pine competitor. Diameter growth of a pine growing in a mixedwood was affected slightly more by another pine than by a spruce of the same size (Pukkala *et al.* 1994).

POTENTIAL FOR REDUCED COMPETITION IN BLACK SPRUCE-JACK PINE MIXED STANDS

Jack pine and black spruce mixtures have the potential of reducing both one- and two-sided competition through crown- and root stratification together with other silvical, morphological, and physiological differences. Jack pine has numerous characteristics that indicate it is intolerant of shade, including a rapid juvenile growth rate. Black spruce is more shade-tolerant and tends to grow more slowly during juvenile stages of stand development. In a spruce-pine mixture, the jack pine typically reaches the canopy first allowing it to allocate resources to diameter growth sooner than black spruce.

Compared to black spruce, jack pine has an open crown, lower LAI, and higher photosynthetic capacity (Körner 2004). Typical LAI values for jack pine range from 1 to 4 m² (surface area to unit ground area) and 1 to 6 m²m⁻² for black spruce (Chen *et al.* 1997). Gower *et al.* (1997) reported values of 1.8 m² m⁻² for jack pine and 5.6 m² m⁻² for black spruce (in mature jack pine stands), where LAI is defined as one half of the total leaf surface area. Photosynthetic capacity refers to the amount of light required to reach saturation point (Vallardes and Niinemets 2008). Jack pine has a photosynthetic capacity of approximately 8 μmol m⁻²s⁻¹; double that of black spruce at 4 μmol m⁻²s⁻¹ (Körner 2004). Even though both jack pine and black spruce require light to perform their physiological processes, they require light in different amounts. Jack pine's lower leaf area allows sufficient light to penetrate the canopy and be captured by the spruce below. Therefore, a stratified mixture of these two species may experience less intense competition by intercepting light at different intensities and locations within the canopy.

Jack pine seedlings grow faster than other boreal conifers and develop relatively deep roots (Rudolph and Laidly 1990). Roots may reach depths of 2.7 m on deep sites, although the bulk of the rooting system consists of laterals restricted to the upper 46 cm of the soil profile (Rudolph and Laidly 1990). Intense competition for soil moisture and nutrients will cause the lateral roots of jack pine to grow downward (Karsh 1986). Compared to jack pine, black spruce has a shallow root system (Fowells 1965). Its roots may reach 60 cm in depth, but most spread laterally at the moss humus interface with the bulk of the roots in the upper 20 cm of the organic horizons (Viereck and Johnston 1990). Two-sided competition may therefore be reduced in black spruce-jack pine mixtures.

COMPETITION INDICES TO DESCRIBE COMPETITIVE INTERACTIONS

Tree growth is influenced by many factors including genetics, tree age, size, and competition with neighbours (Tomé and Burkhardt 1989). “The interpretation and outcome of competition can critically depend on how the competition is measured” (Freckleton and Watkinson 1999). This statement is applicable to the design of an experiment, the selection of the response variable and the quantification of competitive interactions (Weigelt and Jolliffe 2003). Competition has been studied extensively and is often expressed mathematically as a competition index. Competition indices quantify competition by amalgamating several primary response variables (Weigelt and Jolliffe 2003).

There are many advantages in using competition indices to quantify competition. They can be used to express and quantify competition better than a single primary measure (Hunt 1982), because several different measures can be combined to qualify composite ideas (Hunt 1982; Weigelt and Jolliffe 2003). Competition indices can also aid in interpreting complex data and facilitate the presentation of results by condensing experimental data (Weigelt and Jolliffe 2003). However, competition indices must be applied with caution as often the inferences drawn from their use are limited by experimental design (and vice versa) (Vanclay 2006).

Competition indices have many uses. For example, they can be used to indicate how strongly individuals compete (or the intensity of competition) for limited resources. They can also be employed to evaluate how competition by companions influences target plants. Lastly, competition indices can aid in predicting the outcome of competition in directing long term stand composition (Weigelt and Jolliffe 2003).

A variety of competition indices are available to quantify local competition of forest trees (Table 2). Competition indices are typically categorized into distance-independent and distance-dependent indices. Distance-independent indices are simple measures of stand level variables (Shi and Zhang 2003); examples include relative yield, stand density, and basal area. While the distance-dependent indices described in Table 2, could be used as independent variables to predict individual tree growth, the distance-independent indices described have been used to describe effects on yield, rather than growth (with the exception of Lorimer's (1983) index. Distance-dependent refers to those indices which consider the distance between the subject tree and its neighbours and tend to perform better than distance-independent indices (Mailly *et al.* 2003). Distance-independent indices may be adequate in estimating competitive effects in spatially regular pure even-aged stands (Lorimer 1983). In more complex stands, distance-dependent indices take into account spatially explicit variation in the strength of competition among trees (Wagner and Radosevich 1998). Well-known density-dependent indices were developed by Hegyi (1974), Schütz (1989), and Weiner (1984). The majority of mixedwood studies report relative yield, a distance-independent index, while few report distance-dependent indices measures (Forrester *et al.* 2006).

Table 2. Examples of distance-independent and distance-dependent competition indices

Name	Definition	Reference
Distance-Independent Indices		
Absolute Competition Index	$CI_a = Y_{iso} - Y_{mix}$	Wilson and Keddy (1986)
Relative Yield Total	$RYT = RY_i + RY_j$	Harper (1977)
C18	$C18 = \frac{\sum_{j=1}^n D_j}{D_i}$	Lorimer (1983)
Distance-Dependent Indices		
Hegyí's Index	$DCI = \sum_{j=1}^n \left(\frac{D_j}{D_i} \times \frac{1}{DIST_{ij}} \right)$	Hegyí (1974)
Schütz's Index	$Schutz = \sum_{j=1}^n \left[k \frac{H_j - H_i}{CR_j + CR_i} + \left(0.5 - \frac{E_{ij}}{CR_j + CR_i} \right) \right]$	Schütz (1989)
Weiner's Index	$W_r = \sum_{i=1}^n \frac{A_i}{d_i}$	Weiner (1984)
Neighbourhood Competition Index	$NCI = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(DBH_{ij})^\alpha}{(DIST_{ij})^\beta}$	Canham <i>et al.</i> (2004)

Y_{iso}, performance of target plant grown in isolation; *Y_{mix}*, performance of target plant grown with neighbours; *RY_i*, relative yield of species; *R*, search radius ($\approx 3.5 \times$ mean crown radius of canopy trees, *m*); *D_i*, diameter at breast height of subject tree *i*; *D_j*, diameter at breast height of competitor tree *j*; *DIST_{ij}*, distance between subject tree *i* and competitor *j*; *H_i*, height of subject tree *i*; *H_j*, height of competitor tree *j*; *CR_i*, crown radius of subject tree *i*; *CR_j*, crown radius of competitor tree *j*; *E_{ij}*, distance (m) between crown extremities of subject tree *i* and competitor tree *j*; *K*, constant in Schütz's index, *A_i*, cross-sectional area of the *i*th neighbour; *d_i*, distance of the *i*th neighbour; λ_i , species specific competition index that ranges from 0 to 1 allowing for differences among species in their competitive effect; *DBH_{ij}*, dbh of subject tree *i* and competitor tree *j*; α and β , are estimated by the analyses and determine the shade of the effect on dbh and the distance to the neighbour respectively.

Hegyi's (1974) index is computed as the sum of the distance-adjusted relative size ($[dbh_i/dbh_j]/\text{distance}_{ij}$) of potential competitors i within a defined search radius of the subject tree j . Hegyi (1974) used a 3 m search radius, but more recent researchers have used larger search radii (e.g. Clinton *et al.* 1997; Piutti and Cescatti 1997; Canham *et al.* 2004; Bristow *et al.* 2006). The size of the search radius is generally related to the size of the trees being investigated, with stands composed of larger individuals requiring a larger search radius.

Schütz's (1989) competition index attempts to describe one-sided and two-sided competition for resources by defining a zone of influence around each tree. This index differs from Hegyi's because it separates horizontal from vertical competition (Kelty and Cameron 1995). The horizontal component is described by measuring the proximity of crown radii, while the vertical component is evaluated with difference in height (Ung *et al.* 1997).

Mailly *et al.* (2003) compared the ability of a variety of distance-independent and distance-dependent competition indices to predict tree growth increment in old, uneven-aged stands of black spruce. They found that Hegyi's index was superior to Schütz's index based on correlation with basal area increment and reduction of mean square error (MSE). The correlation of Schütz's index to basal area increment was similar to using only neighbourhood density, a distance independent competition index.

Amoroso and Turnblom (2006) used Relative Yield (RY) and Relative Yield Total (RYT) as a distance-independent index of competition to characterize competitive behaviour of Douglas-fir and western hemlock mixtures. The theory behind this index is that if both species use resources in identical ways, the expected RY of each species would be equivalent to its proportional contribution to the mixture, and RYT would be

expected to equal 1. An RYT >1 would indicate either niche separation or the existence of some beneficial relationship between species. An RYT <1 indicates an antagonistic or competitive relationship between species in a mixture (Amoroso and Turnbull 2006).

Canham *et al.* (2004) developed a species-specific index called the “neighbourhood competition index” (NCI) in a study of stands composed primarily of western hemlock and western red cedar. This index is produced using optimization techniques that solve for maximum likelihood estimation (MLE) parameters through an iterative process to determine the values that best fit the model and maximize the likelihood of a given set of data. These values of model parameters that best fit the data, are those that maximize the r^2 of the relationship between observed and predicted radial growth. The parameters used in NCI (as described in Table 2) are defined in Table 3.

Table 3. Maximum likelihood estimation parameters of Canham *et al.* (2004) model.

Parameter	Definition
MaxRG	The maximum PotRG at the peak of the lognormal shape (mm/year)
X_0 (DBH)	Dbh of target tree at which MaxRG occurs
X_b	Determines breadth of function for Equation 1
C	Measures the sensitivity of the subject tree to crowding; at C equals 0, the subject tree is insensitive to crowding
S	Measures the sensitivity of the subject tree to shading; at S equals 0, the subject tree is insensitive to shading
R	Search radius for the inclusion of a competitor tree
α	Relates neighbour dbh to its competitive effect
β	Controls the decline in neighbour effect with distance from the target tree
λ	Species-specific competition index; varies between 0 and 1

To maximize the goodness of fit of r^2 , potential radial growth (PotRG) is estimated using measures of dbh and maximum radial growth (MaxRG) and other parameters estimated by the analysis, using Equation 1.

$$PotRG = MaxRG \exp \left[\frac{-1}{2} \left(\frac{\ln(DBH / X_0)}{X_b} \right)^2 \right] \quad \text{Eq. [1]}$$

A lognormal function is used to describe the shape of the effect of PotRG as it varies with diameter. MaxRG is the maximum PotRG at the peak of the lognormal shape. Potential radial growth, crowding, and shading are combined to calculate the expected radial growth of the subject tree, using Equation 2.

$$Expected\ RG\ (mm/yr) = PotRG\ (mm/yr) - (C \times NCI) - (S \times Shading) \quad \text{Eq. [2]}$$

The species-specific competition index (λ) indicates the variation in the effects of intra- versus interspecific competition. Stadt *et al.* (2007) evaluated several competition and light estimation indices for predicting growth in mature boreal mixed forests composed of trembling aspen, white birch, balsam poplar, lodgepole pine and white spruce and found Canham's index to be superior for all species except aspen. This improvement in predicting diameter growth was attributed to the maximum likelihood estimation (optimization) techniques used to calculate Canham's index.

MANAGING BLACK SPRUCE- JACK PINE MIXEDWOODS

The boreal forest experiences frequent natural disturbances including wildfires (Rowe 1961) and disease and insect outbreaks (Baskerville 1975). Entomological and pathological disturbances aid in maintaining a heterogeneous forest structure (Antos and Parish 2002), especially in areas of the boreal with longer fire cycles (Bergeron and Dansereau 1993; Kneeshaw and Bergeron 1999; Harper *et al.* 2002).

The major insect defoliators affecting pole-sized jack pine are the pine tussock moth (*Parorgyia plagiata* Walker) and the jack pine budworm (*Choristoneura pinus* Freeman) (Rudolph and Laidly 1990). Heavy defoliation over an extended period of time can cause losses in volume growth and mortality (MacLean and McKinnon 1997). Pole-sized jack pine are susceptible to several diseases including needlecast [*Davisomycella ampla*(J.J. Davis) Darker], diplodia blight, and a variety of rust fungi including, sweet fern blister rust (*Cronartium comptoniae* Arthur) and fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) (Rudolph and Laidly 1990).

Generally, insect and disease outbreaks affect only the host trees (Miller 1975); creating gaps within the residual canopy (D'Aoust *et al.* 2004). Canopy gaps created from insect and disease disturbances are essential for the persistence of shade-intolerant trees in mixed-species stands, and release suppressed shade-tolerant trees (Morin 1994).

Kemball *et al.* (2005) demonstrated that single-pass logging resulted in less species diversity and noticeably higher shrub coverage than natural fire and spruce budworm disturbances. Over time, high shrub cover, facilitated by logging, may negatively impact conifer recruitment and lower forest productivity (Kemball *et al.* 2005). They suggest that a viable alternative is harvesting that emulates the stand structure of a severe spruce budworm attack, such as a two-pass harvesting system with sufficient canopy retention to delay shrub development. In a spruce-pine conifer mixedwood this could involve removing the merchantable overstory jack pine, mimicking a jack pine budworm disturbance, while at the same time enhancing growth of black spruce.

Spatial patterns and proportion of each species can play an important role in species interactions and stand development (Kelty 2006). Since root and canopy stratification should contribute to complementarity in jack pine-black spruce mixedwoods, the two species could be intermixed at planting. This would result in a fine-grained spatial pattern (Figure 1a). If species were separated at planting into blocks or multiple rows, interactions that facilitate stable coexistence would be reduced. However, when two species are combined in a fine-grained mixture in an equal proportion as in Figure 1a, the upper canopy species may suppress the subcanopy species to the point where stand productivity will equal that of a pure stand of the dominant species. If this is the case, it is recommended that the proportion of the taller species be reduced in favour of the lower canopy species, as seen in Figure 1b, to attain higher stand productivity (Kelty 2006).

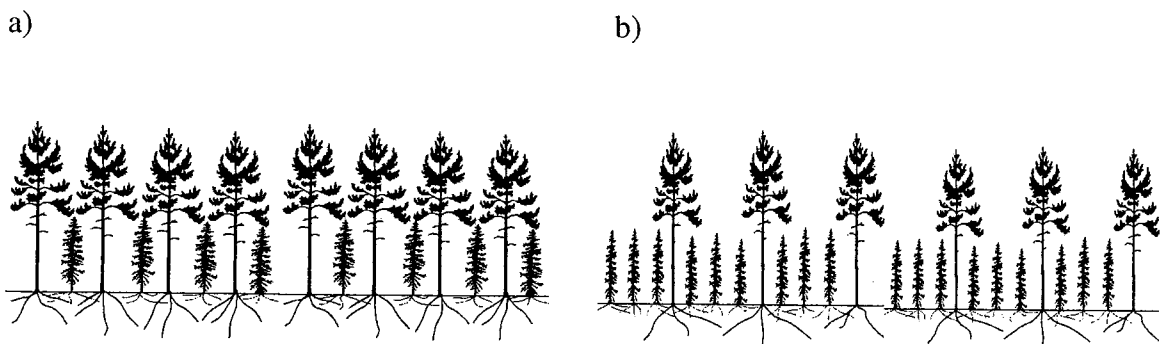


Figure 1. Diagrams of jack pine-black spruce plantation designs; (a) fine-grained mixture with a stratified canopy with an equal proportion of each species; (b) fine-grained mixture as well, but with unequal species proportions.

Competition between species may be reduced for both above- and belowground, resource when species exploit physiological, physical, and temporal differences. Ecological theories of niche, competitive exclusion, competition production coupled with silvical differences suggest that competition may be reduced in jack pine – black

spruce mixed stands through: 1) vertical canopy separation and 2) vertical root separation. Differences are maximized in stands of medium fertility, established at high density, and spatially arranged in a fine-grained mixture in an equal proportion.

MATERIALS AND METHODS

To reiterate, the objectives of this experimental study were: 1) to quantify competition using three distance-dependent competition indices and to determine which index best quantifies competition in a mixed stand, and 2) to determine if root distribution of black spruce and jack pine are affected by a mixture. To reduce confusion, the nomenclature used to describe the methods and discuss the results of above- and belowground competition is displayed in Table 4.

EXPERIMENTAL SITES

This study was conducted at Greta Lake (Gr) and Gamsby Lake (Gb), situated near Geraldton (49° 46 N 86° 55 W; 348.7 m elevation) approximately 300 km northeast of Thunder Bay in Northwestern Ontario. This location has a mean annual temperature of 0.3°C and a mean annual precipitation of approximately 760 mm (Environment Canada 2004).

Locating study stands composed of pure black spruce, pure jack pine, and spruce-pine mixtures on similar soil and site conditions is difficult. Gamsby and Greta were chosen as study areas because: 1) each site had an “all summer planting” of black spruce associated with it, and 2) both areas were harvested at approximately the same time and using similar techniques. Although silvicultural records were unavailable, it is likely that the harvested blocks had been scarified and aurally seeded. In the “all summer plantings”, jack pine volunteers were removed to ensure that the stand remained

pure black spruce. Because of this history, I was able to select stands composed of pure black spruce, pure jack pine, and spruce-pine mixture based on similar soil, vegetation and site conditions among each site, according to the Field Guide to Forest Ecosystem Classification for Northwestern Ontario (Sims *et al.* 1989). Site description included

Table 4. Nomenclature used to describe the results and discuss the results of this study

Description	Nomenclature
Black spruce (as a species)	Sb
Jack pine (as a species)	Pj
Greta site	Gr
Gamsby site	Gb
GrSb	Pure spruce transect at Greta
GrPj	Pure pine transect at Greta
GrMW01	First mixed spruce-pine transect at Greta
GrMW02	Second mixed spruce-pine transect at Greta
GbSb	Pure spruce transect at Gamsby
GbPj	Pure pine transect at Gamsby
GbMW	Mixed spruce-pine transect at Gamsby
Pure black spruce	Sb _p
Pure jack pine	Pj _p
Mixedwood	MW
Mixedwood black spruce	Sb _m
Mixedwood jack pine	Pj _m
Black spruce root biomass	Sb _r
Jack pine root biomass	Pj _r
Percentage black spruce root biomass	% Sb _r
Percentage jack pine root biomass	% Pj _r
Diameter at breast height (1.3 m)	dbh
Stems per hectare	sph

elevation, slope, microtopography, and surface stoniness. Elevation was measured using a Garmin 78 global positioning system unit, and slope was measured with clinometer. The vegetation description included identification and estimation of percent cover of all plant species present in the shrub, herb, and moss layers within a randomly located 1 x 1 m sample plot.

A soil pit was excavated in each study area and an auger sample was taken at stand type. Soil texture, structure, coarse-fragment content, thickness and sequence of soil horizons, and maximum rooting depth were described following the Field Guide to Forest Ecosystem Classification for Northwestern Ontario (Sims *et al.* 1989). The field soil description was used to determine soil drainage class and moisture regime.

Site characteristics for the Greta and Gamsby sites are summarized in Table 5. The Gb and Gr sites had slopes ranging from 0-18 percent. Gr had a slightly finer textured soil (S3, Fresh-Coarse Loamy; Sims *et al.* 1989), was well drained and contained approximately 55% coarse fragments by area in the lower two soil layers. Gb had very little coarse fragments with the exception of gravel in the parent material. This soil is described as a S1, Dry-Coarse Sand (Sims *et al.* 1989) and experiences more rapid drainage due to its coarser makeup. While the Field Guide to Forest Ecosystem Classification for Northwestern Ontario identifies Greta as “Well Drained,” it is likely that the drainage is actually faster due to the large amount of coarse fragments. The Gamsby site had a greater maximum rooting depth, which is likely a reflection of coarse fragment content. The dominant vegetation included *Pleurozium schreberi*, *Vaccinium angustifolium*, *Vaccinium myrtilloides*, and *Ledum groenlandicum* (Table 5).

Table 5. Study site characteristics.

Site	Gamsby	Greta
Elevation (m)	398	358
Slope gradient (%)	18	0
Surface stoniness (%)	0	0
Microtopography	Level	Level
Soil Coarse Fragments (%)	15	60
Rooting depth (cm)	65	55
Soil Type	Dry coarse sand (S1)	Fresh coarse loamy (S3)
Drainage Class	Rapid (2)	Well (3)
Moisture Regime	Moderately dry (0)	Fresh (2)

EXPERIMENTAL DESIGN AND DATA COLLECTION

One central transect 20 m long was established within each stand type at each site. Although direction of travel for each transect was randomly selected, the starting point of each transect was intentionally situated to ensure enough area for transect set-up. A single transect was placed in each of the stand types at each study area (GrSb, GbSb, GrPj, GbPj, GrMW01 and GbMW). A second transect was established in a spruce-pine mixture at Gr to account for the greater variability noted in this stand (GrMW02). Species, diameter at breast height (dbh), crown radius and location of each tree within 10 m of the center line of the transect and a 10 m radius semicircle at the ends of each transect were recorded. The transect design is presented in Figure 2. All trees within 5 m of the central transect with a dbh greater than 8 cm were cored, while trees less than 8 cm dbh were cut down and a disk taken for analysis. Cores and disks were used to determine age and radial growth rate (mm yr^{-1}) over the last 5 years using

the Tree Ring Increment Measurer (TRIM) system. Stands in this study were approximately 25-years-of age at breast height (1.3m).

A subsample of twenty trees per species per transect, representing the range of diameters, were measured for total height and height-to-live crown. Additional trees were measured in the mixed stands as there was more variability among diameters. Using linear regression, height measurements were extrapolated to the remaining trees. While height and diameter relationships are referred to as “curves” due to their non linear shape, the shape of the curve is linear for boreal black spruce and jack pine with breast height diameters of 25 cm or less (see Peng et al. 2001). Using a linear relationship smaller diameters may be underestimated ($\sim < 30$ cm), while larger diameters may be over estimated ($\sim > 30$ cm). The r^2 values for the linear relationship between height and diameter show a good fit, especially for black spruce. The average r^2 values associated with the height and diameter relationships were 0.84 and 0.78 for black spruce in mixed- and pure stands, respectively. While, average r^2 values for the height and diameter relationship for jack pine were 0.57 and 0.40 in mixed- and pure stands, respectively.

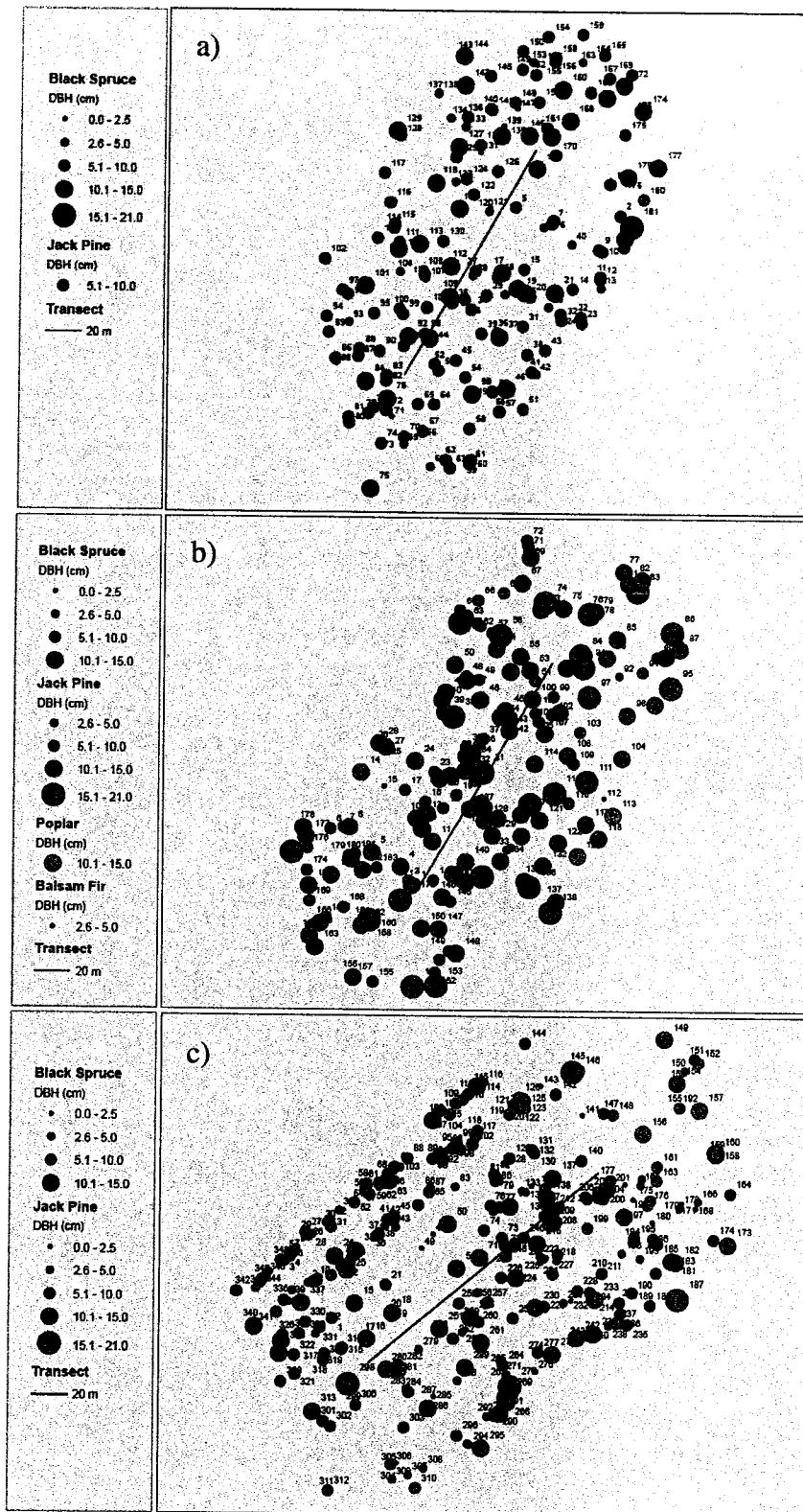


Figure 2. Examples of a) a pure spruce transect, b) a pure jack pine transect and c) a mixedwood transect.

A summary of stand characteristics is presented in Table 6. The density of stems found at the sites and stand types ranged from 2479 - 4776 sph. The mixed sites at Greta had the highest density with values of 4104 sph and 4776 sph, while the Gamsby mixed site had a much lower density of 2479 sph. Density among pure stands ranged between 2479 and 3585 sph. Basal area per hectare was greatest in Pj_p stands followed by MW stands and Sb_p stands, respectively.

Average Sb height and dbh was typically smaller than Pj, with average height values of 4.86 m and 10.41 m and average dbh values of 5.7 cm and 10.1 cm, recorded for Sb and Pj, respectively (Table 6). Overall, Sb individuals appear to be slightly larger in Sb_p stands compared to MW stands, with an average increase in height and dbh of 0.265 m and 1.35 cm, respectively. Jack pine in the pure stand type were on average 1.65 m taller than Pj_m; however, average diameter between stand types was similar. Black spruce in pure stand at Greta were 0.88 m taller and had dbh's 1.5 cm larger; however, the opposite is seen for Sb_m, with Gamsby hosting the larger trees, with height and dbh differences of 0.27 m and 1.35 cm, respectively. Differences in mean height and dbh of Pj_p are also evident between the Greta and Gamsby sites. Overall, the Gamsby site had larger Pj individuals. On average, Pj_p were 1.72 m taller at Gamsby, with dbh's averaging 1.4 cm larger, while differences between height and dbh of Pj_m are 2.99 m and 3.5 cm. The Gamsby site had a sandier textured soil, which may explain size differences between the two sites, as pine species are well-adapted to sandy soils. In addition, the Gamsby site was less dense in terms of stems per hectare than Greta, giving individual trees space to grow in size. Crown radii were similar among species, site, and stand type.

It should be noted that GrPj had a large number of Sb volunteers; however, Pj accounts for 92% of the basal area. In addition, the species mixture of GbMW stand type is not ideal as it was dominated by pine in terms of relative frequency by both sph and basal area. However, in nature it is difficult to find an even mixture, especially if site conditions favour one species over the other. The Sb trees in the GbMW stand were older than the volunteer spruce found in the Pj_p stands. A summary of stand characteristics from the preliminary assessment of the suitability of the sites for this study is presented in Appendix V

Table 6. Summary of stand characteristics for the Gamsby and Greta sites and stand types

Transect	Species	Height (m)		dbh (cm)		Crown Radius (m)		Density		Rel. Freq. (%)		Mean Tree BA (m ²)	Species BA (m ² /ha)	Total BA
		Mean	Std Dev.	Mean	Std Dev.	Mean	Std Dev.	Species	Total	Sph	BA			
GrSb	Sb	5.52	1.7	7.4	2.9	0.85	0.3	2507	2507	100	100	0.005	12.378	12.378
	Pj	n/a	n/a	n/a	n/a	n/a	n/a	0	0	0	0	0.000	0.000	0.000
GbSb	Sb	4.64	1.4	5.9	2.5	0.80	0.2	3123	3123	100	100	0.003	9.923	9.923
	Pj	n/a	n/a	n/a	n/a	n/a	n/a	0	0	0	0	0.000	0.000	0.000
GrPj	Sb	n/a	n/a	3.9	2.6	n/a	n/a	1078	3585	30	8	0.002	1.857	23.241
	Pj	10.82	1.1	9.8	3.4	0.93	0.4	2507	2507	70	92	0.009	21.384	21.384
GbPj	Sb	n/a	n/a	6.5	2.8	n/a	n/a	140	2479	6	2	0.003	0.489	25.884
	Pj	12.54	0.7	11.3	3.3	0.99	0.5	2339	2339	94	98	0.011	25.395	25.395
GrMW01	Sb	4.40	1.6	4.5	2.4	0.70	0.3	2143	4776	45	21	0.002	4.333	20.935
	Pj	8.39	1.1	8.3	3.5	0.87	0.4	2633	2633	55	79	0.006	16.603	16.603
	Sb	4.62	1.3	5.1	2.2	0.87	0.4	1709	1709	42	19	0.002	4.178	4.178
GrMW02	Pj	8.74	1.6	9.1	3.5	0.92	0.4	2395	4104	58	81	0.007	17.873	22.051
	Pj	12.54	0.7	11.3	3.3	0.99	0.5	2339	2339	94	98	0.011	25.395	25.395
GbMW	Sb	5.12	2.2	5.8	3.3	0.84	0.3	630	2479	25	9	0.003	2.189	25.444
	Pj	11.55	1.8	12.2	3.3	0.91	0.5	1849	1849	75	91	0.013	23.255	23.255
Overall	Sb	4.86	1.6	5.7	2.8	0.81	0.3	n/a	n/a	n/a	n/a	0.003	6.600	n/a
	Pj	10.41	2.1	10.1	3.7	0.92	0.4	n/a	n/a	n/a	n/a	0.009	20.902	n/a

COMPETITION INDICES

To quantify local competition at the individual tree level, three distance-dependent competition indices were selected: Hegyi's (1974), Schutz's (1989) and Canham *et al.*'s (2004). Equations are presented in Table 7. The search radius for the inclusion of competitor trees was 5 m, therefore, only trees within 5 m of the central transect were selected as subject trees. A 5 m radius was a practical choice given the size of the transects and the size of the trees being investigated. This resulted in 643 subject trees (GrMW01 = 107; GrMW02 = 98; GrSb = 78; GrPj = 90; GbMW = 92; GbSb = 89; GbPj = 89).

Table 7. List of competition indices used in this study.

Name	Definition	Reference
Hegyi's Index	$DCI = \sum_{j=1}^n \left(\frac{D_j}{D_i} \times \frac{1}{DIST_{ij}} \right)$	Hegyi 1974
Schütz's Index	$Schutz = \sum_{j=1}^n \left[k \frac{H_j - H_i}{CR_j + CR_i} + \left(0.5 - \frac{E_{ij}}{CR_j + CR_i} \right) \right]$	Schütz 1989
Canham's Index	$NCI = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(DBH_{ij})^\alpha}{(DIST_{ij})^\beta}$	Canham <i>et al.</i> 2004

D_i , diameter at breast height of subject tree i ; D_j , diameter at breast height of competitor tree j ; $DIST_{ij}$, distance between subject tree i and competitor j ; H_i , height of subject tree i ; H_j , height of competitor tree j ; CR_i , crown radius of subject tree i ; CR_j , crown radius of competitor tree j ; E_{ij} , distance (m) between crown extremities of subject tree i and competitor tree j ; K , constant in Schutz's index (0.65), λ_i , species specific competition index that ranges from 0 to 1 allowing for differences among species in their competitive effect; DBH_{ij} , dbh of subject tree i and competitor tree j ; α and β , are estimated by the analyses and determine the shape of the effect on dbh and the distance to the neighbour respectively.

Hegyi's and Schutz's indices were calculated using the equations given in Table 7. All trees within a 5 m radius, regardless of size were considered potential competitors and were included in the calculations to determine Hegyi's index. Alternatively, Schutz's index only considers a tree a competitor if:

$$E_{ij} \leq 0.5(CR_j + CR_i) + k (H_j - H_i)$$

Canham *et al.*'s (2004) neighbourhood competition index (NCI), which will be referred to as only Canham's index from this point forward, was calculated according to the formula presented in Table 7. To calculate Canham's index, the parameters α and β were determined using maximum likelihood estimation (MLE) and simulated annealing because the summation terms in the equation make it impossible to estimate the parameters using traditional software packages (Canham *et al.* 2004). This global optimization technique allows a number of parameters in related equations to vary simultaneously over numerous iterations. The analysis was done using .NET software developed by Rob Kushneriuk at CNFER for use with the data I collected. The software written using Delphi for Windows described by Canham *et al.* (2004) was provided to me by Dr. Canham, and then modified as needed to complete the analysis. The overall model seeks to maximize the goodness of fit between observed and predicted radial growth, as measured by r^2 . Radial growth rate, distance to neighbours, dbh, site (i.e., Gr and Gb), stand type, and species identifier data were included in the MLE model for each subject tree. The model was calibrated prior to analysis to reflect the climatic conditions of the study area (e.g. latitude and length of growing season) and the crown geometry of spruce and pine.

In the MLE software I used, twelve parameters were unknown and allowed to vary with each iteration. This means that the outcome varies slightly with each run. Radial growth of each subject tree is predicted based on potential radial growth (PotRG), crowding, and shading. Simulated annealing allows all parameters that contribute to these component sub-models (PotRG, crowding, shading) to vary simultaneously (Canham *et al.* 2004). The assumptions of this analysis are that potential radial growth

varies with dbh and that the effects of crowding and shading will reduce growth in a tree otherwise free from competition (Canham *et al.* 2004). While Canham *et al.* (2004) used a non-linear model to estimate PotRG, the code in the adapted model was changed so that PotRG was predicted based on the relationship between diameter and radial growth using simple linear regression. The MLE software was used to determine the slope and intercept of the dbh vs. PotRG relationship. This is because Canham used a larger range of stand ages, while trees from this study are relatively young and represent a single age. Therefore, the data from this experiment was not broad enough to find the peak of the lognormal (non linear) shape, which made using MaxRG inappropriate. The MLE model was run ten times for each species using 32, 000 iterations. The output was reviewed and the run that best maximized r^2 was chosen for further analysis.

One of the main reasons I chose to use Canham's model is because it includes a species-specific competition index (λ), to capture the effects of competition on a subject tree by its neighbours. To analyze the effects of intra- *versus* intraspecific competition, λ is estimated by the analysis and varies between 0 and 1. The net competitive effect of any individual neighbour is multiplied by λ , to account for differences among neighbouring species (Canham *et al.* 2006). To illustrate, a species that has a strong competitive effect will have a λ value closer to 1, a species with a moderate competitive effect will have a λ around 0.5, and a species with no competitive effect would have a λ of 0.

Using simulated annealing, the parameter estimates differ slightly with each run. Individual parameter estimates may vary wildly from run to run; however over several runs, estimates of terms, such as Canham's competition index (Table 7) and potential radial growth tend to become consistent. All parameters, with the exception of search radius, were free to vary in order to find the coefficients that best fit the model.

ROOT CORES

Root samples were taken from six of the seven transects: GbMW, GbSb, GbPj, GrMW01, GrSb, and GrPj. A total of 60 subject trees were selected for root core sampling: ten trees from each transect. All subject trees were positioned within 5 m of the transect and represented a range of Hegyi's competition index values (3.598 – 40.658 and 0.127 – 280.202 for spruce and pine, respectively). Hegyi's index was chosen because it is the easiest index to calculate and it was found to outperform Schütz's index in a study comparing their ability to predict growth of black spruce (Mailly *et al.* 2003). Root cores were taken using a modified motorized ice auger to a depth of 45 cm below the organic mineral interface. In pure stands two cores were taken for each intensively measured subject tree (Figure 3) and the soil bulked to make one sample. In mixedwood stands four cores were taken (one representing a competitor of each species) and bulked to make two samples (Figure 3). The rationale for using the methodology presented in Figure 3 was to have a consistent sampling procedure for each intensively measured tree. Because the spatial distribution varied, a core was taken equidistant from the subject tree and the closest competitor. Considering that root distribution can be highly variable (e.g. there would be more roots in areas with greater nutrients) and to as a means to acquire a larger amount of root biomass to work with; two cores were taken for each intensively measured tree. A meter on each side of the centre point was chosen because it was far enough away to capture differences, but also still within the zone of influence. Since this sampling design is not random, the inferences from the analysis of the root data is confined to these particular study stands (transects).

Due to time constraints, a subsample of 40 cores was processed in the lab.

Subsample selection was based on maintaining the range of low and high Hegyi's index values, and within the mixedwood stands, a representation of species mixtures within each subject tree neighbourhood. Core contents were separated at seven depths: organic and 0-5, 5-10, 10-15, 15-20, 20-30, and 30-45 cm.

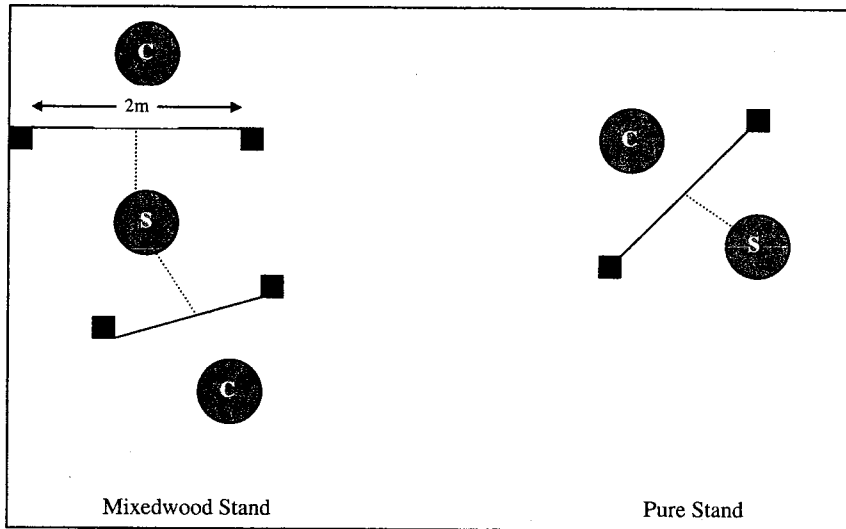


Figure 3. Diagram depicting the methodology used for selecting the position to collect root cores. The subject and competitor trees are denoted by S and C, respectively. Squares (■) show location of root cores.

Each mineral root core sample was sieved with a 2 mm sieve; coarse fragments were removed and weighed. To determine the actual amount of rooting medium within the core sample, the volume of the coarse fragments was subtracted from the volume of the soil of the corresponding core. To determine volume, the density of a subsample of coarse fragments was determined using the specific gravity test. A container with water was placed on a scale and the weight was recorded. A coarse fragment sample was suspended by a piece of thread and completely submerged into the container of water. The increased weight was recorded. Density was determined by dividing the weight of the sample in the air to that of the weight of the displaced water. The average of the

subsample was found to be 2.6 g/cm^3 . The volume of the coarse fragments was determined using the following formula,

$$V = M/D$$

where V , M , and D refer to volume, mass, and density, respectively.

The samples were then passed through smaller sieves to separate roots from the soil. Organic samples were difficult to sieve and were processed by laying the sample out on a brightly coloured tray and picking out roots using tweezers.

Roots were sorted by diameter [small ($\leq 2 \text{ mm}$), medium (2.1-9.9 mm), and large ($\geq 10 \text{ mm}$)] and by 'species' (Sb, Pj, herb/shrub, and unidentifiable). The sorted roots were labeled, bagged and placed in the drying oven for 48 hours at 70°C . Only fine and medium root weights were used in the subsequent analysis of variance. Large root were not included, as their primary function is to support the tree rather than to acquire belowground resources. The remaining soil was air dried and weighed. A five gram air-dried subsample of each was weighed and then placed in the drying oven at 70°C for 48 hours and weighed again to estimate oven-dried-weights for the total sample. Root biomass from each core was then translated into grams of roots per 100g of soil.

DATA ANALYSIS

Linear Regression for Competition Indices

A simple linear regression was performed to determine the relationship between the response variable, radial growth, and each of the competition indices,

$$y_i = \beta_0 + \beta_1 x_i(\text{competition index}) + \varepsilon_i$$

where;

y_i = the value for radial growth for the i th observation

x_i = competition index (Hegyi's, Schutz's or Canham's)

β_0 = the population intercept

β_1 = the population slope and measures change in Y per unit change in competition index

ε_i = the random error associated with the i th observation

The models were fitted using SPSS v16.0 software. To assess the performance of each index, the coefficients of determination (r^2), mean square error, and regression slopes between species for each competition index were compared. Fine root weights and fine plus medium root weights were each run in a preliminary ANOVA and found to have similar results. Fine and medium root weights were chosen to present the results because the root biomass values were greater.

Analysis of Variance for Root Data

Belowground interactions are a function of a species' rooting patterns which are determined primarily by soil conditions and species' genetic makeup (Ong *et al.* 1996). All plant species tend to concentrate their fine root mass in the top 10-30cm of the soil profile, however, studies have shown that some combinations of species do experience belowground niche separation by stratifying their roots. The questions I addressed with respect to the root data are: 1) Does interspecific competition affect the abundance of fine and medium root biomass and, and 2) Does interspecific competition affect the vertical distribution of fine and medium roots? The General Linear Model procedure in Statistical Analysis Software (SAS), v9.1 was used to address these questions.

The experiment follows a factorial design. The model consists of three fixed factors, Site (Gr and Gb), Stand Type (Sb and MW; Pj and MW), and Depth (organic, 0-

5, 5-10, 10-15, 15-20, 20-30, and 30-45 cm). The experimental unit was the bulked root core which is associated with each replicate, the subject tree. The mathematical model for this experiment is presented in Equation 3.

$$Y_{ijk} = \mu + B_i + S_j + BS_{ij} + D_k + BD_{ik} + SD_{jk} + BSD_{ijk} + \varepsilon_{ijk} \quad [\text{Eq. 3}]$$

$$i = 1, 2; j = 1, 2; k = 1, 7$$

Where:

Y_{ijkl} = root biomass of the l^{th} replicate of the k^{th} depth of the j^{th} stand of the i^{th} site

μ = the overall mean

B_i = the fixed effect of the i^{th} site

S_j = the fixed effect of the j^{th} stand

BS_{ij} = the fixed interaction effect of the i^{th} site with the j^{th} stand

D_k = the fixed effect of the k^{th} depth

BD_{ik} = the fixed interaction effect of the i^{th} site with the k^{th} depth

SD_{jk} = the fixed interaction effect of the j^{th} stand type with the k^{th} depth

BSD_{ijk} = the fixed interaction effect between the i^{th} site with the j^{th} stand with the k^{th} depth

$\varepsilon_{(ijk)l}$ = the random effect of the l^{th} replicate within the ijk^{th} treatment combination

The expected mean squares for the linear model are presented in Table 8. Due to the number of fixed factors and replicates, direct tests were not available for any of the factors or their interactions. Conservative tests (allowing a “reject only” framework) were available to test hypotheses, and are presented in Table 9.

Where the three-way ANOVA indicated that Stand Type (e.g. pure and mixed), depth (organic through to 45 cm of mineral soil) and their interaction were the only significant sources of variation for either total root biomass or percentage of root biomass by species, the two stand types (i.e. pure and mixed) were analyzed separately

using a one-way ANOVA to identify significant differences between depths based on Student-Newman Keuls post hoc tests (SNK).

Table 8. Expected Mean Square derivation for Equation 3.

Source	2 F I	2 F J	7 F K	Expected Mean Squares	df
B_i	0	2	7	$\sigma^2 + 14\phi(B)$	(I-1)
S_j	1	0	7	$\sigma^2 + 7\phi(S)$	(J-1)
D_k	2	2	0	$\sigma^2 + 4\phi(D)$	(K-1)
BS_j	1	0	7	$\sigma^2 + 7\phi(BS)$	(I-1)(J-1)
BD_{ik}	0	2	0	$\sigma^2 + 2\phi(BD)$	(I-1)(K-1)
SD_{jk}	1	0	0	$\sigma^2 + \phi(SD)$	(J-1)(K-1)
BSD_{ijk}	1	0	0	$\sigma^2 + \phi(BSD)$	(I-1)(J-1)(K-1)
$E_{l(ijk)}$	1	1	1	σ^2	

Table 9. Hypothesis tests for Equation 3.

Hypothesis	Test Statistic	Reference Distribution
$14\phi(B) = 0$	$MS(B)/MS(\epsilon)$	F(1, 28)
$7\phi(S) = 0$	$MS(S)/MS(\epsilon)$	F(1, 28)
$4\phi(D) = 0$	$MS(D)/MS(\epsilon)$	F(6, 28)
$7\phi(BS)$	$MS(BS)/MS(\epsilon)$	F(1,28)
$2\phi(BD) = 0$	$MS(BD)/MS(\epsilon)$	F(6, 28)
$\phi(SD) = 0$	$MS(SD)/MS(\epsilon)$	F(6, 28)
$\phi(BSD) = 0$	$MS(BSD)/MS(\epsilon)$	F(6,28)
$\sigma^2 = 0$	—	—

RESULTS AND DISCUSSION

COMPETITION INDICES

Different indices illustrate different features of competition. Hegyi's index relies on dbh and crowding (e.g., number of neighbours, distance from neighbour, sph), as does Canham's. However, Canham's index is produced by a MLE model that considers other parameters including species identity. Schütz's competition index differs from Hegyi's and Canham's indices in that it attempts to quantify both horizontal and vertical competitive effects by incorporating crown radii and total height, in addition to crowding.

In total, 643 trees were used for the competition index calculations. As with most indices, the values are unitless, so any comparisons that are made must take that into account. However, with respect to the three indices used in this study, higher values indicate higher levels of competition than lower values. Means for both species in all stand types were very similar; however, the variation (as expressed by Std. Dev. and min/max values) was substantial (Table 10). The largest difference in radial growth between pure and mixed stands occurred between Sb_p and Sb_m (Gamsby). The larger growth (2.4 mm) was associated with the lower index value (36.01) in the Sb_p stand and was found to be 1.06 mm larger than that of Sb_m . The distribution of values of the three competition indices appears to differ between Sb and Pj (Figure 4) and among stand types (Table 10). However; there are two features in common which suggest that a larger number of black spruce individuals are experiencing more intense competition than jack pine. First, for each index, the range of values for spruce is wider than that of jack pine. Second, Sb values appear to be more positively skewed than the Pj values.

Table 10. Descriptive statistics for each competition index by species.

		Greta				Gamsby			
		Sb _p	Sb _m	Pj _p	Pj _m	Sb _p	Sb _m	Pj _p	Pj _m
Avg. Radial Growth (mm)		2.46	1.90	1.20	1.48	2.40	1.34	1.01	1.08
Hegyí	Mean	30.42	29.55	15.76	16.07	36.01	44.70	11.00	9.48
	Std. Dev.	46.04	21.24	10.06	50.32	53.14	44.77	7.55	4.25
	Min. value	3.58	5.27	2.52	3.81	0.13	7.53	3.62	1.30
	Max. value	280.20	130.25	44.11	50.32	229.48	215.90	57.53	21.53
Schütz	Mean	18.20	68.01	35.74	27.74	13.39	123.66	41.92	26.26
	Std. Dev.	9.08	31.46	25.30	15.02	7.90	53.87	24.09	18.47
	Min. value	2.31	6.03	0.00	0.00	1.70	7.82	0.00	0.00
	Max. value	46.65	166.36	107.89	73.86	37.45	182.67	119.39	86.86
Canham	Mean	20.30	65.20	14.43	10.83	42.94	113.63	19.80	19.18
	Std. Dev.	10.45	22.58	3.38	2.74	48.41	36.51	4.68	4.76
	Min. value	7.29	12.78	6.95	5.00	6.07	33.45	9.63	2.76
	Max. value	51.78	111.69	28.82	17.29	28.45	177.47	28.15	28.97

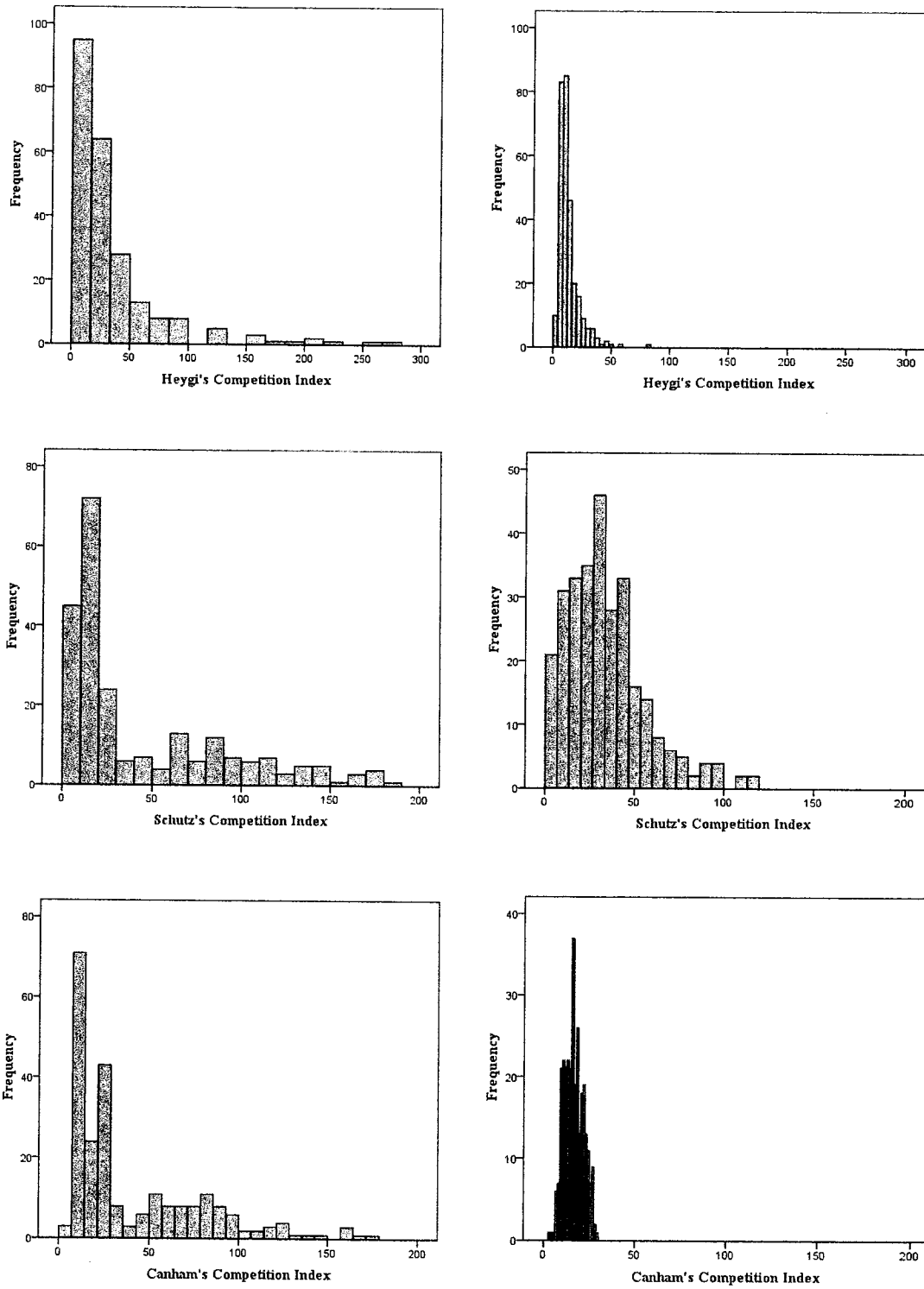


Figure 4: Frequency distribution of the computed competition indices for spruce (left) and jack pine (right).

Based on information presented in Tables 11 and 12, 11 out of 15 of the highest Hegyi's index values for Sb and 10 out of 15 for Pj were found in pure stands. These Sb index values, some of which were in the low- to high 200's, reflect the combination of large numbers of competitors (16 to 47 competitors within the 5 m search radius) and large differences between smaller subject trees (dbh of 1.0 cm) and larger competitor trees (dbh of >15 cm). Alternatively, the largest index values for jack pine subject trees fell between 30 and 60. Interestingly, the number of neighbours was often higher in this group (ranging from 21 to 52) but the difference between diameters is smaller.

The range of Schütz index values for Sb and Pj was smaller than that of Hegyi's (Table 10) and the relative difference in the maxima of the two species was also smaller (3:2 vs. 5:1, Sb:Pj). The highest Schütz values for Sb were all from individuals in mixed stands while highest values for Pj individuals were mainly in pure stands (12 out of 15; Tables 11 and 12). Therefore, there is some agreement with regard to Hegyi's and Schütz's indices for pine but not for spruce. This may reflect the influence of height data on the calculation of the index, since crown radii and number of neighbours were very similar. The trend in relative numbers suggests that the competitive effects of jack pine are larger than those of spruce. That is, both spruce and jack pine are more affected by jack pine than by spruce.

A large difference in the range of Canham's index values between spruce and pine was observed (Maxima of 177.47 and 28.97, respectively; Table 10, Figure 4), as was the ratio (6:1, Sb: Pj). The distribution of values between the two species was also very different. Spruce values were skewed to the right, while pine values appeared more normally distributed (Figure 4). Like Hegyi's index, Canham's competition index uses dbh and distance from neighbour to calculate an index. However, Canham's

competition index includes constants α and β , which are estimated by MLE, and determine the shape of the effect of the dbh and the distance to the neighbour, respectively, on each subject tree.

The range of Canham index values reflects the size and degree of crowding of individuals. The study sites had moderate to high densities (~2500 – 4800 sph). The Sb_p were evenly spatially distributed, while in the mixed stands the distribution was more clustered (Figure 2), resulting in more stems per hectare. These areas of clumping often indicate superior microsite (Stoll *et al.* 1994), which may magnify the effect of competition as measured by the indices. This variation in spatial distribution and the consequence of smaller trees due to crowding explains the larger range of competition indices for black spruce. The smaller range of index values for jack pine may be due to a combination of a more even spatial distribution and larger average size.

Canham's and Schütz's index values appear to be consistent in identifying stand conditions with the most competition; the highest values occurred in mixed stands for black spruce and pure stands for jack pine (Tables 11 and 12). These indices were also the most consistent in identifying the individual trees experiencing the greatest competition, agreeing upon 20 of 30 individuals. For P_j , all three indices were in agreement that P_{j_p} stands are experiencing the greatest competition. However, Hegyi's did not agree with the other indices on individual trees as Hegyi's and Schütz's indices only selected the same individuals three times and Hegyi's and Canham's five times.

Table 11. The fifteen highest index values by competition index with corresponding stand and individual tree characteristics for black spruce.

Index	Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radius (m)	Radial Growth (mm)	Index Value
Hegyí	79	GrSb	23	4.4	3.79	0.61	2.04	280.202
	140	GrSb	25	8.3	6.06	1.19	2.82	251.928
	141	GrSb	25	9.6	6.81	0.72	2.98	216.458
	17	GbMW	26	1.0	2.2	0.46	0.67	215.910
	67	GrSb	23	5.4	4.37	1.00	2.42	190.123
	106	GrSb	26	4.3	3.73	0.80	1.06	180.977
	78	GrSb	23	7.3	5.48	0.89	2.50	165.933
	71	GrSb	19	1.2	1.93	0.67	0.91	165.795
	108	GrSb	22	3.1	3.04	0.36	1.79	132.130
	135	GrMW	47	1.0	2.07	0.61	0.80	130.254
	8	GbSb	24	1.7	2.71	0.43	1.56	128.847
	28	GrSb	22	3.7	3.39	1.01	1.38	122.534
	16	GbMW	23	1.4	2.45	0.35	0.82	117.746
	120	GrSb	16	4.6	3.91	0.55	2.86	96.633
	15	GbMW	27	1.4	2.45	0.46	1.36	93.478
Schütz	149	GbMW	22	3.9	3.98	1.13	0.48	182.672
	136	GbMW	23	3.9	3.98	1.12	0.43	178.911
	6	GbMW	24	1.5	1.94	0.60	0.51	172.462
	92	GbMW	26	2.2	2.94	0.90	0.44	170.314
	25	GbMW	30	3.4	3.02	0.60	2.42	170.263
	135	GbMW	22	3.1	3.49	0.93	0.48	166.359
	90	GbMW	25	3.7	3.36	0.98	0.88	165.785
	147	GbMW	23	4.6	4.95	1.10	0.71	164.232
	89	GbMW	25	2.6	3.18	0.87	0.62	153.274
	153	GbMW	20	7.0	5.88	1.13	2.38	148.409
	93	GbMW	28	7.4	5.08	1.06	0.94	147.935
	159	GbMW	23	8.8	6.96	1.59	1.76	146.714
	17	GbMW	26	1.0	2.20	0.46	0.67	145.653
	21	GbMW	23	1.8	2.69	0.56	1.31	145.453
	95	GbMW	28	1.3	2.39	0.61	1.58	137.595
Canham	25	GbMW	30	3.4	3.02	0.60	2.42	177.473
	17	GbMW	26	1.0	2.20	0.46	0.67	167.768
	159	GbMW	23	8.8	6.96	1.59	1.76	162.619
	16	GbMW	23	1.4	2.45	0.35	0.82	157.903
	21	GbMW	23	1.8	2.69	0.56	1.31	157.187
	15	GbMW	27	1.4	2.45	0.46	1.36	145.942
	51	GbMW	20	9.0	6.56	1.13	2.22	139.061
	144	GbMW	30	8.8	6.98	0.83	1.71	134.155
	138	GbMW	25	1.9	2.75	0.46	0.38	126.232
	146	GbMW	24	6.4	5.76	0.92	1.36	123.247
	6	GbMW	24	1.5	1.94	0.60	0.51	122.302
	149	GbMW	22	3.9	3.98	1.13	0.48	121.945
	147	GbMW	23	4.6	4.95	1.10	0.71	119.994
	148	GbMW	23	7.8	6.37	0.68	0.72	118.028
	142	GbMW	29	9.5	9.96	0.66	2.64	114.949

Table 12. Fifteen highest index values by competition index with corresponding stand and individual tree characteristics for jack pine.

Index	Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radius (m)	Radial Growth (mm)	Index Value
Hegyí	13	GbPj	22	4.0	11.14	0.68	0.83	57.529
	223	GrMW	49	3.1	6.93	0.18	1.96	50.318
	51	GrMW	32	13.4	6.76	1.31	2.36	47.170
	2	GrPj	39	5.2	9.37	0.98	0.26	44.107
	327	GrMW	42	6.8	8.67	0.64	0.31	41.803
	255	GrPj	32	7.0	9.93	0.87	0.76	40.658
	94	GrPj	44	4.1	9.03	0.92	0.92	38.206
	67	GrPj	22	5.8	9.56	0.59	0.34	37.814
	253	GrPj	32	8.3	10.34	0.60	1.22	37.363
	68	GrPj	23	5.6	9.50	0.46	0.41	36.154
	69	GrPj	21	5.5	9.46	0.60	0.72	35.197
	1	GrPj	39	6.0	9.62	0.47	1.42	35.069
	1	GbPj	22	5.5	9.40	0.94	0.57	34.662
	79	GrMW	52	4.9	7.44	0.79	1.08	32.974
	82	GrMW	51	5.1	6.64	0.45	1.17	32.337
Schütz	1	GbPj	22	5.5	9.40	0.94	0.57	119.394
	31	GbPj	28	15.3	13.35	2.22	1.24	117.086
	221	GrPj	27	8.6	8.93	1.18	1.01	107.893
	12	GbPj	22	11.0	11.11	1.33	0.61	107.841
	220	GrPj	37	13.6	11.06	1.55	1.09	99.450
	93	GbPj	20	13.0	12.90	1.84	1.28	97.323
	140	GbPj	29	12.7	12.84	1.90	1.16	96.852
	47	GrPj	38	7.6	10.12	1.32	0.60	96.364
	226	GrPj	36	6.3	9.71	0.93	0.76	92.774
	44	GrPj	39	5.9	9.59	1.14	0.92	90.528
	5	GbPj	20	11.2	12.55	1.85	1.30	90.063
	23	GbMW	31	10.5	10.73	1.42	1.62	86.864
	69	GrPj	21	5.5	9.46	0.60	0.72	81.392
	10	GbPj	21	14.1	12.07	1.42	1.17	81.368
	18	GbPj	27	9.6	12.23	1.24	0.40	76.956
Canham	31	GbPj	28	15.3	13.35	2.22	1.24	27.797
	140	GbPj	29	12.7	12.84	1.90	1.16	23.275
	93	GbPj	20	13.0	12.90	1.84	1.28	22.986
	23	GbMW	31	10.5	10.73	1.42	1.62	21.831
	18	GbPj	27	9.6	12.23	1.24	0.40	19.906
	12	GbPj	22	11.0	11.11	1.33	0.61	17.383
	10	GbPj	21	14.1	12.07	1.42	1.17	16.814
	44	GrPj	39	5.9	9.59	1.14	0.92	15.354
	5	GbPj	20	11.2	12.55	1.85	1.30	15.089
	1	GbPj	22	5.5	9.40	0.94	0.57	14.157
	47	GrPj	38	7.6	10.12	1.32	0.60	13.841
	220	GrPj	37	13.6	11.06	1.55	1.09	13.255
	221	GrPj	27	8.6	8.93	1.18	1.01	11.858
	69	GrPj	21	5.5	9.46	0.60	0.72	9.863
	226	GrPj	36	6.3	9.71	0.93	0.76	9.691

Canham's model produces an index that estimates the magnitude of competition as a function of diameter, distance from neighbour and a species-specific index. The species-specific competition index (λ) indicates the variation in the effects of intra- versus interspecific competition, by partitioning the competitive effects of neighbours into the effects of crowding and shading (Canham *et al.* 2004). The range of λ falls between 0 and 1; zero represents little competitive effect, while a value of 1 represents a strong competitive effect. Black spruce appeared to have little interspecific competitive effect on jack pine with a λ value of 0.0006 (Figure 5a). Intraspecific competition appeared to be strong among the pine with an index value of 0.9973. Based on the λ values calculated, black spruce is experiencing both strong intra- and interspecific competition with λ 's of 0.7457 and 1.000 for spruce and pine, respectively (Figure 5b).

The large confidence intervals reflect the variation in the data among pure and mixed stands, as pure and mixed stands were run together in the MLE model. Large confidence intervals may also be a result of relatively young stands that are still in the early stages of self-thinning, meaning competition may not have had enough time to manifest. It is important to note that the λ is not a traditional statistical test, therefore significance cannot be tested. Rather, λ is a product of the MLE model, which performs a number of runs to find the model that best fits the data. Each run will have a slightly different outcome.

To summarize, λ indicates that there is a strong intraspecific effect within both tree species and while jack pine has a strong competitive effect on black spruce, black spruce has a weak competitive effect on jack pine. These results reflect conditions in the stands types measured, based on stand composition and tree size. This does not imply that spruce would not compete with jack pine for any dbh/distance combination. To

illustrate, it is likely that in a spruce-pine mixture with large spruce and small jack pine, spruce would have a stronger interspecific effect on pine.

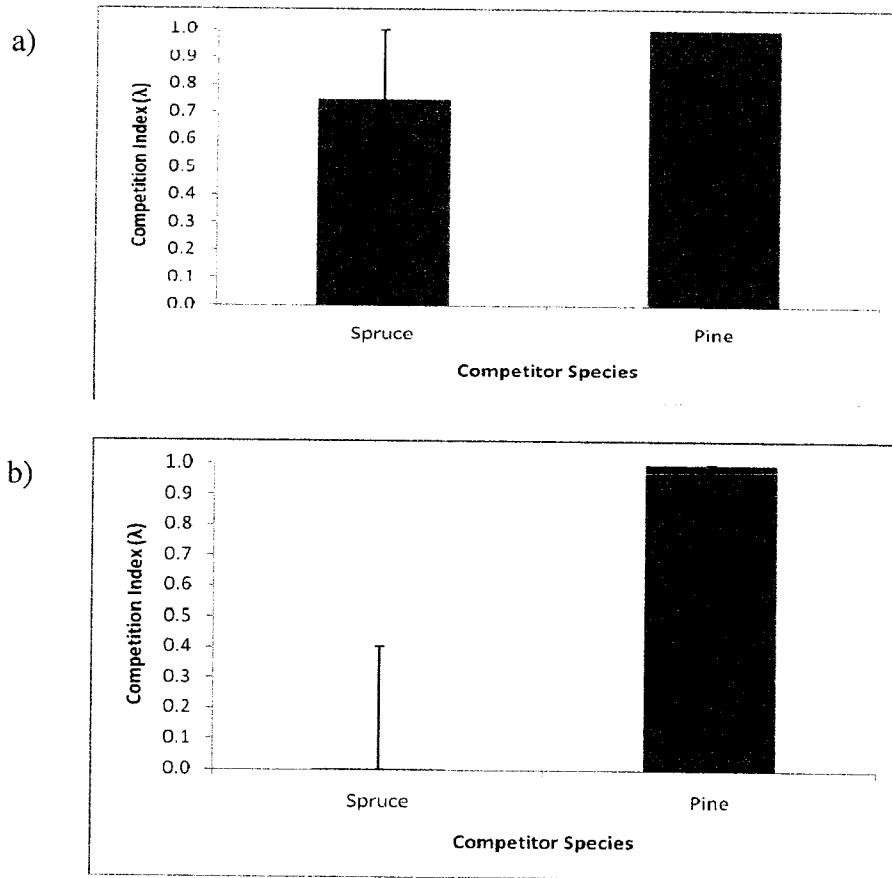


Figure 5. Estimated λ and 95% confidence intervals for the per capita effect of each of the four species of competitors on target species of a) black spruce and b) jack pine.

As previously mentioned, symmetrical or two-sided competition is generally invoked to describe competition for belowground resources. Competition for nutrients is likely to occur over a larger area than aboveground competition for light. Therefore, one could argue that belowground competition would be better measured using stand level distance-independent indices, such as basal area, while aboveground competition is best represented by distance-dependent indices (Ledermann and Sage 2001). Knowing this, one could further argue that the distributions of Hegyi's, Schütz's, and Canham's

competition indices and λ produced by MLE, indicate that that asymmetrical or one-sided competition for light is occurring in these stands. Two of the three indices show that the subcanopy black spruce are experiencing more competition in mixed stands. Under asymmetrical competition trees acquire light resources in direct relation to their relative sizes. Jack pine occupies the canopy in the mixed stands capturing the majority of the light resource, shading spruce. The majority of the jack pine are larger and consequently, acquire an unequal share of the light resources which can exacerbate the size-inequality.

Jack pine experience stronger competitive effects in the pure stands examined because each individual pine is competing with its neighbours for space in the canopy to acquire light, whereas in the mixed stands the spruce are in the understory and do not affect jack pine in their quest for light. This is one explanation as to why black spruce has little effect on shade-intolerant jack pine.

Competition Index as a Predictor of Radial Growth

Radial growth declines with increasing competition as measured by all three indices (Figure 6). The regression analysis found the relationship between radial growth and competition index for all three models to be significant at the 0.05 level. The species identity slightly influenced the strength of the model; black spruce had higher r^2 values in every case, with the exception of Canham's index. However, there was a lot of scatter and r^2 values indicate that there was a lot of unexplained variation; only 4.7 – 10.0% and 5.8 – 33.6% of the variation in radial growth of jack pine and black spruce, respectively, could be explained by the three competition indices calculated (Table 13). It is possible that a non-linear function form may have improved the fit of tree growth versus the three competition indices, which is something to consider in future studies.

Although, the linear relationship can be seen in the scatterplots, clustering of data points suggest that most of the trees at these sites are experiencing relatively little competition. Spruce had higher radial growth in all cases, which may suggest that jack pine is using more of its resources for height growth or because the pine is experiencing more competition for light due to its shade tolerance.

Predicting radial growth from any of the linear regression models would not be advised, as they would perform poorly. Canham's approach using MLE to predict radial considers not only the competition index, which is a measure of crowding, but also a number of other parameters to predict radial growth. In the model I used, these included maximum RG (a function of diameter), a parameter estimated by the analysis that is multiplied by Canham's index ("C"), as well as shading. The scatter that can be seen in the lowest panel of Figure 6 is thus an indication that Canham's index alone, without the inclusion of these other factors, is unlikely to provide accurate estimates of radial growth.

Mean square error (MSE) is often used to determine which regression model best explains the variability in the observations. The model with the lowest MSE is generally interpreted as the best. Hegyi's had the lowest MSE for jack pine, followed by Canham's and Schütz's models, with MSE values of .312, .326, and .331, respectively (Table 13). For black spruce Schütz's index produced the lowest MSE followed by Canham and Hegyi, with values of .490, .591, and .696 (Table 13). The MSE values suggest that of the models tested, no single index outperforms the other in predicting radial growth from a single value in the linear regression model.

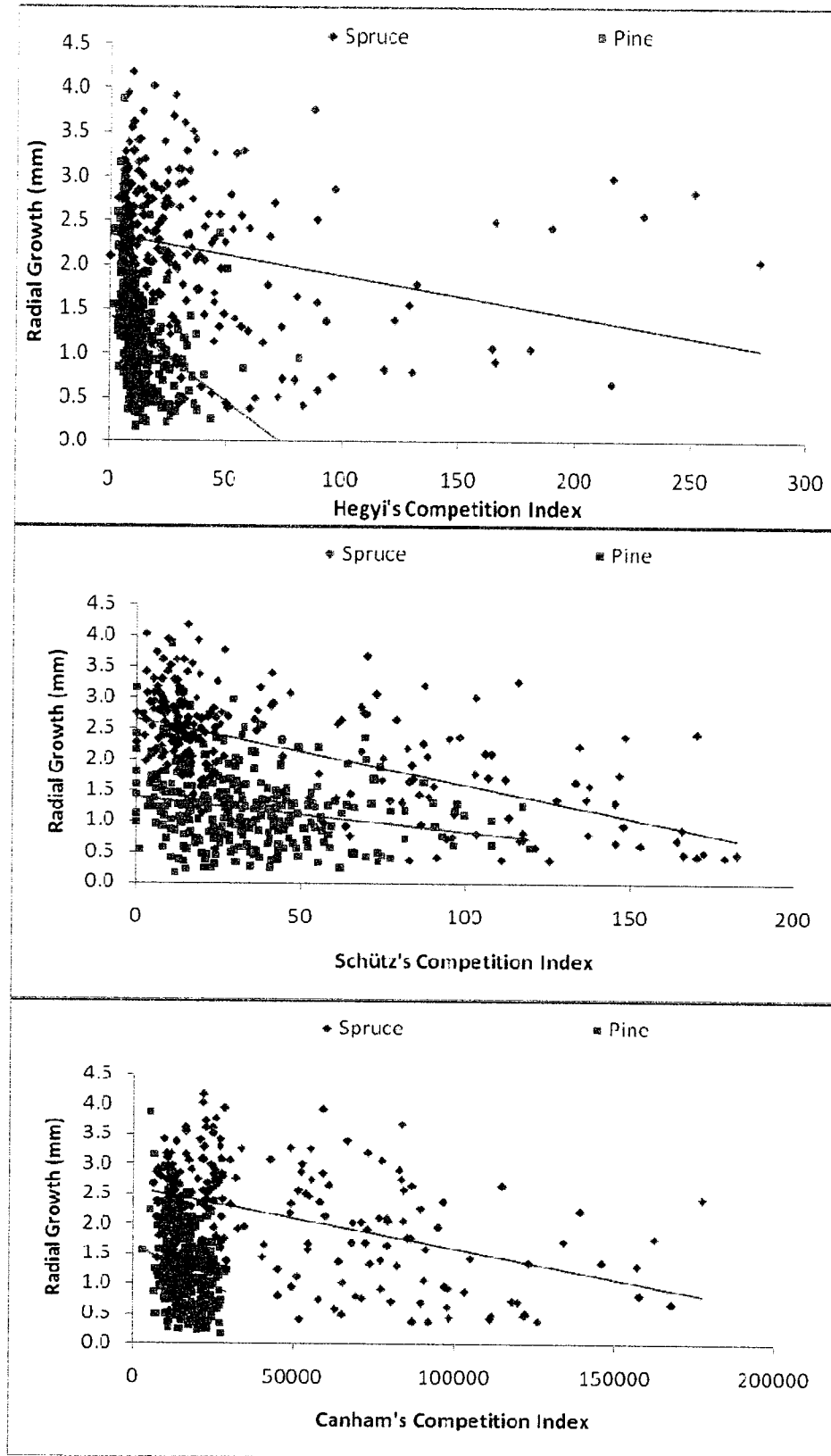


Figure 6. Scatterplots and fitted regression line of radial growth and competition index (Hegyi, Schütz, and Canham, respectively) for black spruce and jack pine.

Table 13. Linear regression coefficients and statistics for predicting radial growth from competition index.

Species	Competition		b_0	b_1	r^2	MSE	P
	Index						
Pj	Hegy		-0.0196	1.4428	0.010	0.312	0.000
	Schütz		-0.0056	1.3774	0.047	0.331	0.000
	Canham		-3.00E-05	1.64E+00	0.060	0.326	0.000
Sb	Hegy		-0.0046	2.3336	0.058	0.696	0.000
	Schütz		-0.0106	2.6449	0.336	0.490	0.000
	Canham		-1.00E-05	2.59E+00	0.200	0.591	0.000

The weak relationship between radial growth and competition index, signified by the low r^2 values suggests that: a) competition may not be strong in these stands, b) these competition indices may not be appropriate for quantifying competition in mixed stands, or c) radial growth is not the best metric for assessing competition in these stands.

These ideas will be examined in further detail below.

- (a) If competition is not strong, this may reflect the complementary growth patterns and resource requirements of the component species or it may suggest that the current stage of stand development does not involve substantial competition.
- (b) Traditionally, competition indices have been used to assess competition in pure stands. Hegyi's and Schütz's indices do not account for species differences; therefore, they may not be appropriate for quantifying competition in mixed stands. Canham's model does account for species differences by including λ and Canham *et al.* (2004) found the model to explain 33-59% of the variation of radial growth in their study of mature western hemlock – western redcedar mixtures in British Columbia. The different outcomes from this study and Canham *et al.*'s (2004) could be a result of stand age (relatively young stands vs.

mature stands) or there may be variation in northwestern Ontario compared to northwestern British Columbia.

- (c) Radial growth tends to decrease as trees enter the sub- and main canopies (Nowacki and Abrams 1997). This may explain the lower radial growth rates (Appendix II) of jack pine compared to that of spruce. The competition indices include diameter or height as growth indicators and do not take into account the rate of growth, which is why jack pine on average had smaller competition indices. Stands undergoing self-thinning experience a reduction in growth rates; however, if this were the cases, inter-tree competition would be very high (Weiner and Thomas 1986) and this is not reflected in the competition indices computed for these stands. These stands are still in the early stages of self-thinning. Because radial growth rates are affected by canopy position and stand development stage, they may not be the best metric to assess competition in these stands. Size differences may also be attributed to factors other than competition including, genetic differences, environmental heterogeneity, and age differences (Weiner and Thomas 1986).

The slopes of spruce and pine were found to be significantly different for all three indices (Table 14). Generally, jack pine exhibited steeper regression slopes compared to black spruce. The difference between the fitted regression line slopes for spruce and pine was most apparent for Hegyi's index (Figure 6). The steep slope of the regression line indicates that as competition increases, it has a greater negative effect on jack pine radial growth, which suggests that pine may be more sensitive than spruce to increasing competition for light and crowding. This is expected as jack pine is a shade-

intolerant tree. Shade-intolerant trees are more sensitive to increasing aboveground competition than a mid-tolerant or tolerant species (Holmes and Reed 1991). Thus, adding more trees to a spruce stand should not have as much of an effect on radial growth as adding more pine to a pine stand.

Table 14. Slopes (B) and t-values calculated to test for differences in slope between species for competition index vs. radial growth shown in Figure 6.

Index	B		t_{stat}
	Spruce	Pine	
Hegyí	-0.0046	-0.0195	3.387*
Schütz	-0.0106	-0.0056	2.71*
Canham	-1.0061E-04	-2.7449E-04	2.312*

*denotes significance

As previously mentioned, Hegyí's, Schütz's, and Canham's indices are not good predictors of radial growth from the linear regression model. This is supported by the weak linear relationships observed between the three competition indices and radial growth (Figure 6). To further support this statement, expected radial growth was predicted using the regression equations for each index, results are displayed in Figure 7. There is a distinct upper boundary to the values that is apparent for all three indices. These upper boundaries coincide with the slope intercept of the regression lines presented in Figure 6, meaning that these models are incapable of predicting radial growth above the slope intercept. It is clear that these regression equations would be inappropriate for predicting radial growth in these stands. However, the strength in Canham's MLE model is that it accounts for not only crowding, shading, and inter-versus intraspecific competition, but it can also predict potential radial growth using

optimization techniques in the MLE model (Figure 8). The adapted MLE model included Canham's competition index and potential radial growth (submodels) and parameters estimated by the analysis that measures the sensitivity of the target tree to crowding and shading to determine expected radial growth. The ability to predict potential radial growth has implications for forest management. Determining future species composition and growth rates of mixed stands is difficult because the target tree will interact differently with different species and because mixtures have received less study than their pure counterparts. Canham's model has the potential to predict future growth which can aid in determining which silvicultural system to employ to meet desired outcomes.

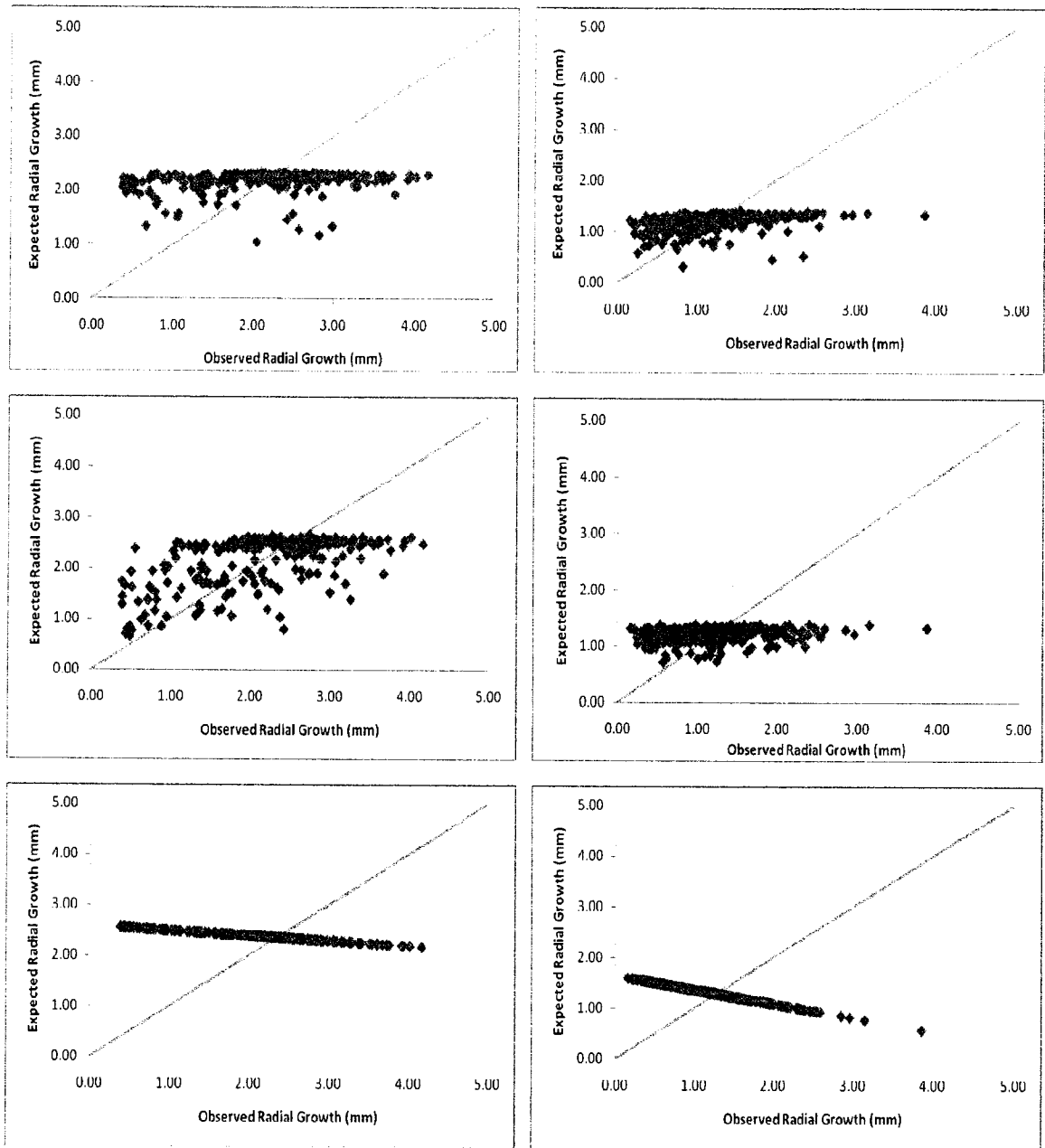


Figure 7. Expected vs. observed radial growth for black spruce (left) and jack pine (right) for Hegyi's and Schütz's, and Canham' competition indices, respectively. Lines are a 1:1 relationship between predicted and observed growth.

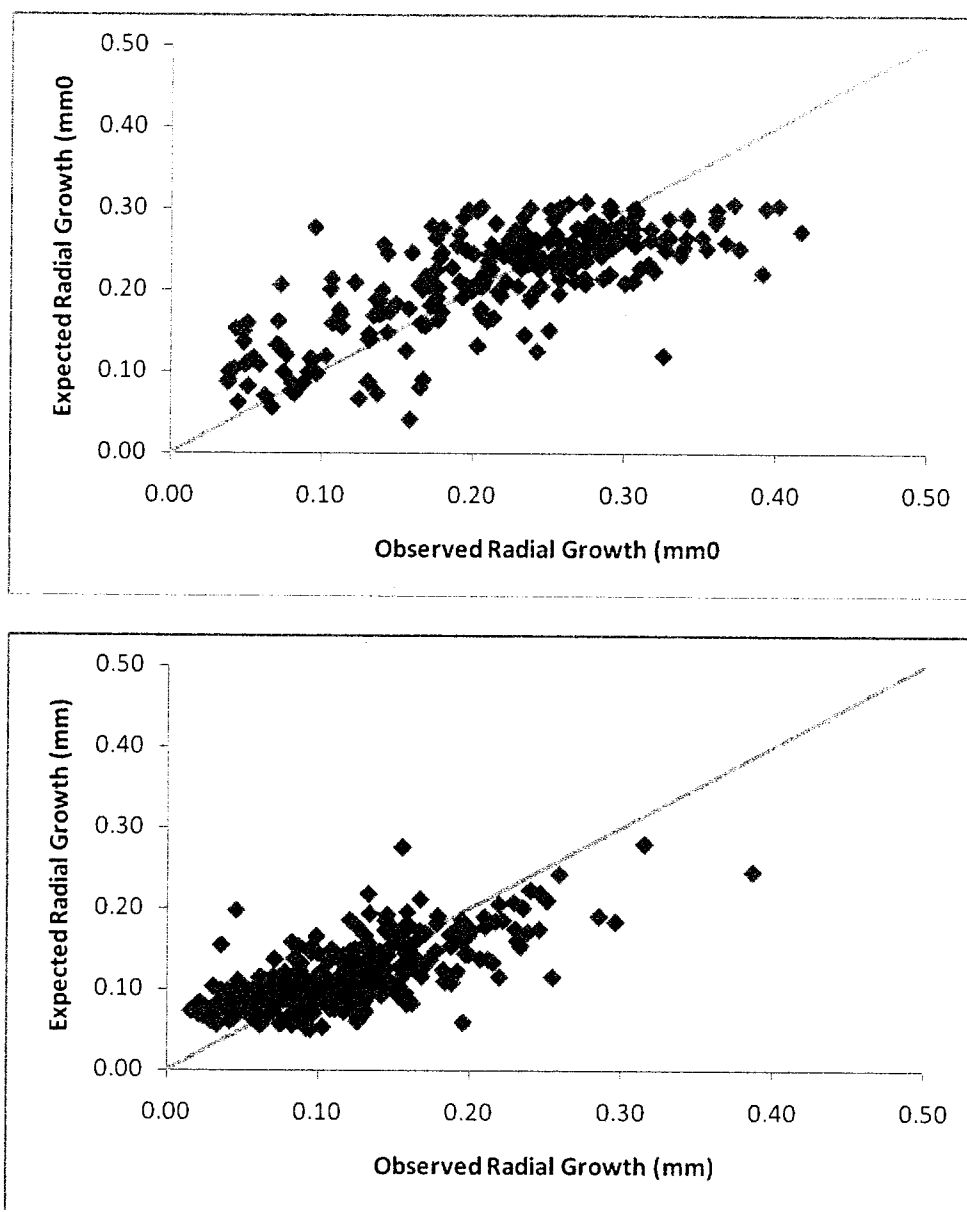


Figure 8. Expected vs. observed radial growth for black spruce (top) and jack pine (bottom) for Canham's adapted maximum likelihood estimation (MLE) model. Lines are a 1:1 relationship between predicted and observed growth.

Using Hegyi's and Schütz's indices you are limited to making inferences about inter- and intraspecific competitive effects, whereas Canham's model allows us to directly measure inter- and intraspecific competitive effects to support inferences.

Canham's model computes a species-specific competition index, depending on the identity of the subject tree and that of its neighbours to assess the effect of species, while Hegyi's and Schütz's ignore the identities of neighbouring trees. Analysis of competitive effects due to species identity will also be useful in the development of silvicultural systems aimed at managing mixed-species stands and need to be accounted for to predict future growth.

While it is more costly and time consuming, in natural mixed stands it is best to use distance-dependent competition indices to account for the irregular spatial arrangement. Assuming uniformity of spatial arrangement can lead to losses in growth and mortality (Norris *et al.* 2001). Knowing the spatial arrangement of the stand and which trees are experiencing intense competition from neighbours will aid in density management decisions, such as commercial thinning. Of the three indices used, Hegyi's is the easiest to compute, especially since dbh is a standard measurement taken for permanent growth and sample plots. While you can substitute dbh for height when computing Schütz's competition index, crown radii measurements are time consuming and the risk of measurement error is high without the proper equipment. Quantifying competition with Hegyi's or Schütz's indices give you a snapshot of competition at one point in time and would be most appropriate for addressing the question "Do I currently have a competition problem?" Canham's index requires the MLE model to be calibrated to reflect the stand conditions and geographic location, requiring a strong modeling background. However, with Canham's model you can not only address the question "Do I currently have a competition problem?" but also "Will I have a competition problem in the future?"

BELOWGROUND COMPETITION

The results from ANOVA and SNK tests of main and interaction effects for both black spruce and jack pine are summarized in Tables 15, 16, and 17. The interaction effects are displayed in Figures 9 for Sb_r , % Sb_r , Pj_r , and % Pj_r , respectively.

Table 15. Summary of F-ratios calculated from ANOVA for black spruce and jack pine root biomass and percentage root biomass**.

Source of Variation	d.f	Black Spruce		Jack Pine	
		Biomass (g/100 g soil)	Percentage (%)	Biomass (g/100 g soil)	Percentage (%)
Site	1	0.18	0.04	1.58	0.52
Stand Type	1	13.90*	135.23*	0.51	8.37*
Depth	6	8.47*	1.17	12.56*	3.44*
Site* Stand Type	1	0.06	0.23	2.53	2.62
Site*Depth	6	0.80	0.50	0.74	0.98
Stand Type* Depth	6	3.67*	0.90	1.83	4.81*
Site* Stand Type* Depth	6	0.17	0.38	0.59	1.08

* indicates significance at the 0.05 level

** A full summary table of ANOVA components is presented in Appendix III and IV for Sb and Pj , respectively.

Table 16. Student-Newman-Keuls tests of main effects for black spruce root biomass and root biomass percentages.

Black Spruce		Root Biomass (g/100 g of soil)			Percentage Root Biomass (%)		
Variable	Level	N	Mean	SNK	N	Mean	SNK
Stand Type	Sb	70	0.0789	A	63	78.3	A
	MW	54	0.0188	B	50	14.3	B
Depth	Organic	18	0.1509	A	16	68.3	A
	0 to 5	18	0.1179	A, B	17	45.3	A
	5 to 10	18	0.0628	B	18	56.7	A
	10 to 15	18	0.0193	B, C	18	46.7	A
	15 to 20	18	0.0086	C	17	40.3	A
	20 to 30	17	0.0016	C	13	47.3	A
	30 to 45	17	0.0022	C	14	44.5	A

*Means with the same letter are not significantly different.

Table 17. Student-Newman-Keuls tests of main effects for jack pine root biomass and root biomass percentages.

Jack Pine		Root Biomass (g/100 g of soil)			Percentage Root Biomass (%)		
Variable	Level	N	Mean	SNK	N	Mean	SNK
Stand Type	Pj	75	0.0893	A	75	92.1	A
	MW	79	0.0983	A	79	82.7	B
Depth	Organic	22	0.0839	B, C	23	71.1	B
	0 to 5	23	0.1737	A	23	86.4	A
	5 to 10	23	0.1741	A	23	92.5	A
	10 to 15	23	0.0905	B	23	86.4	A
	15 to 20	21	0.0706	B, C	21	94.2	A
	20 to 30	22	0.0294	B, C	22	89.8	A
	30 to 45	20	0.0203	C	19	92.3	A

*Means with the same letter are not significantly different.

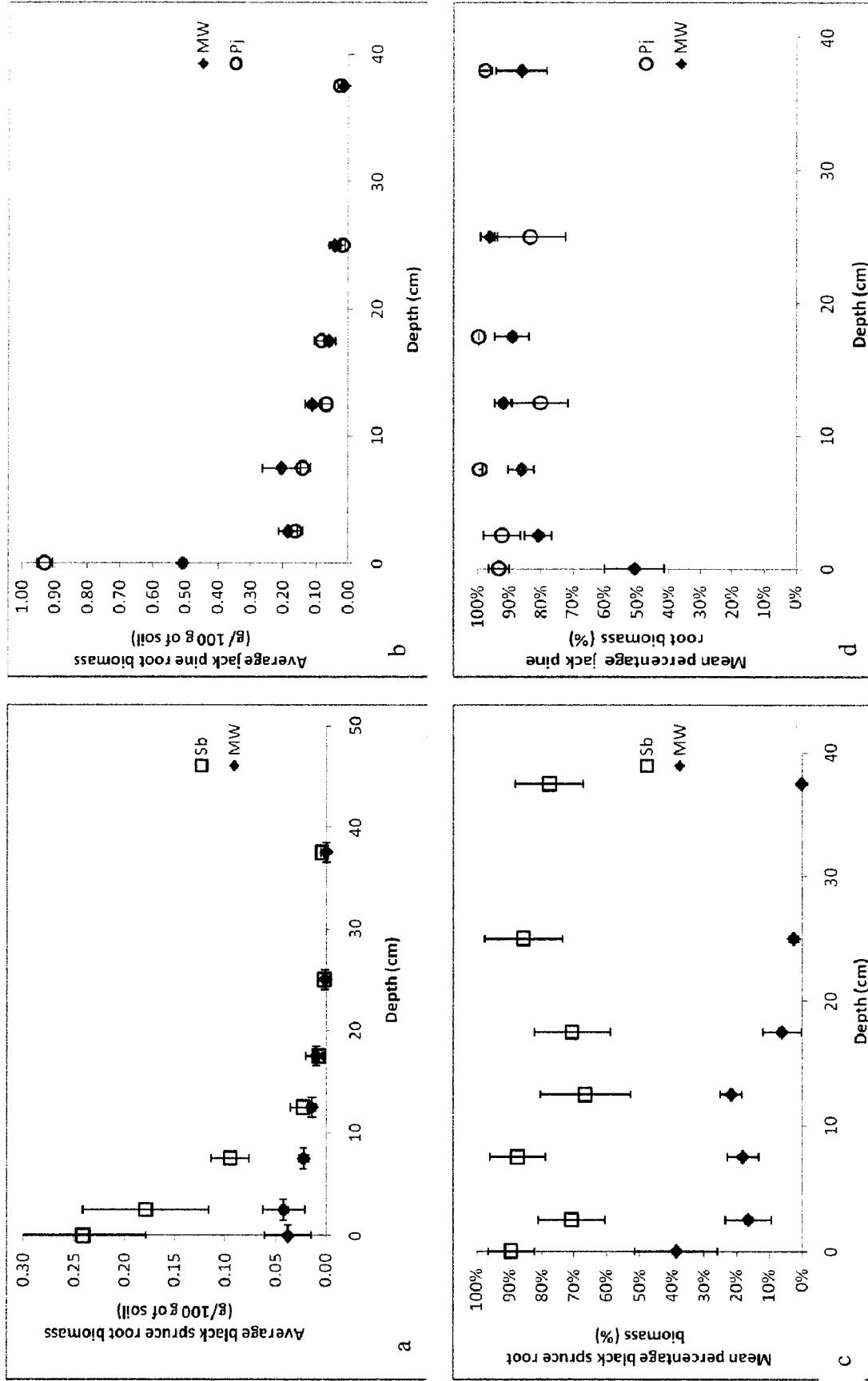


Figure 9. Relationship between depth and a) average Sb root biomass, b) average Pj root biomass, c) average percentage of Sb root biomass, and d) average percentage of Pj root biomass. The associated table is presented in Appendix V.

Black Spruce

Stand Type ($p = 0.0003$), Depth ($p < .0001$), and their interaction ($p = 0.0025$) significantly affected the amount of Sb_r biomass (Table 15). The interaction can be seen in Figure 9a. In this case, there is little difference between layers in the MW stands but a clear decline from top to bottom in pure stands. Pure spruce stands had 4 times more Sb_r than mixedwood stands, which resulted not only in a significant effect of Stand Type but also drove the main effect of Depth.

Black spruce in mixedwood stands have significantly less root biomass. This may be because P_j occupied the site first and had already established their root system forcing the Sb to put their roots wherever there was space to do so, in order to acquire belowground resources. In Sb_p stands, trees placed roots in the upper organic and mineral layers. This coincides with the known silvics of the species. Black spruce has a shallow root system (Fowells 1965) compared to P_j and tends to concentrate the majority of roots in the upper 20 cm of the organic horizons (Viereck and Johnston 1990). Figure 9 reveals an interesting phenomenon between Sb_r and P_{j_r} in the organic soil of mixed stands. In MW stands, average Sb_r in the organic soil was very low (0.040 g); nonetheless, it appears to have a large effect on the amount of P_{j_r} in this horizon. The amount of P_{j_r} in this layer decreased by almost 50% between pure (0.932 g) and mixed (0.507 g) stands, which indicates that Sb_r , although small in quantity greatly affects the distribution of P_{j_r} . This suggests that Sb is a stronger competitor in the organic layer. This is likely a reflection of spruce's adaptation to wet and organic soils.

Significant differences were detected for the main effect of Stand Type ($p < .0001$) on the % Sb_r (Table 15). Post hoc tests show that % Sb_r was greater in pure

stands (Figure 9c). While statistically significant, these results are not ecologically significant, as this would be expected because Pj are not present in these stands.

Jack Pine

Average abundance of Pj_r declined with increasing depth (Table 15). SNK post hoc tests revealed that the upper mineral soil layers (0-10 cm) had significantly more root biomass than the organic and lower soil layers (10-45 cm).

The results suggest that Pj prefer to put their roots in the upper mineral horizons of the soil profile regardless of Site and Stand Type. Jack pine is reputed to lay down a relatively deep taproot (Rudolph and Laidly 1990). However, the bulk of the medium and fine rooting systems are confined to the upper 46 cm of the soil profile (Rudolph and Laidly 1990), unless intense competition for water and nutrients force them to forage deeper parts of the profile (Karsh 1896). Given that the results show that Pj are putting the majority of their roots in the upper mineral soil horizons, it is likely that competition for soil moisture and nutrients is not intense.

Stand Type ($p=0.0045$), Depth ($p=0.0035$), and their interaction ($p=0.0002$) significantly affected the percentage of Pj roots (Table 15). The interaction can be seen in Figure 9d. In this case, there is no difference between relative amounts of roots found at different depths in the Pj_p stands, but the % Pj_r roots found in the organic layer of the MW stands is significantly less than that found in the mineral soil. In other words, Pj roots appear to be less competitive in the organic layer and more competitive at deeper depths in comparison to Sb.

The pure jack pine stand had a significantly higher % Pj_r (Table 17; Figure 9d), which is expected since pine is not sharing the soil with spruce on these sites. The main

effect of Depth reflects the influence of the interaction and the large difference in relative amounts found in the organic layer only.

The results suggest one of two things may be occurring: 1) competition for soil resources at the study sites may not be intense enough to promote complete stratification, or 2) root plasticity and morphology characteristics of jack pine and black spruce may not be such that they are able to utilize soil resources in a spatially noncompetitive manner. Root studies of the morphological plasticity of European beech (*Fagus sylvatica* L.) fine roots have shown adaptations to different levels of competition. Curt and Prevosto (2003) studied rooting patterns of mixed silver birch (*Betula pendula* Roth) and beech stands at different competitive intensities and found that at low levels of competition, fine roots coexist in the same soil layers. Under high competition, beech exhibits vertical stratification of root systems, occupying deeper parts of the soil (e.g. Curt and Prevosto 2003; Bolte and Villanueva 2006). Bolte and Villanueva (2006) studied the impacts of competition on fine root morphology and distribution of European beech and Norway spruce. They found that the abundance of Norway spruce fine root biomass was significantly lower in mixed stands compared to pure stands, which coincides with the results of this study. Complete separation of spruce and beech rooting systems was observed, with Norway spruce dominating the organic and upper 5 cm, while beech increased noticeably from 10-40 cm (Bolte and Villanueva 2006). This is not to say that competition for belowground resources is not occurring. Black spruce did appear to affect the distribution of P_j in the organic layer in MW stands. However, further research under a controlled even mixture is required to determine whether complete stratification occurs and if so, how meaningful is it to the coexistence and productivity of these species.

The alternative is that Sb and Pj at these sites are not able to acquire belowground resources in a spatially noncompetitive manner (Wang et al. 2002), due to morphological characteristics. If this is the case, competition may be negatively affecting the growth of one or both species. The competition index values suggest that Sb is experiencing more intense competition than Pj; however, relative growth rates of Pj appear to be more affected by competition than Sb. It is likely that differences in tree sizes are due to asymmetrical competition for light rather than that for belowground resources.

CONCLUSION

This study employed three distant-dependent competition indices to quantify competition in pure- and mixed stands of jack pine and black spruce. Quantifying competition with Hegyi's or Schütz's indices gives you a snapshot of competition at one point in time and would be most appropriate for addressing the question "Do I currently have a competition problem?" Canham's index is more intensive to calculate; however, with Canham's model you can not only address the question "Do I currently have a competition problem?" but also "Will I have a competition problem in the future?"

In addition, using Hegyi's and Schütz's indices you are limited to making inferences about inter- and intraspecific competitive effects. The strength of Canham's index lies in its ability to predict potential radial growth and to quantify inter- versus intraspecific competition by computing λ from the MLE model. Hegyi's and Schütz's do not consider species differences, which may make them inappropriate for assessing competition in mixed stands.

Black spruce roots vertical distribution did not differ among pure and mixed stands. Black spruce prefers the organic and upper 10 cm of the mineral soil regardless of stand type. While jack pine also prefers upper mineral soil, the majority of root biomass in the lower soil profile are pine. The presence of black spruce roots in the organic layer strongly affected the distribution of jack pine roots in mixed stands. This reinforces the silvics of the species; spruce is a stronger competitor for belowground resources in organic soils, and jack pine is stronger on sandier mineral soils. It is not possible to determine whether complete separation of pine and spruce roots would have occurred under more 'intense' competitive conditions, as the intensity of belowground competition (i.e. resource limitations) were not determined. Therefore, it is

recommended that future studies of this kind perform a measure of nutrient and water availability of the site to complement root biomass data.

Due to physiological, physical, and temporal differences these species are able to coexist. Pure stands of jack pine had the greatest amount of basal area; however, the variable spatial distribution of the species in these stands did not allow pine and spruce to take advantage of individual species differences. The silvics of these species do suggest that there is potential for mixed stands composed of black spruce and jack pine to be more productive than their pure counterparts. Research on competition and thinking about how these two species are able to coexist is a first step toward facilitating management of spruce-pine mixtures in northern Ontario. The next step to complete the story is to implement studies that assess the potential gains in productivity in these stands to encourage policymakers and forest managers to support conifer mixedwood management. It is recommended that forest practitioner's managing jack pine – black spruce mixtures establish stands on sites of medium fertility, at relatively high densities using a fine-grained approach with unequal species proportions (Figure 1).

These results denote responses at a relatively early age, prior to stem exclusion. Long-term measurements are required to track species interactions along all stages of stand development. It is recommended that future studies use managed stands so that species mixtures can be more carefully controlled and differences between species can be maximized. In nature it can be difficult to find even species mixtures, especially if a site favours one species, even slightly, over another. Therefore, the results and inferences taken from this study relate to the specific conditions of the experimental sites and should not be widely extrapolated to other sites, species-mixtures, and stand conditions.

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APPENDICES

APPENDIX I SUMMARY STAND STATISTICS OF
RECONNAISSANCE DATA COLLECTION

Table 18. Summary stand statistics from reconnaissance data collection. The mean represents the average from five plots per stand and site type.

Transect ID	Species	Mean Ht. (m)	Mean dbh (cm)	Density (sph)	Rel. Freq. sph (%)	BA (m ²)	Rel. Freq. BA (%)	Total BA
GbSb	Spruce	5.66	6.5	3100	99	0.038	49	6.17
	Pine	.	1.9	3100	1	0.040	51	
GbPj	Spruce	7.13	7.4	2900	4	0.085	47	13.08
	Pine	12.29	10.6	2900	87	0.096	53	
GbMW	Spruce	5.78	6.6	2300	33	0.040	19	13.05
	Pine	12.56	14.1	2300	59	0.170	81	
GrSb	Spruce	5.96	7.0	3000	99	0.044	92	7.24
	Pine	.	2.3	3000	1	0.004	8	
GrPj	Spruce	3.49	3.3	3700	35	0.012	10	10.4
	Pine	9.32	10.6	3700	65	0.104	90	
GrMW	Spruce	4.97	5.1	4400	44	0.024	21	11.97
	Pine	9.67	10.1	4115	56	0.090	79	

APPENDIX II

SUMMARY OF INDIVIDUAL TREE CHARACTERISTICS AND COMPETITION INDEX DATA

Table 19. Summary table of black spruce individual tree characteristics and competition

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
6	GbMW	24	1.5	1.94	0.60	0.508	72.419	172.462	122302.094
15	GbMW	27	1.4	2.45	0.46	1.364	93.478	136.643	145942.069
16	GbMW	23	1.4	2.45	0.35	0.816	117.746	117.448	157903.294
17	GbMW	26	1.0	2.20	0.46	0.668	215.910	145.653	167768.365
21	GbMW	23	1.8	2.69	0.56	1.308	74.253	145.453	157187.272
25	GbMW	30	3.4	3.02	0.60	2.424	40.629	170.263	177472.721
51	GbMW	20	9.0	6.56	1.13	2.216	11.199	134.458	139061.277
77	GbMW	23	12.8	9.83	0.98	2.048	5.273	44.345	79214.953
89	GbMW	25	2.6	3.18	0.87	0.620	39.861	153.274	97761.566
90	GbMW	25	3.7	3.36	0.98	0.876	28.840	165.785	103184.941
91	GbMW	27	4.9	6.39	0.56	0.964	22.103	56.982	96870.261
92	GbMW	26	2.2	2.94	0.90	0.444	49.990	170.314	98461.159
93	GbMW	28	7.4	5.08	1.06	0.936	15.155	147.935	98173.415
94	GbMW	28	4.5	4.35	0.67	0.380	24.987	125.598	86808.780
95	GbMW	28	1.3	2.39	0.61	1.580	89.107	137.595	91017.398
135	GbMW	22	3.1	3.49	0.93	0.480	30.795	166.359	111686.196
136	GbMW	23	3.9	3.98	1.12	0.428	29.905	178.911	111177.445

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
137	GbMW	23	11.7	8.50	1.17	1.432	7.701	85.806	105014.927
138	GbMW	25	1.9	2.75	0.46	0.384	51.107	111.104	126232.346
142	GbMW	29	9.5	9.96	0.66	2.640	9.719	35.757	114949.253
144	GbMW	30	8.8	6.98	0.83	1.708	10.747	106.899	134155.088
146	GbMW	24	6.4	5.76	0.92	1.356	17.894	127.659	123247.259
147	GbMW	23	4.6	4.95	1.10	0.708	30.506	164.232	119994.301
148	GbMW	23	7.8	6.37	0.68	0.724	15.495	93.993	118027.776
149	GbMW	22	3.9	3.98	1.13	0.480	31.899	182.672	121945.190
153	GbMW	20	7.0	5.88	1.13	2.376	19.487	148.409	96463.548
159	GbMW	23	8.8	6.96	1.59	1.760	7.527	146.714	162619.388
1	GbSb	24	10.3	7.05	1.13	2.376	3.933	2.310	10335.176
3	GbSb	25	5.8	4.78	1.00	2.736	6.650	8.215	10183.167
4	GbSb	24	8.6	6.19	0.94	2.148	4.644	5.618	9830.219
7	GbSb	25	2.5	3.11	0.53	1.652	21.877	19.842	12665.771
8	GbSb	24	1.7	2.71	0.43	1.556	128.847	19.451	12365.117
14	GbSb	25	7.0	5.36	0.81	2.908	8.786	8.387	11683.829
15	GbSb	25	2.4	3.06	0.52	1.132	44.927	20.028	12583.191
18	GbSb	26	1.5	2.61	0.59	0.544	43.669	23.736	11081.168
19	GbSb	26	5.9	4.83	1.19	2.000	7.395	13.963	10443.325
20	GbSb	28	4.7	4.22	0.86	2.076	10.042	15.392	10483.890
26	GbSb	31	6.0	4.88	0.77	2.280	9.100	10.450	12586.934
27	GbSb	22	2.2	2.96	0.61	1.432	40.404	17.257	7290.456
28	GbSb	23	3.6	3.67	0.69	2.384	19.297	8.102	7171.898
32	GbSb	28	6.7	5.23	0.90	1.892	7.380	9.105	14819.409

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
33	GbSb	25	6.5	5.13	0.97	2.308	7.302	12.531	14816.338
40	GbSb	24	5.0	4.37	0.77	2.316	8.320	16.473	12417.791
41	GbSb	25	5.7	4.73	0.78	2.664	8.094	15.412	12273.807
48	GbSb	25	8.3	5.44	1.04	2.848	11.945	8.154	12439.526
49	GbSb	25	8.8	6.29	0.79	2.800	10.910	4.915	12146.971
50	GbSb	23	11.0	8.82	0.65	2.748	5.901	0.000	10695.209
51	GbSb	24	4.5	4.12	0.70	1.064	22.733	13.347	13534.970
52	GbSb	32	3.6	3.67	0.64	1.928	14.597	15.003	12803.502
56	GbSb	24	3.2	3.46	0.71	1.716	38.401	22.524	13782.330
57	GbSb	24	3.9	3.82	0.46	1.992	27.933	12.918	13689.646
58	GbSb	21	6.2	4.98	0.79	2.396	6.260	8.899	10125.205
60	GbSb	24	7.2	5.48	1.26	2.984	6.495	18.104	11912.432
62	GbSb	24	10.3	7.05	0.84	2.052	36.809	4.218	8597.709
63	GbSb	22	4.3	4.02	0.50	2.072	23.099	14.535	13681.765
64	GbSb	22	6.8	5.28	0.65	2.768	15.387	9.175	12665.053
66	GbSb	21	2.9	3.31	0.72	1.392	53.668	25.285	13449.119
76	GbSb	24	6.4	5.08	0.90	2.924	7.172	13.049	10153.722
80	GbSb	23	5.8	4.78	0.68	2.200	6.669	7.558	10796.600
81	GbSb	24	3.9	3.82	0.93	1.664	11.392	20.350	13097.787
89	GbSb	26	8.7	6.24	1.02	2.784	5.852	7.079	8323.088
96	GbSb	26	4.1	3.92	0.67	2.448	11.415	13.657	14265.455
108	GbSb	24	5.0	4.47	1.19	2.112	32.660	23.119	10851.326
109	GbSb	24	9.0	6.44	1.29	3.416	12.630	9.176	9316.899
115	GbSb	25	7.0	5.58	0.76	2.344	6.403	10.538	10346.511

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
116	GbSb	28	1.0	2.40	0.43	1.300	47.350	26.431	14181.513
117	GbSb	27	8.0	5.63	1.21	1.800	5.985	12.114	9156.915
120	GbSb	27	5.0	4.47	0.76	1.748	15.649	16.269	17594.842
121	GbSb	25	8.0	7.15	0.82	2.272	8.246	0.000	15832.604
122	GbSb	27	4.0	4.07	0.73	2.000	10.672	15.617	9540.186
125	GbSb	27	6.0	4.67	0.95	2.560	9.458	14.514	12578.807
126	GbSb	29	5.0	4.47	0.74	2.112	8.503	11.192	7070.766
132	GbSb	22	4.0	3.67	0.73	2.052	15.650	16.678	12176.441
133	GbSb	22	2.0	2.96	0.45	1.308	25.453	17.242	12350.698
134	GbSb	22	2.0	2.76	0.25	1.308	35.572	12.587	12349.968
139	GbSb	23	9.0	6.19	1.20	2.328	4.194	6.615	7525.515
144	GbSb	21	5.0	4.57	1.05	3.104	7.349	14.081	10238.325
146	GbSb	20	4.0	4.07	0.75	2.296	12.910	15.963	10563.951
147	GbSb	20	7.0	5.28	0.84	3.172	6.073	12.503	9942.134
153	GbSb	24	5.0	4.32	0.80	2.436	9.693	12.301	14553.472
154	GbSb	24	8.0	5.63	0.90	2.912	5.412	3.864	7467.011
155	GbSb	24	6.0	4.83	0.60	1.792	6.279	7.295	7820.134
156	GbSb	23	6.0	4.88	1.07	3.372	7.466	19.111	13178.503
159	GbSb	25	9.0	6.24	1.00	2.528	4.710	4.594	10694.767
160	GbSb	20	6.0	4.73	0.70	2.836	6.996	8.243	11076.612
166	GbSb	18	8.0	5.68	1.00	3.172	4.862	6.252	11457.464
171	GbSb	19	6.0	4.62	0.62	2.104	0.127	5.264	13928.630
172	GbSb	19	7.8	5.78	0.72	2.736	4.630	1.703	10825.275
179	GbSb	22	7.5	5.63	0.93	2.792	5.902	6.383	12640.609

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
180	GbSb	20	5.3	4.52	0.75	2.604	7.512	8.381	12060.356
187	GbSb	24	5.2	4.47	0.72	1.856	10.252	14.878	13615.880
201	GbSb	18	5.4	4.57	0.63	2.680	15.658	12.405	12848.301
203	GbSb	18	5.5	4.62	0.46	2.096	15.852	8.201	11185.483
204	GbSb	19	5.7	4.73	0.80	1.776	10.540	14.017	12778.847
205	GbSb	23	7.7	5.73	1.12	2.544	6.318	11.234	12597.075
206	GbSb	23	5.7	4.73	0.77	2.512	22.429	13.380	18110.613
207	GbSb	23	8.4	6.09	0.94	3.056	11.979	7.060	17034.010
209	GbSb	16	7.6	5.97	0.76	3.056	11.979	7.060	17309.075
217	GbSb	17	6.1	4.93	0.78	2.852	6.591	12.277	14387.217
1	GrMW	44	7.5	5.96	1.11	3.196	14.883	87.452	72992.881
17	GrMW	39	1.8	2.60	0.31	0.492	7.546	66.167	64959.306
19	GrMW	25	3.8	4.81	1.34	1.572	44.875	90.336	54387.606
20	GrMW	26	1.9	2.67	1.21	3.260	44.875	115.961	55143.750
21	GrMW	35	8.6	6.80	1.20	3.072	7.574	46.653	42603.892
48	GrMW	39	1.0	1.74	0.45	1.648	7.574	82.932	40591.148
49	GrMW	33	1.1	1.74	0.67	0.800	7.574	103.403	44956.760
74	GrMW	48	6.1	5.46	0.83	2.020	17.226	74.895	68202.245
75	GrMW	54	3.8	3.93	0.74	2.092	38.039	107.775	78952.694
81	GrMW	51	8.7	7.19	0.70	2.868	19.145	40.960	52187.342
128	GrMW	45	1.6	2.47	0.66	0.584	32.337	121.206	62721.043
130	GrMW	42	7.2	7.31	0.80	2.460	20.891	36.357	54772.974
132	GrMW	43	5.7	5.20	0.78	2.736	35.581	69.967	55422.789
134	GrMW	48	3.1	3.46	0.70	1.684	26.858	112.139	67973.344

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
135	GrMW	47	1.0	2.07	0.61	0.796	130.254	137.225	69357.026
140	GrMW	35	5.7	4.44	0.88	3.004	13.525	103.126	52450.515
141	GrMW	21	0.8	1.93	0.32	1.244	13.525	64.550	44916.441
147	GrMW	10	8.6	7.13	0.90	2.756	3.538	25.691	31604.844
162	GrMW	34	4.3	4.26	0.72	2.180	20.330	82.276	48843.857
164	GrMW	12	9.1	7.46	1.26	0.952	8.730	31.529	28748.780
165	GrMW	35	3.3	3.60	0.64	1.124	28.318	86.333	49426.428
178	GrMW	35	1.5	2.40	0.42	0.416	11.591	96.678	51013.269
179	GrMW	36	1.2	2.20	0.30	1.668	11.591	91.274	51776.491
195	GrMW	44	6.8	5.93	1.20	2.364	18.562	74.513	54417.860
197	GrMW	42	1.8	2.60	0.62	0.920	18.562	98.260	58102.404
203	GrMW	37	6.0	5.40	0.45	1.908	30.786	63.542	77115.512
205	GrMW	42	6.6	6.22	1.06	1.684	25.100	83.563	72812.275
206	GrMW	43	7.5	6.40	1.11	2.100	21.012	83.918	72303.460
208	GrMW	54	6.4	5.66	0.98	1.640	26.226	105.955	76439.228
216	GrMW	49	2.1	2.80	0.76	0.764	10.016	133.328	79044.994
217	GrMW	46	8.0	6.73	0.94	2.260	16.992	64.848	71233.482
219	GrMW	47	3.5	4.16	0.54	1.068	49.618	87.001	89264.036
220	GrMW	48	1.3	2.27	0.40	0.376	49.618	113.119	90499.258
221	GrMW	47	2.5	3.58	0.37	0.696	60.338	82.998	91985.892
222	GrMW	48	2.5	3.07	0.60	0.712	79.702	116.363	89424.047
224	GrMW	43	2.1	2.78	0.61	1.024	50.318	117.602	80213.128
226	GrMW	42	9.3	8.57	0.72	2.644	11.556	28.537	65208.679
227	GrMW	43	8.0	6.73	1.22	2.848	13.248	78.798	60825.417

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyi	Schütz	Canham
229	GrMW	48	7.5	6.40	1.20	2.640	13.856	68.252	58951.568
246	GrMW	47	6.3	5.60	0.45	1.952	23.084	62.265	86677.472
247	GrMW	46	4.1	4.13	0.27	1.340	47.449	64.324	94875.983
249	GrMW	35	3.3	3.60	0.45	0.504	28.874	76.966	73591.215
253	GrMW	30	2.8	3.26	0.77	2.340	33.918	95.023	49153.916
259	GrMW	33	5.7	5.20	0.95	2.160	27.145	88.697	76936.261
260	GrMW	33	4.8	4.60	0.55	1.488	34.146	72.729	77324.191
279	GrMW	26	4.9	4.66	0.77	1.400	12.610	60.661	63953.295
281	GrMW	29	6.1	5.46	0.75	3.060	23.003	41.150	66477.318
283	GrMW	21	3.7	3.86	0.96	1.376	24.531	68.320	59645.197
284	GrMW	23	9.0	6.78	0.88	3.392	7.725	23.664	53555.072
288	GrMW	40	3.2	3.53	0.62	2.504	26.998	70.015	83512.477
299	GrMW	26	4.0	4.06	0.73	1.444	13.645	38.542	51262.494
300	GrMW	26	9.1	6.78	0.52	3.672	5.998	12.241	48913.341
301	GrMW	16	5.4	5.00	0.73	2.560	5.998	12.241	28420.938
302	GrMW	17	7.0	6.06	0.44	3.272	5.998	12.241	28452.348
315	GrMW	39	5.9	5.33	0.83	1.768	30.968	55.527	86310.984
316	GrMW	33	4.0	4.06	0.71	2.052	40.563	88.312	84008.411
317	GrMW	37	6.0	5.40	0.77	2.744	23.584	69.259	83354.690
318	GrMW	33	6.8	5.93	0.25	2.904	23.861	41.471	82694.524
319	GrMW	33	2.9	3.33	0.38	1.308	56.852	80.603	82022.959
320	GrMW	33	5.2	4.86	0.59	2.568	41.803	60.901	84147.431
321	GrMW	29	6.4	5.66	1.00	3.916	41.803	60.901	58939.730
331	GrMW	40	3.7	3.86	0.66	1.768	67.955	102.934	85380.321

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
333	GrMW	52	2.4	3.00	0.39	2.028	18.192	16.040	70982.561
1	GrSb	17	11.0	8.64	1.23	3.068	5.817	3.035	21670.079
5	GrSb	11	6.7	5.13	0.99	2.408	5.968	14.199	11113.830
6	GrSb	8	6.4	4.95	0.78	2.192	34.925	11.991	12439.433
7	GrSb	10	9.9	6.99	1.07	2.024	24.848	7.563	10562.023
8	GrSb	11	4.4	3.79	0.74	2.672	26.006	23.908	6071.843
15	GrSb	20	10.0	7.05	0.84	3.608	9.862	14.143	24329.139
16	GrSb	20	10.2	7.16	0.84	3.060	24.449	13.915	29970.053
17	GrSb	22	11.0	7.63	1.47	3.076	30.134	12.432	27222.363
18	GrSb	20	7.8	5.77	1.39	2.788	52.038	36.698	27577.656
19	GrSb	23	11.9	8.15	1.28	2.904	29.088	14.347	25259.255
27	GrSb	24	8.1	6.27	0.96	3.292	57.639	5.031	26867.127
28	GrSb	22	3.7	3.39	1.01	1.380	122.534	52.463	28901.998
33	GrSb	25	9.4	6.70	0.81	2.840	21.624	10.768	27499.891
34	GrSb	24	7.0	5.30	0.63	1.948	28.803	23.934	34618.923
35	GrSb	27	6.0	5.26	1.27	2.324	68.983	44.189	30128.404
36	GrSb	27	7.0	5.30	0.94	3.760	87.949	26.674	25417.996
37	GrSb	27	10.9	7.26	1.26	2.552	56.481	12.878	21625.534
39	GrSb	31	7.7	5.71	0.75	1.404	26.397	16.936	23583.863
44	GrSb	21	10.9	7.57	1.08	3.076	29.400	5.287	21282.957
45	GrSb	23	8.0	5.88	0.76	1.752	15.458	15.302	28276.780
52	GrSb	22	9.4	6.70	1.13	3.604	31.453	11.879	22429.843
53	GrSb	22	6.6	5.07	0.84	2.288	44.615	19.583	22198.579
54	GrSb	19	7.6	5.65	0.83	2.556	14.293	17.159	23175.950

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
64	GrSb	24	6.4	4.95	0.71	2.284	20.928	10.823	17730.187
65	GrSb	25	6.0	4.72	0.83	2.684	23.322	21.601	22834.151
67	GrSb	23	5.4	4.37	1.00	2.420	190.123	20.872	11226.800
70	GrSb	21	7.5	5.59	0.69	2.932	31.709	5.197	9090.078
71	GrSb	19	1.2	1.93	0.67	0.908	165.795	54.113	15413.916
72	GrSb	20	7.0	5.30	0.97	2.652	29.917	19.659	14258.910
76	GrSb	25	10.4	7.28	1.30	2.904	18.571	7.502	17954.170
77	GrSb	21	7.9	5.83	0.84	2.332	32.635	14.730	14946.458
78	GrSb	23	7.3	5.48	0.89	2.496	165.933	19.453	16787.236
79	GrSb	23	4.4	3.79	0.61	2.044	280.202	26.584	17596.729
82	GrSb	28	6.8	5.19	0.94	2.692	70.902	27.707	25136.773
83	GrSb	26	7.7	5.71	1.00	2.412	59.730	23.328	27607.659
84	GrSb	22	10.6	7.40	1.03	3.612	10.023	7.799	15898.025
87	GrSb	22	8.9	6.41	1.05	1.724	37.110	13.841	21532.544
88	GrSb	21	9.8	6.93	0.95	3.292	32.803	7.579	21985.067
90	GrSb	25	8.9	6.41	1.07	2.688	15.385	18.160	26575.707
91	GrSb	20	6.5	5.01	0.90	1.592	32.627	30.164	27302.828
92	GrSb	21	11.5	7.49	0.75	4.020	18.647	2.745	21500.160
95	GrSb	22	7.7	5.71	0.90	3.408	11.947	15.156	20724.494
98	GrSb	22	7.7	5.71	0.75	2.236	43.222	12.873	23836.107
99	GrSb	22	7.4	5.54	0.78	2.400	52.821	17.031	22420.716
100	GrSb	21	7.5	5.59	0.80	2.568	47.406	15.393	23765.949
101	GrSb	17	10.6	7.33	1.12	2.568	47.406	15.393	11883.672
103	GrSb	25	6.7	5.58	0.68	2.384	15.010	16.285	24787.156

Table 19 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
105	GrSb	26	10.7	8.11	0.99	3.412	36.888	2.735	26850.244
106	GrSb	26	4.3	3.73	0.80	1.056	180.977	41.049	25126.563
107	GrSb	25	8.3	6.06	0.58	2.512	89.084	9.963	22721.358
108	GrSb	22	3.1	3.04	0.36	1.788	132.130	23.653	25567.904
112	GrSb	20	11.8	8.09	0.91	2.628	6.270	2.753	25456.687
113	GrSb	18	11.0	7.41	1.27	2.508	7.538	10.695	17269.421
118	GrSb	15	10.6	7.40	0.96	1.964	6.208	2.625	16799.388
120	GrSb	16	4.6	3.91	0.55	2.860	96.633	13.774	6955.287
122	GrSb	13	5.4	3.19	0.86	3.160	11.746	37.449	16078.129
123	GrSb	14	4.3	3.73	0.60	1.216	25.997	18.395	14467.299
124	GrSb	17	5.7	4.55	0.79	2.744	24.563	22.065	19972.614
126	GrSb	22	8.3	6.06	0.82	3.280	10.110	11.139	21881.874
130	GrSb	21	8.5	6.15	1.05	4.168	9.415	15.357	21656.657
132	GrSb	21	8.0	5.88	0.74	3.512	35.595	9.981	24532.003
135	GrSb	22	12.5	7.61	1.29	2.744	18.049	11.752	25237.604
140	GrSb	25	8.3	6.06	1.19	2.824	251.928	23.204	24770.300
141	GrSb	25	9.6	6.81	0.72	2.984	216.458	7.815	23889.279
148	GrSb	25	7.6	5.65	0.78	3.256	54.447	24.410	33448.693
151	GrSb	23	8.4	6.12	0.93	1.908	13.368	21.089	32306.712
161	GrSb	16	7.4	5.54	0.41	2.116	25.513	15.747	27371.268
162	GrSb	14	11.8	8.26	0.95	3.724	13.492	6.026	22302.474
168	GrSb	18	10.2	6.54	1.03	1.932	8.210	16.256	24852.971
170	GrSb	11	6.8	5.19	0.83	3.544	9.146	16.631	16056.741

Table 20. Summary table of jack pine individual tree characteristics and competition index data.

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
1	GbMW	28	9.7	12.78	0.42	0.572	9.243	7.998	16416.261
2	GbMW	22	10.0	10.49	0.72	0.976	7.775	33.002	16560.671
7	GbMW	26	10.1	10.53	0.77	0.400	10.878	37.422	17678.213
8	GbMW	30	10.7	10.82	0.43	1.308	10.694	20.332	19827.886
9	GbMW	31	13.9	12.36	1.08	1.284	6.777	19.990	21991.907
11	GbMW	33	14.1	12.45	0.96	1.008	7.839	10.415	24208.008
12	GbMW	36	16.4	14.16	1.22	1.216	7.450	6.088	28965.540
13	GbMW	35	10.9	10.92	0.72	0.572	11.864	31.122	25391.112
14	GbMW	32	7.8	9.43	0.41	0.616	15.845	33.524	22020.689
18	GbMW	27	12.7	11.78	0.42	0.960	9.818	13.468	23925.674
19	GbMW	26	9.0	10.01	1.02	0.244	15.312	61.898	20844.462
20	GbMW	23	14.0	12.40	0.35	1.276	9.033	9.270	23622.303
23	GbMW	31	10.5	10.73	1.42	1.624	12.624	86.864	21831.322
24	GbMW	30	8.7	11.59	0.25	0.212	16.033	14.943	19825.873
26	GbMW	21	19.7	14.90	1.48	1.672	5.826	6.010	24295.141
27	GbMW	22	13.7	12.26	0.92	0.576	10.201	14.371	25690.303
28	GbMW	31	9.9	10.44	0.48	0.564	20.997	33.288	24045.205
29	GbMW	30	13.5	12.16	0.60	1.588	13.878	22.994	26507.969
30	GbMW	29	11.9	11.40	1.03	0.640	13.672	47.495	24806.971
31	GbMW	31	9.6	10.30	0.53	0.440	19.913	35.671	24201.972
32	GbMW	22	14.2	14.51	1.00	1.652	4.935	6.367	21264.680

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
34	GbMW	14	14.8	12.79	1.21	0.844	3.598	24.173	18416.985
35	GbMW	14	15.2	12.98	1.49	1.252	3.121	28.516	16148.405
43	GbMW	16	10.1	10.53	0.30	0.820	6.987	22.619	16521.594
44	GbMW	16	14.3	12.55	0.78	1.456	4.659	10.599	17794.130
47	GbMW	18	9.3	10.15	0.50	1.248	9.103	30.061	17529.923
48	GbMW	19	11.6	11.25	0.71	1.568	7.248	29.518	19070.039
52	GbMW	20	14.0	12.40	1.41	0.624	7.072	43.176	23348.782
53	GbMW	18	12.5	11.68	0.64	0.632	8.176	25.227	22166.655
54	GbMW	17	11.0	10.97	0.39	0.436	10.106	23.930	19778.125
55	GbMW	16	15.5	13.12	0.72	2.072	5.566	20.788	20693.777
56	GbMW	20	15.2	12.98	1.37	1.408	6.634	20.788	20222.317
57	GbMW	22	10.3	10.63	0.69	0.520	11.353	36.261	18648.171
69	GbMW	29	9.2	10.10	0.99	1.256	14.924	51.982	21438.185
70	GbMW	29	12.4	11.64	1.01	1.008	9.948	36.139	23790.068
71	GbMW	26	16.1	13.41	1.14	1.788	5.110	0.000	18175.558
72	GbMW	24	12.3	11.59	1.02	1.176	6.251	21.755	16476.415
82	GbMW	19	11.9	11.40	0.68	1.444	5.568	12.486	10245.797
83	GbMW	20	4.3	5.96	0.30	1.112	21.529	48.962	7829.317
99	GbMW	29	7.8	9.43	0.39	1.288	12.228	18.086	13709.905
100	GbMW	28	13.7	12.26	0.30	1.364	11.178	5.221	21415.772
101	GbMW	26	14.9	12.83	0.88	1.524	10.585	6.163	22074.533
102	GbMW	26	9.8	10.39	0.57	0.636	11.272	17.915	18821.737
103	GbMW	28	14.6	13.39	1.03	1.708	8.663	4.274	21488.552
104	GbMW	27	8.0	9.53	0.58	0.936	11.439	28.609	16484.725

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
105	GbMW	30	12.0	11.45	0.68	0.716	7.734	18.557	21224.670
112	GbMW	19	13.4	12.12	0.75	1.268	4.544	12.309	20050.362
113	GbMW	25	12.9	11.88	0.94	1.008	6.916	22.934	23403.143
121	GbMW	30	18.3	14.46	0.77	1.588	5.513	0.000	21499.223
123	GbMW	33	11.9	11.40	1.66	0.564	9.690	52.053	21692.396
134	GbMW	25	13.1	11.97	1.22	0.472	8.057	35.774	21309.339
139	GbMW	23	8.9	9.96	0.44	0.524	11.662	29.748	15153.434
140	GbMW	23	16.1	13.41	0.81	1.588	5.205	3.967	16169.495
143	GbMW	31	11.1	12.13	0.59	0.844	8.019	11.582	17619.463
145	GbMW	8	13.8	12.31	1.47	1.556	1.295	15.272	2762.605
150	GbMW	20	18.9	14.08	1.03	2.100	5.450	4.232	16902.446
154	GbMW	22	14.5	12.64	1.02	1.920	6.830	16.300	18615.483
170	GbMW	16	5.4	8.28	0.43	1.316	13.247	60.165	11226.770
171	GbMW	21	12.2	11.54	1.07	1.224	5.644	38.436	17691.174
175	GbMW	13	6.2	8.67	0.75	1.260	8.753	63.673	9422.059
176	GbMW	23	14.2	12.50	1.03	0.872	6.685	23.312	16045.673
177	GbMW	23	9.1	10.06	0.60	0.812	12.060	39.902	13408.519
180	GbMW	25	10.4	10.68	0.78	0.972	8.038	35.411	15995.007
1	GbPj	22	5.5	9.40	0.94	0.568	34.662	119.394	14157.039
3	GbPj	27	9.8	12.27	0.62	1.000	13.549	23.101	20796.624
4	GbPj	25	14.2	13.14	1.29	1.456	6.091	43.938	20557.251
5	GbPj	20	11.2	12.55	1.85	1.296	6.950	90.063	15089.324
9	GbPj	27	13.1	12.59	1.45	1.244	7.246	58.058	20110.724
10	GbPj	21	14.1	12.07	1.42	1.172	5.986	81.368	16813.530

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
11	GbPj	29	12.3	12.76	1.20	1.348	7.488	41.589	21786.350
12	GbPj	22	11.0	11.11	1.33	0.608	13.042	107.841	17383.119
13	GbPj	22	4.0	11.14	0.68	0.832	57.529	56.390	11421.793
16	GbPj	23	8.9	12.10	0.61	1.340	10.859	39.459	16185.501
17	GbPj	20	6.8	11.68	0.91	0.724	9.481	46.251	10424.718
18	GbPj	27	9.6	12.23	1.24	0.400	10.891	76.956	19905.944
19	GbPj	28	5.8	11.49	0.67	0.904	20.308	59.182	16220.831
20	GbPj	31	13.2	12.94	1.32	1.280	9.726	71.230	25803.138
21	GbPj	28	12.9	12.88	0.92	1.288	9.659	47.925	25900.768
22	GbPj	31	6.6	11.65	0.80	0.620	27.627	47.721	19422.830
23	GbPj	31	7.7	11.86	0.30	1.272	21.800	17.165	20680.676
29	GbPj	28	8.3	11.98	0.54	0.524	15.335	35.484	20244.375
30	GbPj	28	10.1	12.33	0.64	0.360	13.368	41.098	23254.924
31	GbPj	28	15.3	13.35	2.22	1.244	7.579	117.086	27796.635
32	GbPj	29	11.2	12.55	0.78	0.712	13.845	40.440	27294.553
33	GbPj	27	12.4	12.78	0.62	0.324	12.145	30.190	26806.686
34	GbPj	27	11.7	12.65	1.17	0.880	13.020	50.844	26561.997
35	GbPj	26	9.2	12.16	0.79	0.240	14.457	40.751	22916.954
36	GbPj	28	9.3	12.18	0.46	0.228	14.097	22.635	22605.846
37	GbPj	31	8.7	12.10	0.77	0.972	14.607	42.071	22922.786
38	GbPj	25	18.9	14.14	1.56	1.708	5.197	25.092	27226.070
42	GbPj	27	11.5	12.61	0.86	0.956	9.219	28.967	23517.090
43	GbPj	28	11.4	12.59	0.75	0.708	11.124	23.393	24624.768
44	GbPj	31	11.8	12.67	0.35	0.160	11.249	11.757	27365.558

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
45	GbPj	30	12.4	12.78	0.91	1.140	10.254	28.074	26559.779
46	GbPj	26	13.6	13.02	0.94	1.020	7.120	18.651	24380.291
47	GbPj	24	10.1	12.33	0.53	0.340	10.829	14.295	19481.739
49	GbPj	27	9.9	12.29	0.67	0.668	10.471	28.390	21155.579
51	GbPj	24	9.1	13.06	1.13	1.080	10.725	37.740	20613.160
52	GbPj	25	14.8	13.26	1.35	0.992	5.762	43.139	19215.601
53	GbPj	26	10.6	12.43	1.37	0.776	9.194	58.234	21987.765
54	GbPj	23	12.2	12.74	1.28	0.880	7.257	34.333	16552.148
55	GbPj	26	12.0	12.71	1.62	1.052	7.462	55.925	21846.883
58	GbPj	22	15.2	13.33	1.18	1.584	6.321	33.133	16845.931
65	GbPj	19	9.0	12.12	0.83	1.584	6.321	33.133	10192.015
73	GbPj	19	10.6	12.43	0.95	1.488	7.493	42.455	17114.930
74	GbPj	15	15.3	13.35	1.79	1.212	4.081	54.244	15229.728
75	GbPj	13	11.4	12.59	1.38	1.280	5.035	53.512	16156.284
76	GbPj	15	17.0	13.69	1.61	2.196	5.062	55.439	23672.246
84	GbPj	19	18.4	14.10	1.50	1.180	4.306	42.411	25677.332
93	GbPj	20	13.0	12.90	1.84	1.284	6.166	97.323	22986.127
94	GbPj	20	16.8	13.24	1.36	1.408	4.953	42.769	25246.759
97	GbPj	19	17.0	13.69	1.38	1.496	3.620	30.656	21241.795
99	GbPj	20	6.3	11.59	0.74	0.652	14.109	56.969	15402.885
100	GbPj	24	10.9	12.49	0.75	1.032	9.042	31.672	22388.796
102	GbPj	20	7.7	11.35	0.19	0.976	12.947	0.000	15828.458
103	GbPj	15	7.7	11.86	0.55	0.768	7.354	14.515	12248.363
105	GbPj	23	9.4	12.20	0.36	0.528	11.077	0.969	18272.486

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
106	GbPj	22	8.5	12.02	0.32	1.112	12.150	0.000	16811.407
107	GbPj	19	14.8	13.26	0.60	1.308	5.133	4.138	18387.616
108	GbPj	17	14.0	12.95	0.94	1.560	4.580	16.629	16069.706
114	GbPj	25	11.9	12.69	1.37	0.876	6.374	31.955	21167.828
119	GbPj	23	15.1	13.31	0.86	0.784	5.617	16.106	23780.983
120	GbPj	19	11.1	12.53	0.33	1.068	7.616	13.129	18127.140
124	GbPj	33	10.8	12.47	1.21	0.572	13.570	58.677	26273.715
125	GbPj	32	13.6	13.02	1.20	1.188	10.279	40.156	28146.086
126	GbPj	23	12.4	12.78	0.92	0.924	8.042	45.290	22645.597
127	GbPj	31	13.2	12.94	1.05	0.616	9.087	39.847	26771.931
128	GbPj	29	12.0	12.71	0.52	1.072	9.832	27.830	25881.192
129	GbPj	25	10.5	12.41	0.81	0.868	9.400	50.958	22352.975
130	GbPj	21	12.7	12.84	0.84	1.348	6.683	26.752	21656.749
131	GbPj	21	4.8	11.29	0.39	0.752	21.156	32.240	13404.008
133	GbPj	21	4.3	11.19	0.28	1.032	24.199	26.676	12679.703
134	GbPj	22	11.9	12.69	1.39	1.472	7.005	45.554	20733.456
140	GbPj	29	12.7	12.84	1.90	1.164	7.572	96.852	23275.443
141	GbPj	21	7.7	11.86	0.76	1.276	14.169	36.295	15054.567
142	GbPj	22	11.0	12.51	0.96	0.956	8.281	35.385	17935.404
143	GbPj	21	10.1	12.33	0.66	1.840	9.801	21.799	16189.538
144	GbPj	19	9.8	12.67	0.72	0.808	8.822	31.839	16510.623
145	GbPj	19	10.3	11.50	0.86	1.132	8.094	62.336	15615.547
146	GbPj	20	7.9	11.90	0.48	1.192	10.356	27.050	14303.292

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
147	GbPj	18	14.4	13.15	1.51	1.904	4.301	43.732	16124.805
148	GbPj	9	13.2	12.94	1.76	0.464	4.301	43.732	9630.937
150	GbPj	22	11.0	12.51	1.31	0.892	6.558	54.003	17734.428
158	GbPj	21	9.8	12.27	1.25	1.844	11.098	35.607	16091.144
159	GbPj	22	17.0	13.35	1.05	1.336	4.518	32.142	18612.866
160	GbPj	24	15.5	13.39	1.39	0.364	7.598	21.030	20970.154
161	GbPj	24	6.2	11.57	0.64	0.800	26.130	22.109	15542.730
170	GbPj	22	8.9	12.10	0.69	1.236	20.729	29.576	17851.676
171	GbPj	24	11.1	12.53	1.24	0.468	14.551	65.909	20307.584
174	GbPj	18	7.7	11.86	0.36	0.652	14.551	65.909	9667.915
15	GrMW	39	12.4	8.58	1.15	1.676	6.601	28.511	10373.939
16	GrMW	34	10.6	9.05	1.02	1.556	7.546	20.728	9704.050
18	GrMW	26	10.7	9.08	1.29	1.952	9.124	11.631	8895.563
50	GrMW	44	10.4	8.99	0.90	1.792	7.011	8.544	9013.395
51	GrMW	32	13.4	6.76	1.31	2.356	47.170	69.386	9621.775
71	GrMW	34	15.0	11.12	1.35	2.468	5.229	7.995	11056.379
72	GrMW	49	9.4	9.89	1.49	0.864	16.535	44.515	14755.452
73	GrMW	46	6.3	8.22	0.85	0.372	22.266	42.836	11253.661
76	GrMW	56	8.8	8.54	1.05	1.036	14.395	41.771	14438.921
77	GrMW	54	8.9	7.20	1.05	1.884	15.098	73.856	13856.393
78	GrMW	48	11.3	10.39	1.00	1.780	11.080	12.161	14444.025
79	GrMW	52	4.9	7.44	0.79	1.084	32.974	41.061	9194.232
80	GrMW	51	7.0	8.79	0.81	0.856	23.936	10.242	10095.098
82	GrMW	51	5.1	6.64	0.45	1.176	32.337	35.837	8296.576

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
129	GrMW	45	9.4	9.14	0.99	1.872	11.459	13.463	10188.804
131	GrMW	41	9.0	8.60	1.04	1.916	16.681	27.881	8755.809
133	GrMW	47	4.8	7.41	0.40	0.560	26.858	34.505	8144.923
136	GrMW	50	7.8	8.26	0.43	0.444	18.058	21.365	12675.029
137	GrMW	39	12.2	9.62	1.30	2.388	8.293	31.873	12949.798
138	GrMW	51	12.4	9.56	0.91	1.380	11.443	24.333	15867.948
139	GrMW	53	10.0	8.88	0.51	1.360	15.679	25.591	15594.266
148	GrMW	15	8.4	8.16	0.93	2.220	4.939	20.404	5023.734
161	GrMW	32	10.0	8.88	1.45	1.240	6.949	43.364	10406.852
163	GrMW	34	9.0	8.60	0.86	0.952	8.730	31.529	8216.020
175	GrMW	38	9.2	8.65	1.20	1.576	11.088	32.872	7796.484
176	GrMW	38	7.8	8.26	1.08	1.184	13.761	31.923	7460.413
177	GrMW	35	9.5	9.65	1.70	1.072	11.591	46.877	11700.416
199	GrMW	52	7.5	7.69	0.82	1.544	14.051	45.636	10364.573
200	GrMW	36	10.3	8.88	0.94	1.448	17.807	25.056	12766.430
201	GrMW	34	13.0	10.24	1.31	0.828	10.623	16.265	13877.388
202	GrMW	36	10.0	8.88	0.96	0.704	16.303	25.200	13055.151
204	GrMW	38	5.8	7.69	0.54	0.488	30.277	28.725	9865.664
207	GrMW	54	9.0	8.60	1.05	0.980	16.819	53.137	15282.095
209	GrMW	54	12.6	9.61	1.13	1.632	12.307	30.430	17292.075
215	GrMW	48	13.0	10.23	1.38	2.012	10.016	29.870	14495.489
218	GrMW	41	4.0	7.18	0.43	0.860	15.704	31.839	6494.651
223	GrMW	49	3.1	6.93	0.18	1.960	50.318	24.968	7481.024
225	GrMW	43	12.7	9.64	1.10	1.448	8.845	27.376	13015.708

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
230	GrMW	47	12.5	9.59	1.47	2.296	7.547	26.332	9766.714
244	GrMW	46	6.1	7.78	0.57	0.484	30.446	34.756	12036.272
245	GrMW	46	8.0	8.31	0.72	0.832	23.124	36.953	13514.613
248	GrMW	46	8.6	10.64	0.55	1.256	16.102	13.590	13889.631
251	GrMW	33	13.4	9.84	1.27	1.332	5.419	21.629	9641.005
252	GrMW	35	8.3	8.40	1.22	0.764	10.330	27.038	10302.584
255	GrMW	28	10.2	8.82	1.12	1.972	8.956	30.985	9939.992
256	GrMW	42	6.8	9.41	0.71	0.996	23.996	15.900	9695.858
257	GrMW	39	8.6	8.59	0.89	2.552	17.079	37.459	10547.336
261	GrMW	41	12.3	9.53	1.04	2.316	7.455	18.718	12486.735
280	GrMW	29	12.3	8.45	0.98	1.996	6.272	11.905	9306.767
282	GrMW	25	12.4	9.56	0.97	2.172	7.878	6.727	9465.973
285	GrMW	27	12.8	8.20	1.26	3.872	5.882	10.735	4995.520
289	GrMW	41	13.7	9.93	1.34	2.860	5.832	16.067	11787.968
298	GrMW	28	16.8	10.80	1.29	3.156	3.811	0.000	6354.791
314	GrMW	37	9.1	8.55	1.16	1.436	16.387	11.965	11092.095
327	GrMW	42	6.8	8.67	0.64	0.308	41.803	60.901	9363.365
329	GrMW	38	4.7	7.94	0.68	0.824	27.913	18.682	7971.760
330	GrMW	52	6.5	7.89	0.41	0.356	27.913	18.682	10012.010
332	GrMW	42	9.4	8.86	0.91	1.164	18.192	16.040	12298.466
1	GrPj	39	6.0	9.62	0.47	1.420	35.069	13.587	11398.628
2	GrPj	39	5.2	9.37	0.98	0.260	44.107	34.638	10833.128
3	GrPj	38	13.0	11.81	0.84	1.488	13.198	7.951	15283.843
4	GrPj	39	2.8	8.62	0.11	0.952	13.198	5.955	8464.326

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
5	GrPj	41	7.0	9.93	0.95	0.220	24.664	20.538	14112.564
6	GrPj	43	8.8	10.50	0.85	1.576	19.074	7.839	17587.896
7	GrPj	46	5.5	9.46	0.90	0.828	32.302	43.015	14697.783
9	GrPj	47	6.8	9.87	0.95	0.924	19.638	30.077	15999.637
21	GrPj	43	12.7	11.72	1.18	1.608	8.140	37.570	18361.431
28	GrPj	41	11.2	11.25	1.44	1.560	11.261	54.934	16737.427
29	GrPj	40	13.6	12.00	1.38	1.248	8.579	47.059	18039.153
30	GrPj	39	15.9	13.49	1.50	2.104	5.893	36.013	18343.881
33	GrPj	47	5.9	9.59	0.28	1.260	29.324	16.980	16060.985
34	GrPj	47	6.5	9.78	0.57	0.288	25.779	23.686	16987.459
35	GrPj	48	15.8	12.69	1.83	2.340	7.685	24.187	20746.428
37	GrPj	45	10.3	11.22	0.75	1.040	11.595	31.462	19466.459
42	GrPj	40	7.3	10.03	0.36	1.224	15.892	33.097	15681.541
43	GrPj	40	15.4	12.56	1.11	2.124	8.717	35.142	22689.466
44	GrPj	39	5.9	9.59	1.14	0.916	29.243	90.528	15354.234
46	GrPj	39	13.7	12.35	1.56	1.392	8.813	26.128	18094.807
47	GrPj	38	7.6	10.12	1.32	0.596	18.547	96.364	13840.835
48	GrPj	38	6.1	9.65	0.67	0.956	23.011	42.818	12319.286
51	GrPj	41	7.1	10.51	0.90	0.476	17.470	65.516	15127.538
52	GrPj	31	15.3	12.08	1.14	2.304	5.762	44.115	15835.542
62	GrPj	9	9.7	10.78	1.13	1.248	5.762	44.115	6946.711
65	GrPj	26	6.4	9.75	0.50	0.692	22.691	51.796	12897.461
66	GrPj	21	11.0	11.19	1.24	0.956	13.483	46.553	12764.675
67	GrPj	22	5.8	9.56	0.59	0.344	37.814	73.443	10625.331

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
68	GrPj	23	5.6	9.50	0.46	0.408	36.154	69.731	11255.913
69	GrPj	21	5.5	9.46	0.60	0.724	35.197	81.392	9863.370
74	GrPj	16	12.3	11.59	1.54	1.996	4.204	69.737	13652.974
75	GrPj	14	12.8	11.75	1.33	1.328	3.451	45.480	12897.027
76	GrPj	15	11.0	12.31	1.05	1.396	4.487	26.373	12055.062
77	GrPj	25	18.0	13.38	1.70	2.516	3.644	32.733	16515.388
78	GrPj	20	17.5	13.22	2.00	2.196	3.454	49.182	14199.319
89	GrPj	36	8.8	10.50	1.36	0.544	11.484	48.653	18070.248
92	GrPj	44	11.8	11.44	0.84	1.220	14.008	15.863	22391.950
94	GrPj	44	4.1	9.03	0.00	0.924	38.206	15.863	13485.234
95	GrPj	46	6.2	9.68	0.36	0.332	28.275	55.390	18468.794
96	GrPj	44	7.1	9.96	0.36	0.416	25.832	49.203	19500.141
97	GrPj	43	11.4	12.80	1.24	1.532	14.020	39.623	23823.153
114	GrPj	34	7.5	12.30	0.91	0.396	25.354	10.366	14843.212
115	GrPj	34	7.7	10.15	0.84	0.372	25.380	13.084	15075.484
116	GrPj	34	5.5	9.46	0.45	0.904	30.939	7.842	12778.687
127	GrPj	32	11.7	11.40	1.38	1.684	9.418	71.887	17568.056
128	GrPj	28	14.4	12.25	1.49	1.932	7.620	64.114	16962.174
129	GrPj	28	7.8	10.18	0.50	0.556	18.456	44.750	14525.472
142	GrPj	21	8.6	10.43	0.84	1.408	6.744	31.966	10006.045
146	GrPj	27	14.8	12.37	1.35	1.456	4.080	8.536	14934.326
148	GrPj	25	10.8	11.12	0.84	0.712	8.425	8.862	14235.469
153	GrPj	28	8.6	10.43	0.37	0.540	13.072	15.124	13756.281
154	GrPj	33	9.8	10.81	0.61	1.084	13.881	8.233	16085.313

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
155	GrPj	33	6.7	9.84	0.68	0.464	22.000	19.987	13570.850
157	GrPj	32	12.4	11.62	1.07	1.736	6.451	5.584	15199.876
163	GrPj	40	10.4	11.00	0.81	0.660	15.396	17.855	18099.527
164	GrPj	40	14.5	12.28	1.30	1.948	9.551	15.890	19268.774
172	GrPj	40	10.3	10.97	0.64	0.888	11.916	26.028	16095.136
173	GrPj	39	13.1	11.84	1.18	1.344	9.111	28.219	19606.288
174	GrPj	41	4.8	9.25	0.67	0.504	20.564	43.043	10156.395
175	GrPj	41	10.8	11.12	1.21	1.352	8.369	37.960	14931.083
177	GrPj	46	12.1	12.63	1.61	1.880	7.973	30.044	16899.282
182	GrPj	39	8.5	10.40	1.10	0.428	15.765	74.318	15786.276
183	GrPj	42	7.2	10.00	0.51	0.916	18.391	41.643	15511.077
185	GrPj	38	6.7	9.84	0.40	0.668	15.800	19.389	13156.643
190	GrPj	38	10.9	11.15	1.27	0.996	8.172	46.151	14318.765
191	GrPj	40	9.9	10.84	1.16	1.448	10.747	52.999	15679.195
192	GrPj	46	12.1	11.53	1.06	1.216	8.930	65.991	17850.274
200	GrPj	39	6.7	9.84	0.82	0.480	12.430	72.982	9850.175
201	GrPj	40	6.8	9.87	0.48	1.212	11.770	42.407	10323.753
210	GrPj	35	7.9	10.22	0.60	1.352	9.863	15.757	10243.999
217	GrPj	37	10.6	11.06	0.90	1.584	9.617	10.729	11378.800
219	GrPj	37	11.8	11.44	0.56	1.652	9.190	26.012	12223.856
220	GrPj	37	13.6	11.06	1.55	1.092	7.875	99.450	13254.697
221	GrPj	27	8.6	8.93	1.18	1.008	8.324	107.893	11857.858
224	GrPj	37	9.7	10.78	0.80	0.888	10.660	53.973	11699.546
226	GrPj	36	6.3	9.71	0.93	0.760	14.822	92.774	9691.980

Table 20 continued...

Tree ID	Site	Neighbour Count	DBH (cm)	Height (m)	Crown Radii (m)	Radial Growth (mm)	Hegyí	Schütz	Canham
237	GrPj	23	16.5	12.91	1.02	2.596	3.467	12.133	11169.030
243	GrPj	22	4.8	9.25	0.62	0.476	21.014	34.903	7011.752
244	GrPj	25	11.5	11.34	1.22	2.968	5.548	29.407	9535.200
245	GrPj	36	7.1	9.96	0.43	1.140	12.858	7.459	12238.720
249	GrPj	37	13.4	10.66	0.96	2.464	7.222	9.004	15856.520
250	GrPj	33	10.0	10.05	0.65	1.144	10.698	16.164	11588.545
251	GrPj	32	9.0	10.56	0.40	1.416	12.709	0.000	11348.510
253	GrPj	32	8.3	10.34	0.60	1.216	37.363	3.275	13191.234
254	GrPj	32	11.6	11.37	0.35	2.156	22.126	0.000	13930.819
255	GrPj	32	7.0	9.93	0.87	0.760	40.658	28.144	11902.337
256	GrPj	32	9.7	10.78	0.71	1.828	24.004	15.844	12340.915
263	GrPj	41	8.3	10.20	0.85	1.212	16.282	8.437	12920.538
267	GrPj	18	16.0	13.24	1.36	2.404	2.523	0.000	12530.540

APPENDIX III

SUMMARY OF ANALYSIS OF VARIANCE RESULTS FOR BLACK SPRUCE

Table 21. Summary of ANOVA components for black spruce root biomass.

Source	d.f	Sum of Squares	Mean Square	F _{calc}	F _{pred}	Sig.
Site	1	0.0014	0.0014	0.18	0.6715	
Stand Type	1	0.1099	0.1099	13.90	0.0003	*
Layer	6	0.4017	0.0669	8.47	<.0001	*
Site*Stand Type	1	0.0005	0.0005	0.06	0.8072	
Site*Layer	6	0.0381	0.0063	0.80	0.5704	
Stand Type*Layer	6	0.1741	0.0290	3.67	0.0025	*
Site*Stand Type*Layer	6	0.0078	0.0013	0.17	0.9853	

*Denotes a significant relationship

Table 22. Summary of ANOVA components for percentage of black spruce root biomass.

Source	d.f	Sum of Squares	Mean Square	F _{calc}	F _{pred}	Sig.
Site	1	0.0031	0.0031	0.04	0.8482	
Stand Type	1	11.4294	11.4294	135.23	<.0001	*
Layer	6	0.5954	0.0992	1.17	0.3279	
Site*Stand Type	1	0.0192	0.0192	0.23	0.6350	
Site*Layer	6	0.2521	0.0420	0.50	0.8089	
Stand Type*Layer	6	0.4575	0.0763	0.90	0.4973	
Site*Stand Type*Layer	6	0.1907	0.0318	0.38	0.8923	

*Denotes a significant relationship

APPENDIX IV

SUMMARY OF ANALYSIS OF VARIANCE RESULTS FOR JACK PINE

Table 23. Summary of ANOVA components for jack pine root biomass.

Source	d.f	Sum of Squares	Mean Square	F _{calc}	F _{pred}	Sig.
Site	1	0.0108	0.0108	1.58	0.2114	
Stand Type	1	0.0035	0.0035	0.51	0.4765	
Depth	6	0.5155	0.0859	12.56	<.0001	*
Site*Stand Type	1	0.0173	0.0173	2.53	0.1144	
Site*Depth	6	0.0303	0.0050	0.74	0.6206	
Stand Type*Depth	6	0.0749	0.0125	1.83	0.0992	
Site*Stand Type*Depth	6	0.0244	0.0041	0.59	0.7342	

*Denotes a significant relationship

Table 24. Summary of ANOVA components for percentage of jack pine root biomass.

Source	d.f	Sum of Squares	Mean Square	F _{calc}	F _{pred}	Sig.
Site	1	0.0205	0.0205	0.52	0.4722	
Stand Type	1	0.3302	0.3302	8.37	0.0045	*
Depth	6	0.8148	0.1358	3.44	0.0035	*
Site*Stand Type	1	0.1035	0.1035	2.62	0.1077	
Site*Depth	6	0.2322	0.0387	0.98	0.4412	
Stand Type*Depth	6	1.1393	0.1899	4.81	0.0002	*
Site*Stand Type*Depth	6	0.2559	0.0427	1.08	0.3774	

*Denotes a significant relationship

APPENDIX V ROOT BIOMASS STATISTICS BY STAND TYPE

Table 25. Summary of root biomass statistics by stand type and species.

Species	Stand Type	Depth (cm)	Root biomass		Root Biomass	
			%	Std. Dev.	g/100 g of soil	Std. Dev.
Sb	MW	Organic	0.387	0.127	0.038	0.023
		0 to 5	0.165	0.071	0.042	0.021
		5 to 10	0.182	0.047	0.022	0.005
		10 to 15	0.218	0.033	0.014	0.004
		15 to 20	0.061	0.059	0.010	0.010
		20 to 30	0.025	0.015	0.001	0.001
		30 to 45	0.000	0.000	0.000	0.000
	Pure	Organic	0.894	0.071	0.241	0.062
		0 to 5	0.709	0.102	0.179	0.062
		5 to 10	0.875	0.086	0.095	0.019
		10 to 15	0.667	0.139	0.023	0.012
		15 to 20	0.706	0.117	0.008	0.004
		20 to 30	0.857	0.120	0.002	0.001
		30 to 45	0.778	0.104	0.004	0.001
Pj	MW	Organic	0.507	0.095	0.507	0.011
		0 to 5	0.810	0.043	0.185	0.028
		5 to 10	0.863	0.039	0.205	0.059
		10 to 15	0.920	0.027	0.110	0.022
		15 to 20	0.892	0.054	0.058	0.018
		20 to 30	0.963	0.027	0.042	0.016
		30 to 45	0.863	0.081	0.014	0.004
	Pure	Organic	0.932	0.032	0.932	0.024
		0 to 5	0.922	0.059	0.162	0.021
		5 to 10	0.992	0.008	0.141	0.022
		10 to 15	0.803	0.087	0.069	0.015
		15 to 20	0.997	0.003	0.084	0.023
		20 to 30	0.834	0.112	0.017	0.005
		30 to 45	0.976	0.023	0.027	0.009