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Stockability, relative density and productivity: investigating their link in boreal mixedwoods

By

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Abstract

I explore and evaluate the use of indicators of density and stand composition in analyzing key aspects of the dynamics of boreal stands comprised primarily by trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss. in western Canada. First, using repeated measures data, I examine static and dynamic maximum size-density relationships (MSDR) for both pure and mixed stands of these species. Then, I evaluate the usefulness of density indicators in explaining understory light availability in mid-rotation and mature boreal pure and mixed stands, including examination of stand density index (SDI) based on the MSDR previously developed. Furthermore, I also test the usefulness of SDI and other density indicators in explaining trembling aspen, white spruce, and stand periodic annual increment in volume. Finally, I evaluate the usefulness of stand characteristics, including density and composition, in predicting the probability of survival of individual trees and saplings in boreal stands experiencing self-thinning. Results show that MSDR can be developed for mixed and pure boreal stands, and that a three-dimensional surface is the most suitable approach for their development. Stand composition and site quality are factors influencing MSDR. I also found that understory light is fairly variable in these stands, and that density and/or SDI are able to explain about 30 % of this variation. Total periodic annual increment in volume appears to be determined by the maximum stockability of these stands, and decreases in either aspen or spruce stocking, or both, result in reductions in PAI. Finally, one-sided competition, rather than two-sided, is the determining factor affecting individual tree survival,

regardless of species. While basal area and/or SDI of larger trees captures these effects, individual tree growth rates serve better as indicators of survival probability.

Preface

This Ph.D. Dissertation contains the results of research conducted at the Department of Renewable Resources of the University of Alberta, Edmonton, Canada. A shortened version of Chapter 2 has been published [Reyes-Hernandez, V.; Comeau, P.G.; and Bokalo, M. 2013.Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. For. Ecol. Manage. 289:300-311]. While I was the leading investigator, responsible for all major areas of concept development, data compilation, and analyses, as well as manuscript composition, Phil G. Comeau was involved in all the stages of concept development and data analysis, and contributed substantially to manuscript edits. Mike Bokalo was involved in stages of data analysis and contributed to manuscript edits.

I was also the principal investigator for the studies conducted in Chapters 3, 4, and 5, where I was responsible for all major areas of concept development, data compilation and analysis, as well as manuscripts writing and composition. Phil G. Comeau was involved in all of the stages of concept development and data analysis; he also contributed extensively to manuscripts edits. Alejandro Velazquez contributed to manuscript edits for some sections of Chapter 2 (biomass component) and edits to Chapter 3.

Philip G. Comeau was the Supervisory author of the entire research project, and was involved throughout the project in concept development, manuscript writing, and edits.

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Chapter 1 General introduction

1.1 Background

The circumpolar boreal zone constitutes one of the largest and most important biogeoclimatic areas in the world covering about 627 million hectares in North America, half of which is forested land (Brandt, 2009). In Canada, the boreal forest occupies the largest forested area of the country (Rowe, 1972) and it is the suitable habitat for *Picea glauca* (Moench) Voss. (white spruce), and *Populus tremuloides* Michx. (trembling aspen), tree species that are able to grow either in pure or in mixed stands. Other associated tree species for instance *Populus balsamifera* L. (balsam poplar), *Betula papyrifera* Marsh. (white birch), *Picea mariana* (Mill.) BSP. (black spruce), and *Abies balsamea* (L.) Mill. (balsam fir) are frequently found in the same ecosystem in varying proportions. In the western share of Canada, the boreal forest usually occupies relatively medium to rich nutrient soils in fresh to moist sites (Jerabkova *et* al., 2006).

Commonly known as boreal mixedwoods, associations between trembling aspen and white spruce are frequently found in upland mesic sites in western Canada (Rowe 1972; Lieffers *et* al. 1996), representing an ecologically and economically vital component of the landscape. Approximately forty percent of Alberta's land is covered by boreal mixedwood forests, with about seventy percent assigned to private companies for extraction of aspen for pulp and paper and white spruce for sawlogs (Alberta Environmental Protection, 1998). Boreal mixedwood stands may occur at both the landscape and stand spatial scale. Edaphic conditions, glaciation events and disturbance regimes are the main forces shaping the boreal mixedwoods at the landscape level (Haeussler *et* al., 2004), whereas discrete and continuous patches, or a mixture with a vertical stratification are formed by the component species at the stand level (MacDonald, 1996).

It is suggested that promotion of boreal mixedwoods might have numerous advantages over their conversion to either pure trembling aspen or pure white spruce stands (Comeau *et* al., 2005). Mixedwood stands are generally more diverse, support a greater structural diversity for other organisms, and they may experience less damage due to partial disturbances such as insect outbreaks and diseases (i.e. higher ecological resilience) than monospecific stands (Cumming 2001; Chen and Popadiouk 2002). Boreal mixedwood stands also provide a wide variety of ecosystem services and sustainable management objectives, such as supporting structural diversity, increasing carbon sequestration, facilitating ground water and stream recharge, providing habitat for wildlife, among many others (Peterson and Peterson 1992; Comeau *et* al. 2005).

Mixtures of trembling aspen and white spruce may also be more productive than monocultures of the same species, since aspen holds nutrients within the stand, improves nutrient cycling owing to their litter properties, and increases availability of light to the forest floor (MacDonald 1996; MacPherson *et* al. 2001). Overstory aspen might also help to reduce damage by wind and temperatures to the white spruce, as well as reduce competition from grasses and other vegetation (MacDonald 1996; Comeau *et* al. 2005). From an economic perspective, mixedwoods may be more valuable by supplying both aspen and white spruce products (*i.e.* fiber), so that mixed stands can satisfy more diverse market demands and be able to provide a variety of products (Comeau *et* al., 2005). There is also apparently potential for reduced costs for establishing a new stand, as it is suggested that less effort is needed when growing a mixed stand than a pure spruce stand after replacing disturbances (Man and Lieffers, 1999).

However, despite the advantages that mixtures of trembling aspen and white spruce might represent, mixedwood management is a relatively new silvicultural approach to western Canada, and more research is needed to support its implementation overall within the context of more demanding markets and societies. The creation or promotion of mixtures of these two species is highly dependent on the maximization of their ecological and economic benefits, aiming at the same time yield goals for each of the component species (Comeau *et* al., 2006).

1.2 Maximum mean size-density relationships in stands of plants

Models of forest growth and stand dynamics commonly assume that space is the primary 'resource' that limits growth and development of individuals; individuals interact with their closest neighbors and stand density might be a good indicator of how plants respond to competition in crowded populations. However, density by itself might not always be the best indicator of the way in which plants interact and compete as they develop, and descriptions of the relation between density and the size of individuals (size-density relationships) have been used to explore stand dynamics and also as the basis for the development of relative density indices in forest management (Lhotka and Loewenstein, 2008).

Development of these indices is based on the premise that plants will respond to density depending on their absolute and relative size, shape, and growth rate. Since the level of crowding is a restrictive factor for individuals’ growth, in forestry this maximum mean tree size-density relationship has been used as a measure of stockability, which is the maximum number of trees that can be developed to a specified dimension under certain growing conditions (DeBell *et* al.1989; Harms *et* al. 1994; Harms *et* al. 2000).

The process of self-thinning is an important aspect in the dynamics of plant populations. Density-dependent mortality is the result of an insufficient supply of resources for plant growth and development, either for individuals or for entire stands (Del Rio *et* al., 2001). Exploration and analysis of maximum mean size-density relationships in populations of plants is a useful tool in forest ecology and silviculture, because it can help to indicate the demands for resources and the need of growing space for individual trees. A relationship between maximum average size (quadratic mean diameter, D_q) and total density (number of trees per hectare, N) was first described for tree populations by Reineke (1933), in which the upper boundary is a straight line on logarithmic scales and is given by:

$$\ln(N) = \beta_0 + \beta_1 \ln(D_q) \qquad \textbf{(1.1)}$$

Where: β_0 and β_1 are the intercept and slope of the self-thinning line, respectively.

Reineke (1933) investigated this relationship for 14 tree species growing in pure stands under different conditions and proposed its application in characterizing a ‘Stand Density Index’ (SDI). SDI is defined as the number of trees in any site at a reference diameter of 25.4 cm (10 inches), and is calculated using the equation:

$$SDI = N\ (Dq/25.4)^{r} \qquad \textbf{(1.2)}$$

Where: N=trees per hectare, Dq=Quadratic mean diameter, r=-1.605

Patterns illustrating the relationships between maximum mean plant weight and density of survivors were first described for several plant species by Kira *et* al. (1953) and Shinozaki and Kira (1956). Yoda *et* al. (1963) further generalized this relationship and proposed the -3/2 power-law or self-thinning rule. The rule states that in a monoculture experiencing density related mortality, the maximum average dry weight per individual (w) is related to total plant density (N); on logarithmic scales this relationship is restricted by a straight line which could be depicted by the approximation:

$$w= K_1N^{-a} \qquad \textbf{(1.3)}$$

Where K_1 and a are constants, and the value of ***a*** was found to be empirically and theoretically to lie near to -3/2 when mean plant biomass is used.

Since average stem volume (or average tree biomass) is the most representative characteristic of carrying capacity in stands of trees (Zeide, 2005), and because both biomass and volume have a close isometric relationship, that is $\mathbf{v \propto w^{1.0}}$ (Drew and Flewelling, 1977), they have frequently been used to describe both maximum size-density relationships and self-thinning (White, 1981). Both characteristics are also commonly applied in the development of thinning prescriptions in forest management.

Although the self-thinning law is widely considered to be one of the most important contributions to plant ecology, it has also been subject of scrutiny and discussion (Bi *et* al. 2000; Zhang *et* al. 2005). It is based on three fundamental assumptions (Drew and Flewelling 1977; White 1981; Weller 1987b; Zeide 1987): a) that weight is a direct power function of the cube of some particular dimension of the plant; b) that constant shape or geometrical similarity is maintained by plants throughout their entire life cycle (*i.e.* the relationship between plant weight and a linear dimension is constant); and c) that self-thinning occurs only when the total stocking of a stand equals or exceeds 100% of its potential (maximum "stockability"). However, discrepancies in at least one of the assumptions might be anticipated for long-lived organisms such as trees (White 1981; Weller 1987b). Moreover, an invariant slope of -1.5 appears purely theoretical and has been subject of constant debate (Bi and Turvey, 1997).

Originally developed for even aged plant populations, there have been attempts to apply both Reineke's relationship and the self-thinning law to mixed and uneven-aged stands of trees (Puettmann *et* al. 1992; Torres-Rojo and Velazquez-Martinez 2000). A number of studies in mixed stands suggest that Reineke's SDI (Reineke, 1933) can be useful as a measure of site utilization and competition between component species in mixedwood stands, since it is related to light capture (Vales and Bunnell, 1988) and it is independent of species composition (Curtis, 1970); SDI is closely related to the “self-thinning rule” (Yoda *et* al., 1963) and is believed to be independent of the effects of stand age and ecological site characteristics (Long, 1985). In fact, indexes based on size-density relations (like Reineke’s SDI) are independent of site quality and stand age (Curtis, 1970) which allows comparing levels of growing stock independent of these factors (Long and Daniel, 1990). Results have suggested that the self-thinning concept and consequently SDI should hold for the entire community and not for each of the component species separate (Yang and Titus, 2002). A response surface instead of a single line would be more suitable for mixed species stands of trees, which may also allow for exploration of the effects of site, species and other factors on the relationship.

1.3 Boreal mixed stands dynamics and productivity

The typical four stages of development of forest ecosystems are also part of the dynamics of boreal mixedwoods: stand initiation, stem exclusion, canopy transition, and gap dynamics (Chen and Popadiouk, 2002). The early development of mixedwood stands is mainly influenced by the severity of the disturbance, the availability of seed and/or the availability of vegetative reproductive organs (Lieffers *et* al., 1996).The boreal mixedwoods are a disturbance-dependent ecosystem in which wildfires are the main factor that shapes the landscape (Chen and Popadiouk, 2002). Following a major disturbance (*i.e.* wildfires, clearcut) intolerant species such as trembling aspen takes over the site and is the dominant component for up to 60 years. Due to its shade tolerance, white spruce can grow under a trembling aspen canopy during early years; white spruce will gradually take over the site as the stand develops, and a stratified canopy can be the result. Competition and facilitation might play a significant role between these two species (Man and Lieffers 1999; Comeau *et* al. 2005; Filipescu and Comeau 2007a; Filipescu and Comeau 2007b).

Growth and productivity of individual trees and forest stands have been shown to be related to stand occupancy mainly through the amount of canopy leaf area (Dean and Baldwin, 1996). However, since actual measurements of canopy foliage are usually difficult, time consuming and expensive to achieve in forests, measures of relative density are often used as surrogates to estimate site occupancy and resources utilization by species and stand components (Dean and Baldwin, 1996). Indeed, some studies have suggested a strong relationship between stand density index (SDI) and canopy foliage for even aged stands (Long and Smith, 1990).

Higher productivity of trembling aspen and white spruce boreal mixtures than for pure stands of the same species has been suggested, owing in part to their higher total densities (MacPherson *et* al., 2001). Other mechanisms that could lead to an increased productivity in boreal mixedwoods include: differences in shade tolerance, physical canopy separation, differences in phenology and changes in utilization of soil and other resources (Man and Lieffers, 1999). The existence of a stratified canopy when two species with differences in shade tolerance grow together might represent a great advantage by capturing and using a greater proportion of the light available than a mono specific stand (Kelty, 1992). However, the expected higher productivity of mixed stands has been difficult to demonstrate using actual data and stands, perhaps due to wide variation in stocking (in relation to size-density relationships) that occurs in many boreal mixed stands.

Owing to their dominant position in a forest environment, overstory canopy composition and structure are expected to have a significant influence on the understory environment mainly through its influence on light transmission, litter composition and leaf morphology (Hart and Chen, 2006). It has been suggested that light is the most common limiting resource that influences understory vegetation cover and richness in forests (Jennings *et* al., 1999). Although air temperature and humidity in the understory is also influenced by canopy structure (Sharpe *et* al., 1996), it seems that those factors are correlated with light (Barkman, 1992), and variation in understory light regimes can be used as a single factor to explain microclimatic variations in the understory (Barbier *et* al., 2008). Overstory canopy cover and species composition influence understory light levels (Lieffers and Stadt 1994; Hart and Chen 2006) and as a consequence it might also have a strong influence on understory plant communities and tree regeneration (Comeau *et* al. 2004; Bartemucci *et* al. 2006; Hart and Chen 2006).

The fact that differences in species' ecological requirements and variation in species proportions, age, site, and other factors, influence component species growth rates, and consequently stand structure makes it difficult to develop reliable descriptions of the dynamics of mixed species stands. As a result, single measures of stand structure such as mean basal area, average diameter, total density and others, which are frequently used in characterizing the dynamics of mono-specific, even-aged stands, are often limited in their usefulness in mixed stands due to their inability to indicate space and/or resources utilization. Other measures of crowding (*i.e.* stand density index-SDI) have been proposed to be better at representing the potential impact of each stand component (species, size class, etc.) on the dynamics of mixed species forests.

1.4 Thesis outline and objectives

This thesis is structured in six Chapters, with four main Research Chapters that follow this introductory Chapter. The overall objective of this Dissertation is to explore the use of measures of density and relative density, based on maximum size-density relationships such as Reineke's equation (Reineke, 1933) and the self-thinning law (Yoda *et* al., 1963), as approaches to clarifying the dynamic performance of two boreal tree species with differences in ecological requirements, namely *Populus tremuloides* Michx. (trembling aspen) and *Picea glauca* (Moench) Voss. (white spruce).

Since it is required to investigate if suitable explanations can be developed for size-density relationships of these stands, in **Chapter two** I examine static and dynamic limit concepts for maximum size-density relationships, as described by Weller (1987a, 1990), and expanded by VanderSchaaf and Burkhart (2007a, 2007b). The main objectives of Chapter two are: 1) to test whether the slope of the maximum size-density relationships agrees with the theoretical values of -1.605 proposed by Reineke (1933) or -1.5 proposed by Yoda *et* al. (1963); 2) To explore the effects of stand composition and site quality on maximum size-density relationships in boreal mixedwoods and; 3) To test if competition, as opposed to stochastic events, is a common driver of changes in density in spruce, aspen and mixedwood stands in the boreal mixedwoods region of Alberta.

In **Chapter three** I explore whether or not stand structure and composition, as well as other stand characteristics can explain variation in understory light for mid-rotation and mature mixed and pure boreal stands of trembling aspen and white spruce. Some of the indicators of competition evaluated in this chapter are: total stand basal area, basal area per hectare by deciduous and spruce components, total density per hectare, density by species (spruce and deciduous), percentage of basal area for deciduous and spruce, and relative density by species represented by Reineke's SDI. In this Chapter, I also explore the potential link between understory light transmission and the position and slope of maximum size-density relationships boundary lines (dynamic self-thinning lines) for boreal mixed stands experiencing density-related mortality.

In **Chapter number four**, I analyze the relationships between periodic annual increment in volume (Iv) of trembling aspen (Iv_{aw}), white spruce (Iv_{sw}) and total stand (Iv_{tot}), with selected stand attributes in mid-rotation and mature pure and mixed natural unmanaged boreal stands, comprised primarily of trembling aspen and white spruce. Stand attributes such as total stand basal area, basal area by component species, average spruce and aspen height, Stand Density Index (dynamic SDI) total and by component species, and stand composition represented by the percentage of basal area in aspen and spruce, are tested for in alternative models pursuing to explain the variation in PAI in volume by component species in pure and mixed stands.

Finally, in **Chapter five** I explore the suitability of individual tree and stand characteristics for predicting the probability of survival of white spruce and trembling aspen in boreal stands experiencing density-related mortality. I explore the potential usefulness of absolute individual tree size represented by diameter at breast height and the square of diameter at breast height, and indicators of stand density, structure and composition. Models of probability of survival for individual trees in self-thinning stands are developed in this chapter. I also evaluate the effects of inter and intra specific competition, as well as one-sided and two-sided competition, in defining which trees survive and which trees die in this type of stands, experiencing density-dependent mortality. The final chapter (Chapter 6) summarizes and concludes from results of all of the main research chapters, and gives insights into future research.

1.5 References

Alberta Environmental Protection. 1998. The boreal forest natural region of Alberta. Natural Resources Services. Recreation and Protected Ares Division. Edmonton, AB.

Barbier, S.; Gosselin, F.; and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved- A critical review for temperate and boreal forests. For. Ecol. Manage. 254:1-15 doi:10.1016/j.foreco.2007.09.038

Barkman, J.J. 1992. Canopies and microclimate of tree species mixtures. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (eds). The ecology of mixed-species stands of trees. Blackwell Scientific Publications. Oxford, UK. pp:181-188

Bartemucci, P.; Messier, C.; and Canham, C.D. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Can. J. For. Res. 23:1969-1979.

Bi, H.; Wan, G.; and Turvey, N.D. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. Ecol. 81(6):1477-1483.

Bi, H.; and Turvey, N.D. 1997. A method of selecting data points for fitting the maximum biomass-density line for stands undergoing self-thinning. Aus. J. Ecol. 22:356-359.

Brandt, J.P. 2009. The extent of the North American boreal zone. Environ. Rev.17:101-161.

Chen, H.Y.H.; and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Reviews. 10:137-166.

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

Comeau, P.G.; Kabzems, R.; McClarnon, J.; and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle. 81:559-574.

Comeau, P.; Filipescu, C.N.; Kabzems, R.; and DeLong, C. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern B.C. Can. J. For. Res. 34:2277-2283.

Cumming, S.G. 2001. Type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecol. Appl. 11:97-110

Curtis, R.O. 1970. Stand density measures: an interpretation. For. Sci. 16:403-414.

Dean T.J.; and Baldwin Jr., V.C. 1996. The relationship between Reineke’s stand-density index and physical stem mechanics. For. Ecol. Manage. 81:25-34.

DeBell, D.S.; Harms, W.R.; and Whitesel, C.D. 1989. Stockability: a major factor in productivity differences between Pinus taeda plantations in Hawaii and the southeastern United States. For. Sci. 35(3):708-719.

Del Rio, M.; Montero, G.; and Bravo, F. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142:79-87.

Drew, T.J.; and Flewelling, W. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. 23(4):517-534.

Filipescu, C.; and Comeau, P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Haeussler, S.; Bartemucci, P.; and Bedford, L. 2004. Succession and resilience in boreal mixewood plant communities 15-16 years after silvicultural site preparation. Fore. Ecol. Manage. 199:349-370.

Harms, W.R.; Whitesell, C.D.; and DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126(1):13-24.

Harms, W.R.; DeBell, D.S.; and Whitesell, C.D. 1994. Stand and tree characteristics and stockability in Pinus taeda plantations in Hawaii and South Carolina. Can. J. For. Res. 24:511-521.

Hart, S.A.; and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. Critical reviews in plant sciences. 25:381-397.

Jennings, S.B.; Brown, N.D.; and Shell, D. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. Forestry. 72:59-73.

Jerabkova, L.; Prescott, C.E.; and Kishchuk, B.E. 2006. Nitrogen availability in soil and forest floor of contrasting types of boreal mixedwood forests. Can. J. For. Res. 36: 112 – 122.

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed species stands. In: M. J. Kelty, B. C. Larson and C. D Oliver (eds). The ecology and silviculture of mixed species forests. pp 125-141. Kluwer Academic Publishers. Dordrecht. 287 p.

Kira, T.; Ogawa, H.; and Zakazaki, N. 1953. Intraspecific competition among higher plants. I Competition-yield-density interrelationship in regular dispersed populations. J. Inst. Polytech. Osaka City Univ. 4:1 -16.

Lieffers, V.J.; Macmillan, R.B.; MacPherson, D.; Branter, K.; and Stewart, J.D. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72:286-292.

Lieffers, V.J.; and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Lhotka, J.M.; and Loewenstein, E.F. 2008. An examination of species – specific growing space utilization. Can. J. For. Res. 38: 470 – 479.

Long, J.N. 1985. A practical approach to density management. For. Chron. 61:23-27.

Long, J.N. and Daniel, T.W. 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For. 5:93-96.

Long, J.N.; and Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var *latifolia* forests: the influence of site quality and stand structure. J. Appl. Ecol. 27:847-856.

MacDonald, G.B. 1996. The emergence of boreal mixedwood management in Ontario: background and prospects. In: Advancing boreal mixedwood management in Ontario. Ed: C.R. Smith and G.W. Crook. Natural Resources Canada. CFS. Sault Ste. Marie, Ontario. pp 11.

MacPherson, D.M.; Lieffers, V.J.; and Blenis, P.V. 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For. Chron. 77:451-356

Man R.; and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75:505-513.

Peterson, E.B.; and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Can. For. Serv. North. Cent. Spec. Rep. 1. 252 pp.

Puettmann, K.J.; Hibbs, D.E.; and Hann, D.W. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: extension of size-density analysis to species mixture. J. Ecol. 80:449-458.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Rowe, J.S. 1972. Forest regions of Canada. Publication No 1300. Dep. Environ. Can. For. Serv. Ottawa, ON.

Sharpe, F.; Shaw, D.C.; Rose, C.L.; Sillet, S.C.; and Carey, A.B. 1996. The biologically significant attributes of forest canopies to small birds. Northwest Sci. 70:86-93.

Shinozaki, K.; and Kira, T. 1956. Intraspecific competition among higher plants. Logistic theory of the C-D effect. J. Inst. Pol. Osaka City Univ. 7:35-72.

Torres-Rojo, J.M.; and Velázquez-Martínez, A. 2000. Índice de densidad relativa para rodales coetáneos mezclados. Agrociencia. 34: 497-507.

Vales, D. J. and Bunnell, F.L. 1988. Relationships between transmission of solar radiation and coniferous forest stand characteristics. Agric. For. Meteorol. 43:210-233.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007a. Using segmented regression to estimate stages and phases of stand development. For. Sci. 54(2): 167-175.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007b. Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope. For. Sci. 53(3):435-442.

Weller, D.E. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the -3/2 power rule of self-thinning. American Naturalist 133(1):20-41.

Weller, D.E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs. 57(1):23-43.

Weller, D.E. 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. Ecology 68(4):813-821.

White, J. 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89:475-500.

Yang, Y.; Titus, S.J.; Huang, S. 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Model. 163:209-222.

Yoda, K.; Kira, T.; Ogawa, H.; and Homuzi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants). J. Biol. Osaka City Univ. 14:107-129.

Zeide, B. 2005. How to measure stand density. Trees. 19:1-14. doi 10.1007/s00468-004-0343-x

Zeide, B. 1987. Analysis of the 3/2 power law of self – thinning. For Sci. 33 (2): 517-537.

Zhang, L.; Bi, H.; Gove, J.H.; and Heath, L.S. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. Can. J. For. Res. 35: 1507-1514. doi: 10.1139/X05-070

Chapter 2 Analysis of maximum size-density relationships for boreal pure and mixed stands of trembling aspen and white spruce[1]

2.1 Introduction

The relationship between the number of individuals per unit area and their average size was first described for tree populations by Reineke (1933) using density and quadratic mean diameter (equation 2.1); Reineke further applied this concept in development of a Stand Density Index (SDI), defined as the number of trees in any site after transformation to a reference diameter of 25.4 cm (equation 2.2). Kira *et* al (1953), Shinozaki and Kira (1956) and Yoda *et* al. (1963) developed an analogous general relationship for plant populations using mean weight and density (equation 2.3). This relationship has been termed as the self-thinning rule or self-thinning law. In both cases, the upper frontier was found to be delimited by a straight line with a ‘constant’ slope of -1.605 for the density-diameter, and -1.5 in the case of mean weight-density relationship, regardless of species, site quality, and age.

$$\ln (N) = \beta_0 + \beta_1 \ln (D_q) \qquad \textbf{(2.1)}$$

Where: β_0 and β_1 are the intercept and slope of the self-thinning line, respectively.

$$SDI = N (D_q/25.4)^r \qquad \textbf{(2.2)}$$

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Where: N=trees per hectare, D_q=Quadratic mean diameter, r=-1.605

$$w = K_1 N^{-a} \qquad \textbf{(2.3)}$$

Where K_1 and a are constants, a=1.5

The basis of the original self-thinning concept is related to the carrying capacity of a site in terms of plant biomass. As the population approaches this carrying capacity, individual growth will continue only if the density is reduced (Kimmins, 2004). The intercept in equation 2.3 represents a limit for the amount of biomass that can be accumulated in the defined space and supported by the available resources on the site (Lonsdale and Watkinson, 1982). Harper (1977) and White (1980) showed that site quality can influence the intercept of the maximum size-density line and it is now widely accepted that the intercept of this line can vary from one plant species to another. The assumed invariance of the slope regardless of species, age and site quality (Jack and Long 1996) has been subject of more discussion (Zeide 1987; Weller 1989; Bi and Turvey 1997; Zhang *et* al. 2005).

It has been shown that the slope of the relationship can vary depending upon changes in species, site, age, and other variables (Weller 1987a; Zeide 1985, 1987). More recent studies have shown that the slope and/or the intercept is not constant across site index (Bi 2001; Weiskittel *et* al. 2009), nutrient availability (Morris 2003), climate (Comeau *et* al., 2010), stand age (Ogawa 2005; Zeide 2005), or stand origin and stand composition (Weiskittel *et* al., 2009). The original thinking of a constant and universal slope regardless of species, environment and age proposed by Reineke (1933) and Yoda *et* al. (1963) seems now unsuitable (Pretzsch and Biber 2005; Pretzsch 2006; Schutz and Zingg 2010), at least for trees that grow over wide ranges of geography and site conditions.

Weller (1987a, 1990) suggests that controversial results had been due to the application of two different concepts which he further defined as the static and the dynamic thinning lines. The static thinning line (also called the species boundary line) operates in all stands of a species across sites, tree sizes, genetics, thinning, etc. In this case, maximum tree densities across an array of average tree sizes are delimited with a line of constant slope notwithstanding all of the factors mentioned above (*i.e.* this represents the more upper limit that may be achieved for the population of stands included in the analyses). Observations used to derive the static thinning line are not necessarily from the same stand; rather they can be a collection of observations obtained from many different stands (VanderSchaaf and Burkhart, 2007b).

The dynamic thinning line, on the other hand, is a limit that operates in an individual crowded stand (VanderSchaaf and Burkhart, 2007a), and represents how each individual stand self-thins. As a consequence, each stand has its own unique dynamic thinning line with its own slope and intercept value. Much of the past work on the analysis of MSDR has been based on the delimitation of a static thinning line, and although both limits can coincide this is not necessary. In contrast to the static thinning line, the slope and intercept values of the dynamic thinning line can be affected by a number of factors such as climate, site quality, initial density and spatial arrangement of individuals (Weller, 1990). VanderSchaaf and Burkhart (2007b) further expanded this concept and proposed species boundary line II, which is obtained from multiple observations coming from crowded stands experiencing density-dependent mortality (such as the dynamic thinning line), and its slope would represent on average how all those stands self-thin.

Although the concepts of MSDR and self-thinning were developed and applied to mono-specific, even-aged plant stands, attempts have been made to apply them in mixtures of species and in uneven-aged stands of trees (Puettmann *et* al. 1992; Torres-Rojo and Velazquez-Martinez 2000; Woodall *et* al. 2005; Ducey and Knapp 2010a, 2010b). These and other studies have emphasized that both concepts should hold for the entire stand and not for each separate species (Yang and Titus, 2002). In the case of a two-species mixture the self-thinning line should be visualized as a response surface with both intercept and slope varying as the proportion of the two species change (Puettmann *et* al., 1992). Since species mixtures can be more productive, in some cases, than monocultures (Man and Lieffers 1999; Chen *et* al. 2003; Pretzsch *et* al. 2010), an effect of stand composition on the MSDR for mixed species stands would be anticipated when species with differences in shade tolerances and resource requirements grow together. However, this effect can be verified only if information on stand composition is available and tested for (Puettmann *et* al., 1992).

The development of MSDR requires objective selection of data points, use of appropriate data and proper analyses. The statistical techniques used to develop

MSDR have varied among studies and include ordinary least squares regression (OLS), reduced major axis, quantile regression, first difference models and mixed models (Zhang *et* al. 2005; VanderSchaaf and Burkhart 2007b). Regression using an OLS approach is sensitive to data selection and may produce self-thinning lines with inappropriate slopes. Quantile regression, deterministic frontier and stochastic frontier function (SFF) regression are currently preferred over OLS for this type of analysis (Zhang *et* al., 2005). SFF is useful to perform statistical inferences on the model parameters, as well as to test for the effects of covariates and deal with some of the problems associated with data that might have autocorrelated errors (Zhang *et* al. 2005; Weiskittel *et* al. 2009). In contrast to techniques such as OLS that intersect data, SFF encloses or envelops data which enhances its power in defining the frontier (Bi, 2004). On the other hand, mixed modelling is considered to be the best approach for examining data that could show autocorrelated errors and heterocedasticity (Littell *et* al., 2006) as may be the case when using repeated measurements coming from remeasured permanent sample plots. This approach also allows testing for effects of site, age and other factors on size-density relationships.

In this Chapter, I apply the static and dynamic thinning line concepts of Weller (1987a, 1990) and their extension by VanderSchaaf and Burkhart (2007b) to explore and analyse MSDR for pure and mixed stands of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) in western Canada. The main objectives were to: (1) determine the upper static and dynamic limits of the MSDR for mixed trembling aspen and white spruce stands based on Reineke’s work (density-quadratic mean diameter relationship) and the self-thinning law (mean biomass-density and mean-volume-density relationships); (2) examine the effect of stand composition, site quality and other site characteristics on both static and dynamic limits; 3) determine whether mixed stands can support greater total tree densities than pure stands; and 4) evaluate and demonstrate the potential application of MSDR in boreal mixedwood stands .

2.2 Methods

2.2.1 Data

Data from permanent sample plots (PSPs) established in pure trembling aspen, pure white spruce and mixed stands of both species in the boreal forest of Alberta, Canada were used in this research. PSPs from the Central Mixedwoods, the Dry Mixedwoods, and the Northern Mixedwoods ecological sub-regions, as well as few plots from the Foothills Natural Region were included in the analysis (Beckingham and Archibald 1996; Forest Management Branch 2005). Although variable in size (0.1 to 0.2 ha), establishment date and re-measurement interval, establishment and measurement of these PSPs followed rigorous standards (Forest Management Branch, 2005). These data were collected by Alberta Sustainable Resource Development, Alberta Pacific Forest Industries and Weyerhaeuser Canada. Most PSPs are 0.10 ha in area (31.62 x 31.62 m), with all tree species (Aw =aspen, Pb = balsam poplar, Bw= white birch and Sw= white spruce, and others) taller than 1.3 m in height or larger than 2.5 cm in diameter at breast height tagged and measured at time intervals ranging between 3 to 10 years. The following plot characteristics were compiled: quadratic mean diameter (QMD) by species; weighted total quadratic mean diameter (D_q) (equation 2.4); composition, expressed as the percentage of basal area by species, aspen (BA_{aw}), white birch (BA_{bw}), balsam poplar (BA_{pb}), deciduous total (BA_d), white spruce (BA_{sw}) and other species (PB_o); number of trees per hectare by species as indicated before, and for all species (TPH); average height (m), total basal area per hectare ($m^2 \cdot ha^{-1}$ by species and total); Reineke's stand density index (SDI) (equation 2; calculated for each species and size class within each plot, and summed to obtain a single SDI value per plot). In addition, site quality indicators were also available, including soil moisture (M_{or}) and soil nutrient regimes (N_{ur}). M_{or} and N_{ur} are quantitative indicators of site productivity, representing the availability of moisture and the amount of nutrients essential for plant growth, respectively, on a site (Beckingham and Archibald, 1996). Five levels (classes) for M_{or} and four levels for N_{ur} were assigned in the current data set. A more detailed description as well as methodologies utilised for their determination are provided by Beckingham and Archibald (1996).

Individual tree gross total volume (m^3) was calculated using individual tree volume equations available for Alberta's tree species (Huang, 1994) and individual aboveground biomass (kg of organic dry mass) was calculated using tree biomass equations available for Canada's tree species (Lambert *et* al., 2005). Both volume and biomass were scaled-up to per-hectare values and used to calculate mean values per stand (mean tree values).

Weighted quadratic mean diameter

$$D_q=((QMD_{aw}*BA_{aw})+(QMD_{bw}*BA_{bw})+(QMD_{pb}*BA_{pb})+(QMD_{sw}*BA_{sw}))/100 \quad \textbf{(2.4)}$$

Where: D_q= weighted quadratic mean diameter in cm; QMD_{aw}, QMD_{bw}, QMD_{pb}, BA_{aw}, BA_{bw} and BA_{pb} are as explained in text above.

Plots with more than 10% of basal area in species other than trembling aspen or white spruce were removed from the data set. In total, 2496 individual measurements from 879 plots were available. Natural logarithm transformations of the data were performed and they were used in further analyses. Table 2.1 summarizes information for the plots included in each analysis of the study. Figure 2.1 illustrates the approximate distribution of the PSPs in relation to natural subregions within the boreal forest region of Alberta. All analyses were performed with SAS® ver. 9.2 for windows (SAS Institute, 2010). The relationships between total density and quadratic mean diameter, mean tree biomass and total density, as well as between mean tree volume and total density were analyzed for the combined data set to define both the static and the dynamic limits according to Weller (1987a, 1990) description.

2.2.2 The Static thinning line

The static thinning line representing the species MSDR boundary line I, was fit using a stochastic frontier regression function (SFF) with PROC QLIM of SAS® ver. 9.2 for windows (SAS, 2010), on the observations showing the single highest SDI from each plot. SFF has been suggested as a powerful statistical technique to analyse potentially heteroscedastic data when we wish to test for the effect of multiple covariates and when we want to use all of the available data (Bi *et* al. 2000; Weiskittel *et* al. 2009). The SFF general equation takes the following form (Zhang *et* al., 2005):

$$y_i = \log Q_i = \alpha + \beta x_i + \varepsilon_i \qquad \textbf{(2.5)}$$

$$y_i = \alpha + \beta x_i + (v_i - u_i) \qquad \textbf{(2.6)}$$

Where $(v_i - u_i)$ is the combined error term with $u_i > 0$ and v_i unrestricted. The two error term components are assumed to be independent and identically distributed. I tested for the effects of stand composition, age, moisture and nutrient regime specifying a half-normal-model option for the model. The following general form was used for density-diameter relationships:

$$\ln(TPH)=\beta_0+\beta_1*\ln(D_q)+\beta_2*\ln(BA_d)+\beta_3*\ln(M_{or})+\beta_4*\ln(N_{ur})+\beta_5*\ln(age) \qquad \textbf{(2.7)}$$

Where ln = natural logarithm, TPH is total density, D_q is weighted quadratic mean diameter, BA_d is the percentage of basal area in deciduous, M_{or} is moisture regime, N_{ur} is nutrient regime, and age is an estimation of the stand age at the time of measurement.

The general equation used for both the mean biomass-density and mean volume-density relationships is as follows:

$$\ln(w)=\beta_0+\beta_1*\ln(N)+\beta_2*\ln(BA_d)+\beta_3*\ln(M_{or})+\beta_4*\ln(N_{ur})+\beta_5*\ln(age) \qquad \textbf{(2.8)}$$

Where: *w* is mean tree biomass (substituted with *v* to represent mean tree volume), N is total density, BA_d is the percentage of basal area in deciduous, M_{or} is moisture regime, N_{ur} is nutrient regime, and age is an estimation of the stand age at the time of measurement.

All first-order interactions were also tested. Because of the possible presence of autocorrelations that may influence the estimated standard errors of model parameters (Bi, 2001), likelihood ratio tests (LR) were used to test for the significance of parameters in models 2.7 and 2.8.

2.2.3 The dynamic thinning line

Analysis of the MSDR dynamic thinning line was performed in two stages. In the first stage, plots with at least 5 re-measurements were retained and size-density trajectories were constructed for each plot by graphing ln D_q over ln TPH for all available measurements. To minimize the potential subjectivity in determining which plots were undergoing self-thinning, the non-linear model (equation 2.9) proposed by Hann *et* al. (2003) was fit to each individual plot to model both the linear (self-thinning) and the non-linear (onset of self-thinning) segments of the size-density trajectory. This was done using PROC NLIN of SAS ver. 9.2. The first part (linear section) is the inverse relationship between total density (trees per hectare) and quadratic mean diameter originally developed by Reineke (1933), whereas the second part models the curvilinear portion of the size-density trajectory, also known as the onset of self-thinning (Poage *et* al. (2007). The model was fit individually to each plot. When the non-linear model did not converge, either because of the strong linear behaviour of their trajectories or because of the small number of observations available per plot, I fit the linear section alone using PROC REG of SAS, as described by Poage *et* al. (2007). Further details of this methodology are found in Hann *et* al. (2003) and Poage *et* al. (2007). Plots with less than 5 re-measurements were analyzed only with linear regression. The non-linear model takes the following form:

$$ln(D_q) = \beta_0 + \beta_1 * ln(TPH_f) - \left(\frac{(\beta_0 * \beta_2)^2}{\beta_0 + \beta_1 * ln(TPH_i) - ln(Dq_i)}\right) * e^{\beta_3 * ln\,(TPH_i) - ln(TPH_f)} \quad \mathbf{(2.9)}$$

Where: D_q = final weighted quadratic mean diameter; TPH_f = final total density; TPH_i = initial total density; D_{qi} = initial weighted quadratic mean diameter; β_0, β_1, β_2 and β_3 are model parameters.

Despite multiple attempts to fit equation 2.9 to the data, the full non-linear model only converged successfully in three cases. Figure 2.2 presents individual stand size-density trajectories for the three plots for which the model 2.9 fit successfully, showing the dynamic component of the self-thinning line, the density-independent mortality stage and the divergence stage of self-thinning according to VanderSchaaf (2010). The final selection of plots was based on parameter estimates obtained with either of the two procedures (non-linear and linear regression) and their confidence intervals following Hann *et* al. (2003) criteria:

a) Values of $\beta_1 < -0.5$ being what we would expect in a 'normal' self-thinning plot (like the reciprocal of Reineke's SDI exponent value);

b) Values of $\beta_1 > -0.5$ indicating a plot that is not undergoing self-thinning; and

c) Values of $\beta_1 = -0.5$ indicating constant basal area.

A visual inspection of points was also performed so that only those observations that were showing trends that are consistent with the density-dependent mortality stage of the self-thinning trajectory were used for further analyses. The plot selection process, based on parameter estimates obtained with either of the two procedures (non-linear and linear regression), visual inspection and the use of their confidence intervals, resulted in 179 plots out of a total of 879 being identified as undergoing self-thinning with 653 observations (in total) available for subsequent analyses to determine the dynamic MSDR using mixed models. However, due to some inconsistencies either in biomass or in volume values, only 173 plots (with 600 observations in total) were used for the mean biomass-density and mean volume-density relationships analyses.

To represent the behaviour of those plots undergoing self-thinning, and to estimate the average slope of the dynamic thinning line a mixed model as described by VanderSchaaf and Burkhart (2007a) was used (fit using PROC MIXED of SAS). The general model used for the density-diameter relationship was:

$$ln(TPH) = (\beta_0 + \mu_{0i}) + (\beta_1 + \mu_{1i}) * ln(D_q) + \varepsilon \qquad \textbf{(2.10)}$$

Where β_0 and β_1 are the fixed effects parameters associated with the slope and intercept, assumed to be Normal $(0,\sigma_0^2)$; μ_{0i} and μ_{1i} are cluster-specific (plot) random effects to be predicted, assumed to be Normal (0, σ_1^2); and ε is the random error term assumed to be Normal (0, σ^2I).

The general model used for the mean biomass-density and mean volume-density relationships was:

$$ln(w) = (\beta_0 + \mu_{0i}) + (\beta_1 + \mu_{1i}) * ln(N) + \varepsilon \qquad \textbf{(2.11)}$$

Where β_0 and β_1 are the fixed effects parameters associated with the slope and intercept, assumed to be Normal (0,σ_0^2); μ_{0i} and μ_{1i} are cluster-specific (plot) random effects to be predicted, assumed to be Normal (0, σ_1^2); and ε is the random error term assumed to be Normal (0, σ^2I); ln is natural logarithm; N is total density, and *w* is mean tree biomass (or *v*= mean tree volume).

Individual plot behaviour is accounted for by allowing both the slope and the intercept to vary by plot. Use of mixed models also allows estimation of the population average MSDR dynamic thinning line slope (VanderSchaaf and Burkhart 2007b; VanderSchaaf 2010). Due to the presence of unequally spaced measurements in the plots, and because a preliminary analysis of the covariance structure for the random effects showed that correlation among repeated measurements from the same subject (plot) decreases over time, a spatial-Gaussian variance-covariance matrix structure for random effects was used (Littell *et* al., 2006), whereas an unstructured variance-covariance matrix was assumed for the random error term. The effects of deciduous basal area, site quality (soil moisture and soil nutrient regime) and age were also tested as fixed effects (covariates and interactions).

2.3 Results

2.3.1 The static thinning line for maximum density and quadratic mean diameter

Estimates of the intercept and slope for the MSDR static thinning line based on model 2.7 are given in Table 2.2. Figure 2.3 illustrates how the line is positioned above the self-thinning plots. LR tests showed that the slope (β_1= -1.96) is significantly different from Reineke's 'b' value of -1.605 when using quadratic mean diameter as the main predictor of maximum density (Table 2.2). LR tests also showed that the percentage of basal area in deciduous species has a significant positive effect on the intercept of the static MSDR line (Table 2.2). Composition also has a significant negative effect on the slope of the static line (Table 2.2), as indicated by its negative value in the interaction term. The other covariates tested did not have significant effects on either the slope or the intercept in this static model. Although σ_v^2 shows a relatively high value this seems to be reasonable for forests stands due to the large spatial and temporal variation over their life and growth span (Bi *et* al., 2000). Even though the reduction in AIC values for equation 2.7 with the addition of covariates (Table 2.2) is small, the inclusion of covariates and interactions does improve the model fit and performance.

2.3.2 The static thinning line for mean biomass and mean volume

Estimates of intercepts and slopes of the static thinning line for both mean biomass and mean volume are presented in Table 2.3. Figure 2.4 illustrates the positioning of the estimated static line only for the mean biomass-density relationship (continuous black line) with respect to the data points used to fit it. LR tests showed that slope values for both relationships are flatter and significantly different than the value of -1.5 proposed by the self-thinning law (β_1=-0.98 for mean biomass and β_1=-1.01 for mean volume). A considerable reduction in Akaike's Information Criterion (AIC) values showed a significant effect of other covariates on the slope and the intercept for both mean volume and mean biomass static lines (Table 2.3). Basal area in deciduous species (%) as well as soil nutrient regime showed significant positive effects on the intercept of the two static lines (Table 2.3).

Percent of basal area of deciduous species had a significant negative effect on the slope for both mean biomass- and mean volume-density relationships. Nutrient regime had a positive effect on the slope for the tree biomass-density static line (results not shown). However, this effect was negligible and the overall performance of the model did not improve, which was evident based on higher AIC and standard error values in the model (not shown) (Table 2.3, model with covariates and interactions). None of the other covariates tested (moisture regime, age, and percentage of basal area of species other than trembling aspen and white spruce) showed any significant effect either on the slope or on the intercept for both mean tree biomass- and mean volume-density relationships.

2.3.3 The dynamic thinning line for maximum density as a function of quadratic mean diameter

Estimates of the average dynamic MSDR based on equation 2.10 are provided in Table 2.4. Figure 2.3 also shows how the average dynamic thinning line is positioned with respect to the plots used for its determination, and its location respecting the MSDR static thinning line. On average, a significantly steeper slope than the theoretical value of -1.605 proposed by Reineke (1933) was obtained when using density as a predictor of quadratic mean diameter ($\beta_1 = -1.73$; 95% confidence interval for $\alpha=0.05$ [-1.797, -1.661]). Slope values for individual plots, obtained using a mixed modelling approach ranged from -0.99 to -2.8 with intercepts ranging from 9.4 to 15.7.

The intercept of the dynamic thinning line is negatively influenced by the percentage of basal area in deciduous species (Table 2.4). Results also indicate that soil nutrient regime has a positive effect on the intercept and a negative influence on the slope of the self-thinning line. However, although nutrient regime was statistically significant the goodness of fit of the model did not improve when including either the variable alone or its interaction term with the slope (*i.e.* similar AIC and AICC values were obtained for the model that included both the main effect and the interaction and for the model without them; both are shown in Table 2.4). The inclusion of covariates (main effects: percentage basal area in deciduous and nutrient regime; interaction: soil nutrient regime and quadratic mean diameter) in the general model (Model 2.10) marginally improved its performance, as shown by an improved distribution of residuals (Figure 2.5). None of the other covariates tested (age, soil moisture regime and percentage basal area of other species) significantly influenced either the intercept or the slope of the dynamic upper limit.

2.3.4. The dynamic thinning line for maximum mean biomass and mean volume as a function of total density

Estimates of the average dynamic thinning line for mean tree biomass-density and mean tree volume-density are presented in Table 2.5. Figure 2.4 illustrates how the dynamic mean biomass density line is placed with respect to the static limit. Figure 2.6 shows the positioning of the dynamic thinning line with respect to some of the plots used to derive it. Flatter and significantly different slopes than Yoda's self-thinning law slope value of -1.5 were obtained (β_1=-1.25 for mean biomass and β_1=-1.39 for mean volume).

Values of the intercept for both dynamic lines were negatively influenced by the proportion of deciduous component (Table 2.5). A decrease in AIC and AIC corrected values (AICC) as well as an improved distribution of residuals (Figure 2.7) indicated that stand composition was important in explaining variation in the intercept for both relationships (mean volume- and mean biomass-density). A statistically significant negative effect of the percentage of basal area in deciduous on the slope value for the mean biomass-density relationship was also found (results not shown), which implies that a steeper or more negative slope would be expected as the deciduous component increases. However, the addition of this variable did not improve model performance and its effect was small (AIC and AICC showed a small decrease with respect to the general model but increased in relation to the model shown in Table 2.5). No significant effects of other covariates (age, soil moisture and soil nutrient regime, percentage of other species than aspen and white spruce) were detected on the slope. Slope values for individual stands obtained with proc mixed varied from -1.82 to -0.91 for the mean biomass-density relationship, and from -1.83 to -0.93 for the mean volume-density relationships; intercept ranged from 10.3 to 17.9 for mean biomass- and from 4.4 to 11.8 for mean volume-density relationship.

2.4 Discussion

In this study I used two different techniques to elucidate potential differences between the static and the dynamic self-thinning lines, as defined by Weller (1987a, 1990). The two approaches (SFF and mixed models) gave steeper slopes than Reineke (1933) value of -1.605, and slopes were steeper for the static than for the dynamic limit (for density-quadratic mean diameter relationship). In addition, shallower slopes than the self-thinning law value of -1.5 were obtained in both static and dynamic limits for mean biomass- and mean volume-density relationships. Approximately 20 % of the total number of plots available for this study had at least one measurement located in the linear portion of the dynamic thinning line (173 plots out of the 879); this seems to be consistent with the fact that these data come mainly from medium age or old stands that either have been historically understocked or which have completed self-thinning prior to the first measurement. Results suggest that competition related mortality is an important event even in mid-successional and older mixedwood stands such as the ones included in these datasets, and it is expected to be even more important in younger mixed stands.

The observed effects of stand composition and soil nutrient regime on size-density relationships (for both static and dynamic limits) for pure and mixed boreal stands of trembling aspen and white spruce are similar to recent results reported for other tree species (Weiskittel *et* al., 2009). These results contribute to our understanding of the behaviour of boreal mixed stands undergoing self-thinning, supporting the idea of a self-thinning response surface instead of a straight line either for mixed species stands (Puettmann *et* al., 1992) or for stands growing over a gradient of site productivity (Bi, 2001). Analyses of both relationships showed consistent results, although a minor difference was detected respecting the probable effect of one covariate on one of the size-density relationships that we explored (*i.e.* positive effect of soil nutrient regime only on the slope of mean biomass-density relationship). However, the ability to detect effects of site quality may have been limited by the fact that most of the stands that I analysed were located on a medium soil nutrient regime with only a few located either in very poor or in very rich sites (Figure 2.8). The concentration of plots in the submesic (4) to subhygric (6) soil moisture regime classes, with most plots being mesic (5), may also be a reason why soil moisture regime was not significant in any model. The addition of more sites with a broader range of soil nutrient and soil moisture regimes may help to elucidate this effect.

2.4.1 The static thinning line for density-diameter relationships

Analyses from total density-quadratic mean diameter relationships support the suggestion that the self-thinning line varies within a region and with changes in stand composition (Weiskittel *et* al. 2009). Results show that the position (intercept) of this MSDR thinning line is influenced positively by the proportion of deciduous species, and that the slope becomes steeper as the deciduous component increases (β_3=-0.124, Table 2.2). This suggests that, in general, for any given value of weighted quadratic mean diameter, D_q, stands with higher percentage of basal area of deciduous species (% BAd) would be able to support more trees (Figure 2.9). Similar maximum densities are expected for mixed and pure white spruce stands. These results also indicate that pure or nearly pure trembling aspen stands will self-thin faster than pure or nearly pure spruce stands (Figure 2.9).

Site quality (soil moisture regime and soil nutrient regime) did not influence either the slope or the intercept of the static thinning line. This outcome might seem inconsistent with other recent studies (Bi 2001; Weiskittel *et* al. 2009) in which site productivity or site quality was found to significantly influence either the intercept or the slope of the MSDR species boundary line, or both. Most of these sites are located in a region with only limited variation in climatic factors such as mean precipitation (ranging from 400 to 550 mm/year) and soil types (Beckingham and Archibald, 1996). In addition, soil nutrient and soil moisture regime might be seen as subjective estimators of site quality, inferred from observations of topographic position and soil properties. The use of a more objective indicator of site productivity for mixed stands, as well as a wider range of sites in terms of site quality would be more useful to in exploring effects of these factors.

Many researchers have proposed that the MSDR static thinning line is the concept more closely linked to the original idea proposed by Reineke (1933) and Yoda *et* al. (1963), and that this static upper limit should be considered as a species constant applied across different stands growing in a variety of conditions in a region (Weller, 1990). However, this study indicates that both slope and intercept for density-diameter relationship static upper limit vary at least with changes in stand composition.

2.4.2 The interspecific mean biomass- and mean volume-density thinning line

Although most of the observations that I used to derive the mean biomass-density static thinning line fell below the estimated line (Figure 2.4), a few points are still located above this limit. By definition, the compound error term in equation 2.6 (v_i - u_i) has an asymmetric distribution with a negative mean (Bi *et* al., 2000). Therefore, most residuals would be expected to be negative with the corresponding observations falling below the estimated line. Nevertheless, it is possible to have positive residuals (Bi *et* al., 2000) in which case there will be observations and residuals above the estimated static line (Figures 2.4, and 2.10). However, these observations and residuals do not represent a substantial portion of the dataset I utilized as is also observed in both figures. External factors, such as an unexpected increase in availability of nutrients (for instance fertilization), might have a positive random effect on the maximum biomass frontier, influencing the existence of positive residuals (Bi *et* al., 2000). In the case of natural unmanaged stands, such as the ones analyzed here, it appears very unlikely to have an abrupt increase in availability of nutrients. An unanticipated longer growing season affecting biomass production (Bi *et* al., 2000), or the existence of unique sites in terms of their productivity appear as more suitable explanations for the existence of positive residuals and points above the biomass upper frontier, as local variation in competition and mortality within each stand will have effects on their overall growth rates and productivity (Kenkel 1988; Kenkel *et* al. 1997).

The interspecific MSDR or static thinning line was formulated as a boundary that applies across different stands and it is considered to be independent of site quality (Weller, 1990). Differences in the position and slope of interspecific self-thinning lines could be related in this case to differences in how biomass is accumulated across stands (Weller, 1989). The finding in this study of significant effects of stand composition and nutrient regime on the intercept and slope for both mean biomass- and mean volume-density relationship agree with and support previous results respecting the effect of site characteristics and stand composition on the interspecific thinning line (Bi 2001; Morris 2002; Morris 2003; Weiskittel *et* al. 2009).

My results suggest that better quality sites (*i.e.* higher soil nutrient regime) are able to support more biomass as has been suggested in other studies (Gholz, 1982). A positive effect of the deciduous component on the intercept of the static thinning line suggests that pure or nearly pure deciduous stands are able to accumulate a greater amount of aboveground biomass before self-thinning starts. The significant negative effect of composition on the slope of the static line also indicates that pure or nearly pure deciduous stands will self-thin faster than pure spruce stands. These results indicate that changes in maximum mean biomass-density relationships across stands are likely to occur as a consequence of changes in stand composition and site quality.

2.4.3 The estimated self-thinning surface for boreal mixedwoods based on SFF

The performance of equations 2.7 and 2.8 obtained with stochastic frontier function regression, for both density-quadratic mean diameter and mean biomass-density relationships (Tables 2.2 and 2.3, model with covariates and interactions) is illustrated in Figures 2.11 and 2.12. They show the estimated self-thinning surface based on diameter-density-species proportion relationship (Figure 2.11), and on mean biomass-density-species proportion (Figure 2.12) covering sites within the full range of species proportions of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.) included in the datasets. Changes in slope and intercept are observed as the proportion of the deciduous component changes.

2.4.4 Determination of self-thinning plots

The use of subjective approaches for analysing MSDR and the self-thinning law has been a matter of longstanding concern (Westoby 1984; Weller

1987; Bi *et* al. 2000; Zhang *et* al. 2005). I attempted to objectively determine which plots were undergoing self-thinning and subsequently define which observations were in the density-dependent mortality stage using a statistical approach (Poage *et* al., 2007). My results illustrate that the methodology is helpful when individual plots clearly depict both the non-linear and the linear sections of the theoretical size-density trajectory of self-thinning plots (Figures 2.2 and 2.3), and when stands have a minimum of 5 consecutive measurements. Although most of the plots in the data set had more than the minimum required measurements to fit the non-linear model, they did not describe both linear and non-linear sections of the size-density trajectory and only the linear portion of model 2.9 could be fit to these plots. Nevertheless, selection based on use of plots with multiple measurements located along the linear portion of the size density trajectory provides for objective selection of plots for analysis of dynamic self-thinning lines.

2.4.5 The dynamic thinning line for density-diameter relationships

These results show that the position of the average dynamic thinning line for density-quadratic mean diameter is slightly below the static or species boundary line (β_0=12.34 for the dynamic and β_0 = 13.53 for the static; Figure 2.3). The intercept of this dynamic thinning line decreases as the percentage of basal area of deciduous species increases, and increases as site quality improves (Table 2.4). This finding is consistent with Weller's idea (1990) respecting the influence of population and site characteristics on self-thinning of individual stands. A steeper slope was also obtained for the static than for the dynamic thinning line (β_1=-1.96 vs. β_1 =-1.73) as also observed by Weller (1990). The intercept and the slope of the dynamic thinning line can be influenced by spatial arrangement of seedlings at establishment (Peet and Christensen, 1980), differences in initial stand conditions (Reynolds and Ford, 2005), changes in soil fertility (White 1981; Westoby 1984; Zeide 1985) and differences in ambient light levels (Hutchings and Budd 1981; Westoby and Howell 1981). In addition, the slope of the dynamic thinning line can be influenced by the way in which plants modify their shape and how they accumulate biomass as they grow (Weller 1987, 1990).

Although both the slope and intercept values of the dynamic thinning line obtained using mixed models show a wide range of variation, the 'average' slope value in the general model (model 2.10) suggests that an increase in total quadratic mean diameter of 1% is associated with a decrease in the total number of trees per hectare of 1.73% on the log scale. This increase in diameter with the concomitant decrease in total density might be accelerated as the sites become richer (better quality) as suggested by the interaction term. While the effect of the deciduous component seems to be rather small (β_2=-0.026, Table 2.4 model with covariates only), these effects suggest that, in general, as the percentage of deciduous species increases at the stand level, both mixed stands and stands moving towards pure spruce will achieve slightly higher maximum densities for a given diameter before density-dependent mortality occurs.

Although including two additional parameters in the model (β_3 and β_4, Table 2.4, model with covariates and interactions) does not represent an additional improvement of the model's fit (*i.e.* similar AIC and AICC values for both models), the significance of soil nutrient regime in the model indicates that local characteristics have an influence on how an individual stand develops and approaches the density-dependent mortality stage. Because most of the self-thinning plots I analysed are located in medium quality sites (nutrient regimes 3 and 4, Figure 2.8), the inclusion of additional sites expanding the range of variation in site quality might help to clarify the effect of this factor on MSDR dynamic thinning lines.

2.4.6 The dynamic thinning line for mean biomass- and mean volume-density relationships

The position of the average biomass-density dynamic thinning line is below the static line (Figures 2.4 and 2.6), although the intercept for the former is higher than that for the static (model with no covariates, β_0=13.91 for the dynamic and β_0=12.4 for the static). A steeper slope was also obtained for the dynamic than for the static line (model with no covariates, β_1= -0.98 static vs. β_1=-1.25 for the dynamic). The intercept of the dynamic thinning line declines as the deciduous component increases as indicated in Table 2.5 (β_2, model with covariates). This implies that at the stand level, pure aspen or mixed stands with higher amounts of deciduous might be able to pack more mean biomass for a given density before self-thinning occurs.

2.4.7 Causes of variation in intercepts and slopes of dynamic thinning lines

As opposed to the static line the dynamic thinning line is not considered as a constant relationship applying across all stands growing in a specific region, rather it is influenced by a number of factors (Weller 1987a, 1990). Intercepts, slopes, or both, of dynamic thinning lines appear to be influenced by soil fertility (White 1981; Westoby 1984; Zeide 1985; Morris 2002), spatial arrangement of seedlings at establishment (Peet and Christensen, 1980), variations in initial stand conditions (Reynolds and Ford, 2005), changes in plant shape and biomass accumulation (Weller 1987a, 1990), differences in light intensity, light availability and use of the available light (Hutchings and Budd 1981; Westoby and Howell 1981; Lonsdale and Watkinson 1982; Hutchinson 1983), as well as tolerance and self-tolerance of species (Zeide 1985, 1987; Pretzsch and Biber 2005).

Boreal mixedwood forests are a disturbance-dependent ecosystem in which wildfires are the main factor shaping the landscape, and where disturbances and competition are the main ecological processes that modify stand dynamics (Chen and Popadiouk, 2002). Following a major disturbance (*i.e.* wildfires, clearcutting) trembling aspen regenerates profusely with initial densities over 100000 stems$\cdot$ha^{-1}, but by age 10 densities drop to about 10000 stems$\cdot$ha^{-1} due to self-thinning (Peterson and Peterson, 1992). Trembling aspen grows faster than white spruce and dominates the site for up to 60 years (Chen and Popadiouk, 2002); meanwhile, white spruce can survive in the understory owing to its ability to utilize light of lower intensities (Lieffers and Stadt, 1994). In these stages, and with the existence of spruce in the understory, competition from trembling aspen reduces white spruce growth (Filipescu and Comeau, 2007a).

However, aspen can also exert facilitative effects on young white spruce (Man and Lieffers 1999; Comeau *et* al. 2005). Competitive and facilitative interactions between these two species are thought to fluctuate with stand age, site and other factors (Filipescu and Comeau, 2007a). This interaction between competition and facilitation could lead to dynamic relationships between spruce growth and competition from trembling aspen (Filipescu and Comeau, 2007b). Nevertheless, because white spruce can survive and grow (albeit perhaps more slowly) underneath a closed canopy of aspen, and it has been shown that understory spruce exerts no influence on overtopping aspen (MacPherson *et* al., 2001) one would expect that mixed stands would carry higher stocking and have a larger intercept than single species stands. Mixedwood stands should also, for this reason and by virtue of phenological separation, competitive reduction and other factors (Man and Lieffers, 1999), be more productive than single species stands.

Changes in the intensity of inter- and intra-specific competition and the interchange of competitive and facilitative interactions, influence the performance of these two species growing in mixtures from their behaviour growing in pure stands, as previously suggested for other tree species (Garber and Maguire 2004; Amoroso and Turnblom 2006). In the same way, modifications of essential tree allometric relationships might occur with associated alteration of trees achieving maximum potential size (Weiskittel *et* al., 2009). Changes in allometric relationships of plants through time (e.g. changes in height-to-crown width ratio or live crown ratio) and the degree of overlap between neighbours are thought to influence the position and slope of self-thinning lines (Norberg, 1988). Stoll *et* al. (2002) suggest that changes in shape and allometry of trees through time are two of the most important factors determining variation of self-thinning, mainly by altering the speed at which dimension hierarchies are created and consequently affecting the dynamic thinning line.

Examination of potential changes in live crown ratios was performed for some PSPs for which there was available data of crown length and crown width. However, many of these sites were not included in the plots for which MSDR were analysed, and inconsistencies due to measurement errors and other factors were detected during initial exploration. No important or clear trends were detected. The existence of better quality information on crown dimensions in stands undergoing self-thinning is necessary to support further exploration of this subject.

Tolerant species will have higher intercepts than broad-leaved trees either because they are capable of packing more biomass per unit of canopy volume (Lonsdale and Watkinson 1983; Westoby 1984), or because of differences in crown shape (Harper, 1977). If light availability and intensity (Hutchinson, 1983), and light use by plants are factors that influence the dynamic thinning line, tolerant species that are capable of using lower intensity light (*i.e.* diffuse light) will have a higher intercept than intolerant species (Hutchinson, 1983). The finding in this study of significant effects of the percentage of basal area of deciduous species on intercept of the static thinning line suggests: a) an increase in the ability of biomass packing in stands with a higher proportion of deciduous species than in stands with higher proportion of white spruce before density-dependent mortality sets in and, b) that for any value of quadratic mean diameter (D_q), stands with a higher percentage of basal area in deciduous will support higher maximum densities than stands with more white spruce. This is not consistent with expected differences between these two species. Further examination of relationships between crown architecture, light capture, site characteristics, species composition and size-density relationships are required to better understand the processes involved in the variation of dynamic thinning lines in boreal mixtures.

Analyses of MSDR for western Canadian boreal tree species have been previously developed. Lieffers and Campbell (1984) reported the the slope of the relationship between tree biomass and density for 23-57 year-old trembling aspen stands is flatter than the theoretical value suggested by the self-thinning law. Yang and Titus (2002) developed maximum size-density functions for separate and combined trembling aspen, white spruce and lodgepole pine (*Pinus contorta* var *latifolia* Engelm.) sites, by using data from 699 PSPs in Alberta. They suggest that when the MSDR is calculated for the three species taken as a whole, the slope takes a value close to Reineke's slope of -1.605; however, no effects of site quality on the relationship were found. In a recent study, Bokalo *et* al. (2007) presented results from analysis of 9 years of measurements on regenerated trembling aspen stands undergoing self-thinning; they suggest that for these young aspen stands, the traditional representation of Reineke's relationship showed a slope significantly different from -1.605 when using root collar diameter instead of diameter at breast height. They also found that the slope of the maximum mean tree volume-density line was -1.731 rather than -1.5, as suggested by the self-thinning law.

However, these studies did not make a differentiation between the static and dynamic concepts suggested by Weller (1987, 1990). Furthermore, they do not assess the potential effects of stand composition on MSDR in these mixed stands. Stand density models which are usually constrained by using MSDR species thinning lines (Puettmann *et* al., 1993), need to make use of a relationship that best quantifies how individual stands self-thin; hence, the slope of the relationship needs to reflect the average self-thinning pattern of individual stands (VanderSchaaf and Burkhart, 2007b).

2.5 Conclusions

Results from this study indicate that maximum size-density relationships can be developed for mixed as well as for pure boreal stands. Stand composition has a significant effect on both slope and intercept of the static thinning lines evaluated in this study. In addition, stand composition as well as nutrient regime have a significant influence on dynamic thinning lines, which indicates that local differences in stands including species proportions and site quality are important in explaining how individual stands develop and approach self-thinning. As other authors have suggested, a multidimensional response surface is useful for explaining MSDR in mixed species stands and also permits examination of the influence of site, history and other factors on these relationships. This study also helps to emphasize the fact that maximum stocking densities (stockability) generally decline as the proportion of intolerant aspen in the stand decreases.

MSDR developed in this study can be used in management of boreal mixedwoods at least 25 years old growing on medium nutrient regimes, owing to the sample size, and ranges in sizes and densities that they were developed from. In particular, the slope of the dynamic thinning line best represents, on average, the self-thinning behaviour of individual plots, which is often desirable in stand density models (VanderSchaaf and Burkhart, 2007), particularly when stand and site variables can be used to explain changes in thinning behaviour. Relationships presented here can be used in the development of stand density management diagrams and models for mixedwood stands.

In addition to management for timber production, these diagrams could also be useful in manipulating stand densities to improve habitat features through promoting growth of understory. However, additional data, including accurate measurements of tree crown dimensions, with a better representation of poor and rich soil qualities as well as data from younger stands and stands regenerating after clearcutting are needed for further investigation of these relationships.

2.6 References

Amoroso, M.M.; and Turnblom, E.C. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36:1484-1496.

Beckingham, J.D.; and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Special Report No 5. Natural Resources Canada. Canadian Forest Service-Northern forestry Centre. Edmonton, AB.

Bi, H. 2004. Stochastic frontier analysis of a classic self-thinning experiment. Aus. Ecol. 29:408-417.

Bi, H. 2001. The self-thinning surface. For. Sci. 47(3):361-370.

Bi, H.; Wan, G.; and Turvey, N.D. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. Ecol. 81(6):1477-1483.

Bi, H.; and Turvey, N.D. 1997. A method of selecting data points for fitting the maximum biomass-density line for stands undergoing self-thinning. Aus. J. Ecol. 22:356-359.

Bokalo, M.; Comeau, P.G.;and Titus, S.J. 2007. Early development of tended mixtures of aspen and spruce in western Canadian boreal forests. For. Ecol. Manage. 242(2-3):175-184.

Brandt, J.P. 2009. The extent of the North American boreal zone. Env. Rev.17:101-161.

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

Chen, H.Y.H.; Fu, S; Monserud, R.A.; and Gillies, I.C. 2008. Relative size and stand age determine *Pinus banksiana* mortality. For. Ecol. Manage. 255:3980-3984. doi:10.1016/j.foreco.2008.03.040

Comeau, P.G.; White, M.; Kerr, G.; and Hale, S.E. 2010. Maximum density-size relationships for Sitka spruce and coastal Douglas-fir in Britain and Canada. Forestry. 83(5):461-468. doi:10.1093/forestry/cpq028

Comeau, P.G. 1996. Why mixedwoods? In: P.G. Comeau & K.D. Thomas (eds). Silviculture of temperate and boreal broadleaf-conifer mixtures. pp: 1-5 B. C. Min. For. Land Manage. Handbook 36. Victoria, B. C.

Comeau, P.G.; Kabzems, R.; McClarnon, J.; and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. For. Chron. 81(4):559-574

DeBell, D.S.; Harms, W.R.; and Whitesel, C.D. 1989. Stockability: a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern United States. For. Sci. 35(3):708-719.

Del Rio, M.; Montero, G.; and Bravo, F. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142:79-87.

Drew, T.J.; and Flewelling, W. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. 23(4):517-534.

Ducey, M.J.; and Knapp, R.A. 2010a. Rapid assessment of relative density in mixed-species stands of Northeastern United States. Int. J. For. Res. Vol. 2010. 8 p. doi: 10.1155/2010/212068.

Ducey, M.J.; and Knapp, R.A. 2010b. A stand density index for complex mixed species forests in the northeastern United States. For. Ecol. Manage. 260:1613-1622. doi:10.1016/j.foreco.2010.08.014.

Filipescu, C.; and Comeau, P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Forest Management Branch. 2005. Permanent Sample plot (PSP) field procedures manual. Alberta Sustainable Resource Development. Public Lands and Forest Division. Edmonton, AB.

Franco, M.; and Kelly, C.K. 1998. The interspecific mass-density relationship and plant geometry. Proc. Nat. Acad. Sci. – USA. 95(13):7830-7835.

Garber, S.M.; and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. For. Sci. 50(1):92-105.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecol. 63:469-481.

Hann, D.W.; Marshall, D.D.; and Hanus, M.L. 2003. Equations for predicting height-to-crown-base, 5-year-diameter-growth-rate, 5-year height-growth rate, 5-year mortality rate, and maximum size- density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest. Res. Contribution 40, Forest Research Laboratory, Oregon State University, Corvallis, OR. 83 pp.

Harms, W.R.; Whitesell, C.D.; and DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126(1):13-24.

Harms, W.R.; DeBell, D.S.; and Whitesell, C.D. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Can. J. For. Res. 24:511-521.

Harper, J. L. 1977. Population biology of plants. School of Plant Biology. University College of North Wales. Academic Press. London. 892 pp.

Huang, S. 1994. Individual tree volume estimation procedures for Alberta: methods for formulation and statistical foundations. Forest Resources Information Branch. Land and For. Serv. Technical Report # 1. T/288. Edmonton, AB. 80 pp.

Hutchings, M.J.; and Budd, C.S.J. 1981. Plant competition and its course through time. Bioscience 31(9):640-645.

Hutchinson, M. 1983. Ecology’s law in search of a theory. New Scientist. 98:765-767

Jack, S.B.; and Long, J.N. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. For. Ecol Manage. 86:205-220.

Kimmins, J.P. 2004. Forest Ecology: a foundation for sustainable forest management and environmental ethics in Forestry. 3rd edition. Prentice Hall. 611 p.

Kira, T.; Ogawa, H.; and Zakazaki, N. 1953. Intraspecific competition among higher plants. I Competition-yield-density interrelationship in regular dispersed populations. J. Inst. Polytech. Osaka City Univ. 4:1 -16.

Kenkel. N.C.; Hendrie, M.L.; and Bella, I.E. 1997. A long-term study of *Pinus banksiana* population dynamics. J. Veg. Sci. 8:241-254.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology. 69:1017-1024.

Lambert, M.C.; Ung, C.H.; and Raulier, F. 2005. Canadian national tree aboveground biomass equations. Can J. For. Res. 35:1996-2018. doi:10.1139/X05-112

Lhotka, J.M.; and Loewenstein, E.F. 2008. An examination of species-specific growing space utilization. Can. J. For. Res. 38: 470 – 479.

Lieffers, V.J.; Macmillan, R.B.; MacPherson, D.; Branter, K.; and Stewart, J.D. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72:286-292.

Lieffers, V.J.; and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Lieffers, V.J.; and Campbell, J.S. 1984. Biomass and growth of *Populus tremuloides* in northeastern Alberta: estimates using hierarchy in tree size. Can. J. For. Res. 14:610-616.

Littell, R.C.; Milliken G.A.; Stroup, W.W.; Wolfinger, R.D.; and Schabenberger, O. 2006. SAS® for mixed models, Second Edition. SAS Institute Inc. Cary, N.C. 814 pp.

Lonsdale, W.M.; and Watkinson, A.R. 1983. Plant geometry and self-thinning. J. of Ecol. 71(1):285-297.

Lonsdale, W.M.; and Watkinson, A.R. 1982. Light and self-thinning. New Phytologist. 90(3):431- 445

MacPherson, D.M.; Lieffers, V.J.; and Blenis, P. V. 2001. Productivity of aspen stands with and without a spruce understorey in Alberta’s boreal mixedwood forests. For. Chron. 77:351-356.

Man, R.; and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75(3):505-513.

Morris, E.C. 2003. How does fertility of the substrate affect intraspecific competition? Evidence and synthesis from self-thinning. Ecol. Res. 18:287-305.

Morris, E.C. 2002. Self-thinning lines differ with fertility level. Ecol. Res. 17:17-28.

Norberg, R.A. 1988. Theory of growth geometry of plants and self-thinning of plant populations: geometric similarity, elastic similarity, and different growth models of plant parts. American Naturalist. 131:220-256.

Ogawa, K. 2005. Time-trajectory of mean phytomass and density during a course of self-thinning in a sugi (*Cryptomeria japonica* D. Don) plantation. For. Ecol. Manage. 214:104-110

Osawa, A.; and Allen, R. 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology 74(4):1020-1032.

Peet, R.K.; and Christensen, N.L. 1980. Succession: a population process. Vegetatio 43(1/2):131-140.

Perry, D.A.; Oren, R.; and Hart, C.S. 2008. Forest Ecosystems. Second Edition. The John Hopkins University Press. Baltimore, MD, USA. 606 pp.

Peterson, E.B.; and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Can. For. Serv. North. Cent. Spec. Rep. 1. 252 pp.

Poage, N.J.; Marshall, D.D.; and McClellan, M.H. 2007. Maximum stand density index of 40 western Hemlock-Sitka spruce stands on southeast Alaska. West. J. Appl. For. 22(2):99-104.

Pretzsch, H. 2006. Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands. Oecologia. 146:572-583. DOI 10.1007/s00442-005-0126-0

Pretzsch, H.; and Biber, P. 2005. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51 (4): 304-320.

Pretzsch, H.; Block, J.; Dieler, J.; Dong, P.H.; Kohnle, U.; Nagel, J.; Spellmann, H.; and Zingg, A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67(712). doi: 10.1051/forest/2010037

Puettmann, K.J.; Hibbs, D.E.; and Hann, D.W. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: extension of size-density analysis to species mixture. J. Ecol. 80:449-458.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Reynolds, J.H.; and Ford, D. 2005. Improving competition representation in theoretical models of self-thinning: a critical review. J. Ecol. 93: 362- 372.

Rowe, J.S. 1972. Forest regions of Canada. Publication No 1300. Dep. Environ. Can. For. Serv. Ottawa, ON.

Saunders, M.K.; and Puettmann, K.J. 2000. A preliminary white spruce density management diagram for the Lake states. Staff paper series No 145. College of Natural Resources. University of Minnesota. St. Paul, Minnesota. USA. 13 pp

SAS. 2010. Statistical Analysis System for windows, V 9.2. SAS-Institute, Inc. Cary, N.C. USA.

Schutz, J.P.; and Zingg, A. 2010. Improving estimations of maximal stand density by combining Reineke's size-density rule and the yield level, using the example of spruce (*Picea abies* (L.) Karst.) and European Beech (*Fagus sylvatica* L.). Ann. For. Sci. 67:507 12 pp.

Smith, D.J.; and Woods, M.E. 1997. Red pine and white pine density management diagrams for Ontario. Tech. Report # 48. Ontario Ministry of Nat. Res. Sault Ste. Marie, ON. 31 p.

Shinozaki, K.; and Kira, T. 1956. Intraspecific competition among higher plants. Logistic theory of the C-D effect. J. Inst. Pol. Osaka City Univ. 7:35-72.

Stoll, P.; Weiner, J.; Muller-Landau, H.; Muller, E.; and Hara, T. 2002. Size symmetry of competition alters biomass-density relationships. Proc. R. Soc. Lond. B. 269:2191-2195. doi: 10.1098/rspb.2002.2137

Torres-Rojo, J.M.; and Velázquez-Martínez, A. 2000. Índice de densidad relativa para rodales coetáneos mezclados. Agrociencia. 34: 497-507.

VanderSchaaf, C.L. 2010. Estimating individual stand size-density trajectories and a maximum size-density relationship species boundary line slope. For. Sci. 56(4): 327-335.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007a. Using segmented regression to estimate stages and phases of stand development. For. Sci. 54(2): 167-175.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007b. Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope. For. Sci. 53(3):435-442.

Weiskittel, A.; Gould, P.; and Hailemariam, T. 2009. Sources of variation in the self-thinning boundary line for three species with varying levels of shade tolerance. For. Sci. 55(1):84-93.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? - a reply to Osawa and Sugita. Ecology. 71(3): 1204-1207.

Weller, D.E. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the -3/2 power rule of self-thinning. Am. Nat. 133(1):20-41.

Weller, D.E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs. 57(1):23-43.

Weller, D.E. 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. Ecology 68(4):813-821.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167-225.

Westoby, M.; and Howell J. 1981. Self-thinning: the effect of shading on glasshouse populations of silver beet (*Beta vulgaris*). J. Ecol. 69:359-365.

White, J. 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89:475-500.

White, J. 1980. Demographic factors in populations of plants. In: Demographic and evolution in plant populations. O. T. Solbrig (ed.). Blackwell Sci. Publications, Oxford. pp: 21-48.

Woodall, C.W.; Miles, P.D.; and Vissage, J. S. 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. For. Ecol. Manage. 216: 367-377. DOI:10.1016/j.foreco.2005.05.050

Yang, Y.; and Titus, S.J. 2002. Maximum size-density relationships for constraining individual tree mortality functions. For. Ecol. Manage. 168:259-273.

Yoda, K.; Kira, T.; Ogawa, H.; and Homuzi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants). J. Biol. Osaka City Univ. 14:107-129.

Zeide, B. 2005. How to measure stand density. Trees. 19:1-14. DOI 10.1007/s00468-004-0343-x

Zeide, B. 1987. Analysis of the 3/2 power law of self – thinning. For Sci. 33 (2): 517-537.

Zeide, B. 1985. Tolerance and self-tolerance of trees. For. Ecol. Manage. 13:149-166.

Zhang, L.; Bi, H.; Gove, J.H.; and Heath, L.S. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. Can. J. For. Res. 35: 1507-1514. doi: 10.1139/X05-070

Table 2.1 Summary of attributes of the plots included in each analysis as indicated.

Analysis	n	Variable	Mean	SD	Min	Max
Static	879	Total density (TPH)	1619	1902	62	19800
		Quadratic mean diameter (D_q, cm)	22.9	6.9	4.6	49.9
		Total basal area ($m^2 \cdot ha^{-1}$)	40.4	12.7	12.2	118.3
		Age (years)	102	39	17	324
		Deciduous basal area (%)	53.7	34.8	0.06	100
		Moisture regime	---	---	2	9
		Nutrient regime	---	---	2	5
		D_q deciduous (cm)	22.4	9.6	0.0	54.3
		D_q white spruce (cm)	19.2	10.8	0.0	67.5
		SDI total	649	264	8	2654
		Volume per hectare ($m^3 \cdot ha^{-1}$)	341.7	126.8	0.7	734
		Biomass per hectare ($Kg \cdot ha^{-1}$)	184835	59092	763.961	551526
		Tree mean volume (m^3)	0.37	0.27	0.003	1.57
		Tree mean biomass (Kg)	199	144	6.0	1235
Dynamic (diameter)	179	Total density (TPH)	1338	1130	198	13813
		Quadratic mean diameter (D_q, cm)	22.9	5.8	7.0	40.8
		Total basal area ($m^2 \cdot ha^{-1}$)	43.8	10.4	12.8	76.1
		Age (years)	106.2	34.2	25	264
		Deciduous basal area (%)	53.1	35.1	0.10	100
		Moisture regime	---	---	4	8
		Nutrient regime	---	---	2	5
		D_q deciduous (cm)	23.8	8.2	0.0	59.9
		D_q spruce (cm)	18.4	9.9	0.0	45.9
		SDI total	837.2	209.7	287	1686
Dynamic (Biomass & volume)	173	Total density (TPH)	1341	1136	198	13813
		Quadratic mean diameter (D_q, cm)	22.9	5.7	7.0	40.8
		Age (years)	106	34	25	264
		Deciduous basal area (%)	53.2	35.2	0.1	100
		Moisture regime	---	----	4	8
		Nutrient regime	---	----	2	5
		Biomass per hectare (kg/ha)	198947	46109	46527	379840
		Volume (m^3/ha)	375.7	106.6	80.7	842.9
		Tree mean volume (m^3)	0.39	0.23	0.015	1.33
		Tree mean biomass (kg)	206.9	120.1	10.5	830.2

n= # of plots; 879 observations were used for analysis of static boundary; 653 observations for the dynamic diameter-density, and 600 obs for dynamic mean biomass and mean volume relationships; SD=standard deviation; max=maximum; min=minimum; $D_q=((QMD_{aw}*BA_{aw})+(QMD_{bw}*BA_{bw})+(QMD_{pb}*BA_{pb})+(QMD_{sw}*BA_{sw}))/100$, where: D_q=weighted quadratic mean diameter of the plot; QMD_{aw}, QMD_{bw}, QMD_{pb} and QMD_{sw} are quadratic mean diameter of aspen, birch, poplar and spruce, respectively; and BA_{aw}, BA_{bw}, BA_{pb} and BA_{sw} are percentage of basal area in aspen, birch, poplar and spruce respectively; SDI total= Stand Density Index of the plot.

Table 2.2 Parameter estimates for the maximum density-diameter relationship (static thinning line) of boreal mixedwood stands using SFF and equation 2.7 without and with covariates as indicated.

Model	β_0	β_1	β_2	β_3	σ_v^2	σ_u^2	AIC
No covariates	13.53 (0.139)	-1.96* (0.044)	---	---	0.279 (0.014)	0.578 (0.027)	1039
With covariates	12.04 (0.372)	-1.49 (0.117)	0.39 (0.090)	-0.124 (0.029)	0.281 (0.014)	0.564 (0.027)	1024

n=879 observations. A half-normal model was used. * Significantly different from -1.605 at $\alpha=0.05$ (using LR tests); standard errors are shown in parenthesis; σ_v^2 = two-sided error term; σ_u^2 = one-sided error term. AIC= Akaike's Information Criterion; β_0=intercept, β_1=lnD$_q$, β_2=lnBAd and β_3=lnD$_q$*lnBAd, all parameters shown are significant at $\alpha=0.05$.

Table 2.3 Parameter estimates for the maximum biomass (w) - and volume (v)-density relationships (static limit) for boreal mixedwood stands using SFF regression and equation 2.7 as indicated

Model	Dependent Variable	β_0	β_1	β_2	β_3	β_4	σ_v^2	σ_u^2	AIC
No covariates	w	12.4 (0.123)	-0.98* (0.018)	---	---	---	0.14 (0.009)	0.66 (0.019)	836
	v	6.37 (0.159)	-1.01* (0.023)	---	---	---	0.138 (0.011)	0.818 (0.023)	1149
Covariates with interactions	w	10.22 (0.322)	-0.707 (0.046)	0.446 (0.076)	0.287 (0.060)	-0.067 (0.011)	0.139 (0.009)	0.631 (0.019)	779
	v	3.92 (0.357)	-0.69 (0.051)	0.484 (0.083)	0.348 (0.065)	-0.077 (0.012)	0.109 (0.011)	0.796 (0.022)	1062

n=879 observations. A half-normal model was used; standard errors are shown in parenthesis; ln=natural logarithm; σ_v^2 = two-sided error term; σ_u^2 = one-sided error term. AIC= Akaike's Information Criterion; model covariates & interactions - biomass: β_0=intercept, β_1=lnN, β_2=lnBAd, β_3= $\ln N_{ur}$ and β_4=lnN*lnBAd; model covariates & interactions-volume: β_0=intercept, β_1=lnN, β_2=lnBAd, β_3=$\ln N_{ur}$, β_4= lnN*lnBAd; all parameters shown are significant at α=0.05; *significantly different than -1.5.

Table 2.4 Estimates of the maximum density-diameter relationship dynamic thinning line for boreal mixedwood stands using mixed-effects models and equation 2.10 as indicated.

Model	Parameter							AIC	AICC
	β_0	β_1	β_2	β_3	β_4	μ_{0i}	μ_{1i}		
No covariates	12.34 (0.112)	-1.73* (0.035)	----	----	----	1.399 (0.215)	-0.411 (0.065)	-1141.3	-1141.2
With covariates	12.49 (0.124)	-1.74 (0.035)	-0.026 (0.009)	----	----	1.410 (0.217)	-0.414 (0.066)	-1140.8	-1140.7
With covariates-interactions	11.01 (0.787)	-1.27 (0.244)	-0.026 (0.009)	1.26 (0.664)	-0.393 (0.206)	1.377 (0.214)	-0.405 (0.065)	-1140.8	-1140.7

n= 179 plots, 650 observations; AIC= Akaike's information criterion; AICC=AIC corrected; all parameters are significant; * significantly different from -1.605; standard errors are shown in parentheses. β parameters are fixed effects (β_0=intercept; β_1=slope (weighted quadratic mean diameter); β_2=percentage of basal area in deciduous; β_3=nutrient regime; β_4=interaction between quadratic mean diameter-nutrient regime; μ's are random effects covariance estimates (μ_{0i}=associated to intercept; μ_{1i}=associated to slope).

Table 2.5 Estimates of the maximum biomass (*w*) - and volume (*v*) - density relationship (dynamic thinning line), for boreal mixedwoods using mixed-effects models and equation 2.11 as indicated

Model	Dependent variable	Parameter					AIC	AICC
		β_0	β_1	β_2	μ_{0i}	μ_{1i}		
No covariates	*w*	13.91 (0.161)	-1.25* (0.0223)	---	1.965 (0.456)	-0.267 (0.065)	-820.0	-819.9
	v	8.603 (0.192)	-1.39* (0.026)	----	3.187 (0.679)	-0.414 (0.092)	-660.3	-660.6
Covariates	*w*	13.941 (0.159)	-1.23 (0.022)	-0.047 (0.012)	1.830 (0.448)	-0.247 (0.063)	-828.7	-828.6
	v	8.614 (0.188)	-1.349 (0.026)	-0.078 (0.013)	2.828 (0.644)	-0.370 (0.089)	-685.2	-685.1

n= 173 plots, 600 observations; AIC= Akaike's information criterion; AICC = AIC corrected; all parameters shown are significant; β parameters are fixed effects (β_0 = intercept; β_1 = slope (total density); β_2 = % basal area in deciduous for model with covariates; μ's are random effects covariance estimates (μ_{0i} = associated to intercept; μ_{1i} = associated to slope). * Significantly different than -1.5. No significant interactions were found.

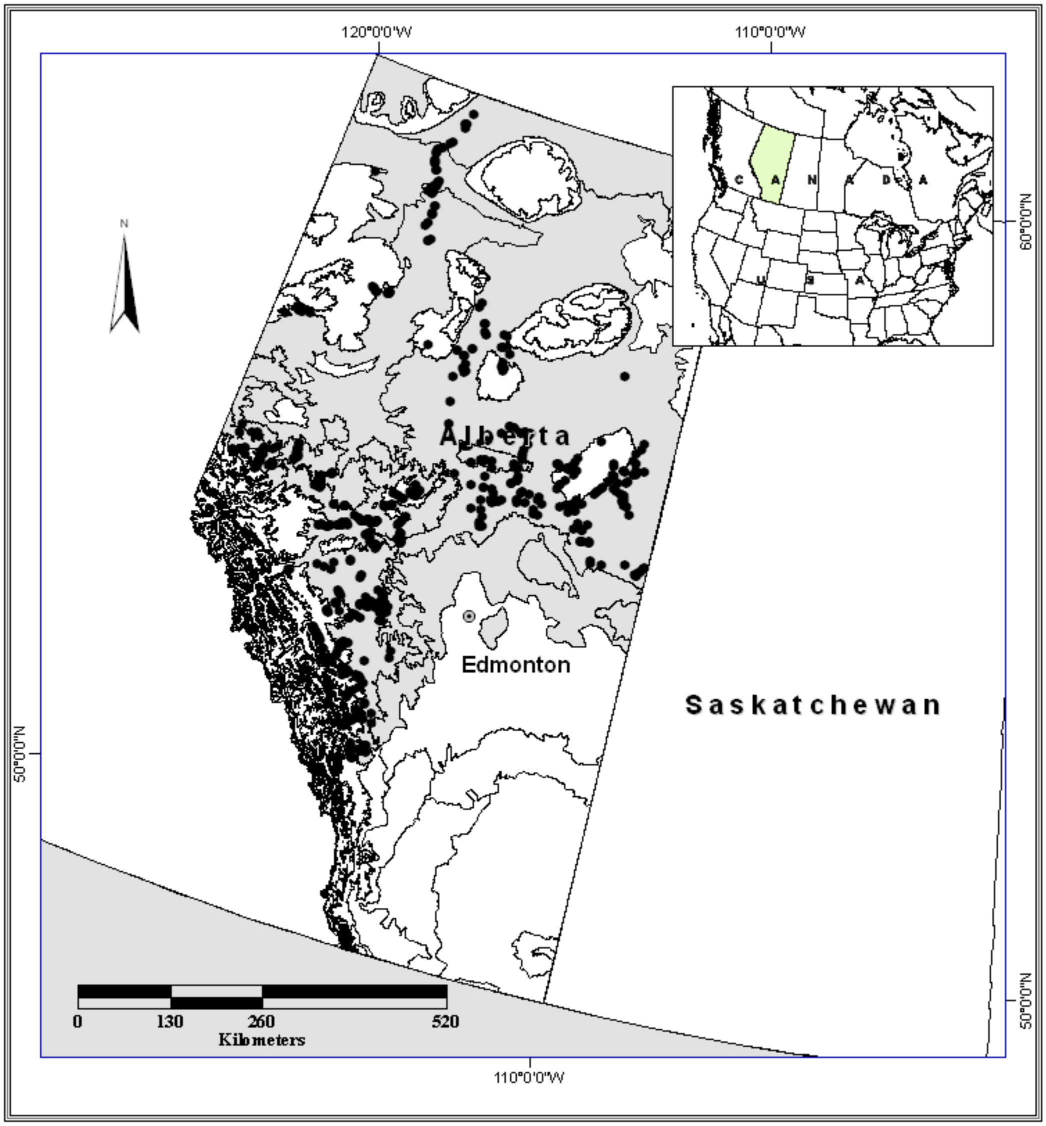


Figure 2.1 Alberta's natural subregions showing location of plots that were used in this study. Regions include the Central, the Dry and the Northern Mixedwoods, as well as the Lower Foothills. Dots indicate areas sampled which might represent one or more permanent sample plots.

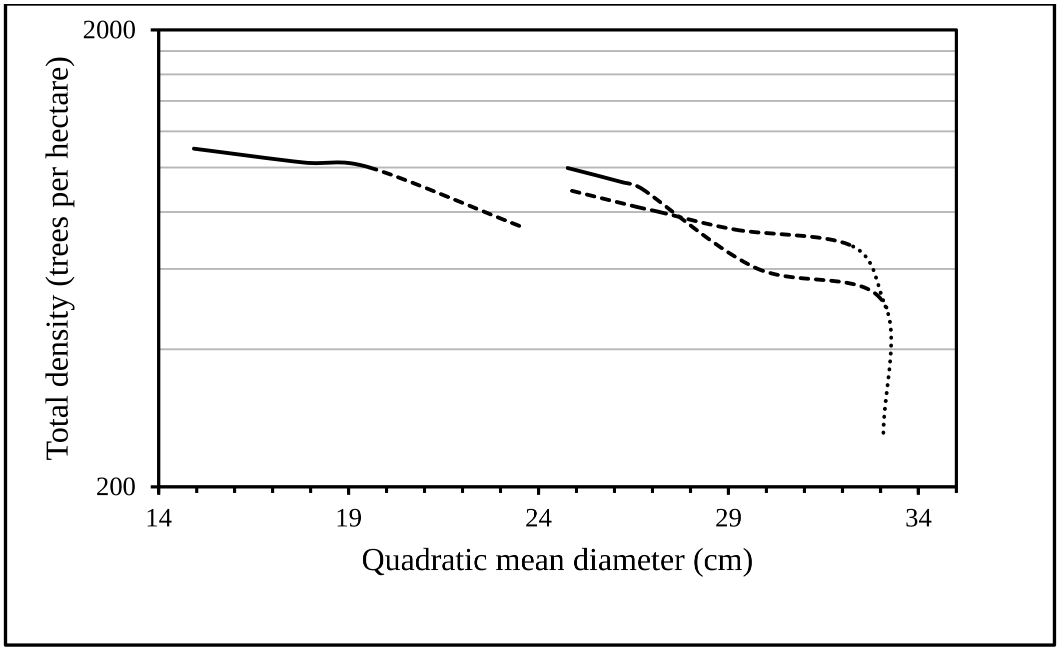


Figure 2.2 Diagrams showing individual size-density trajectories of plots for which the non-linear model (Equation 2.8) fit successfully; the dashed section indicates the dynamic thinning section of self-thinning; the upper portion of the trajectory (continuous line) depicts the density-independent mortality stage and the lower portion (dotted section) the divergence stage of self-thinning.

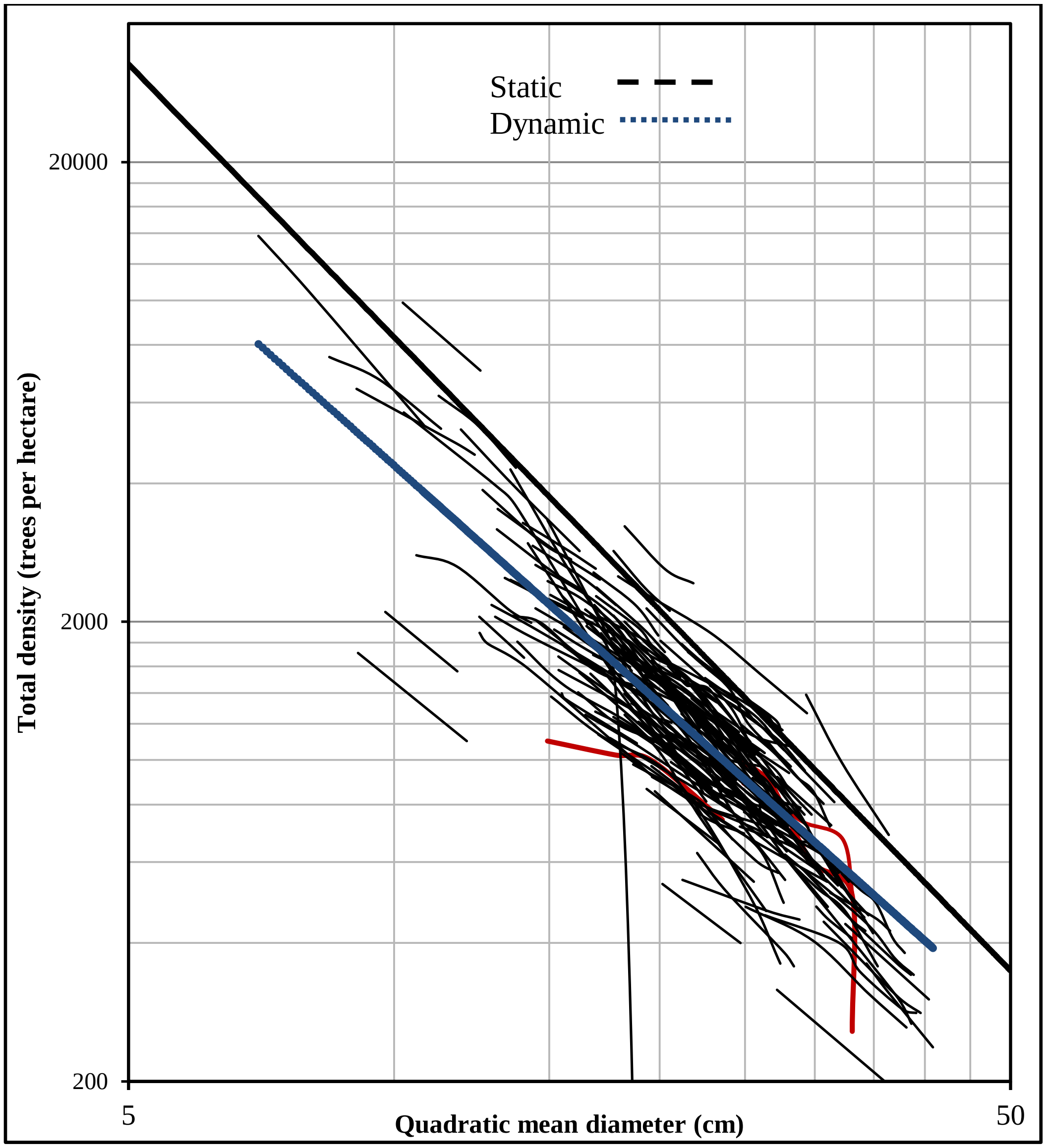


Figure 2.3 The static (black dashed-line) and average dynamic (blue dotted-line) maximum diameter-density relationships of boreal mixed stands as calculated by SFF regression (model 2.7-no covariates) and mixed models (model 2.10-no covariates), respectively. Parameter estimates are provided in Tables 2.2 and 2.4. Size-density trajectories of PSPs are shown. Plots that fit the non-linear model (model 2.9) are shown in dark red and plots that fit the linear model are shown in black.

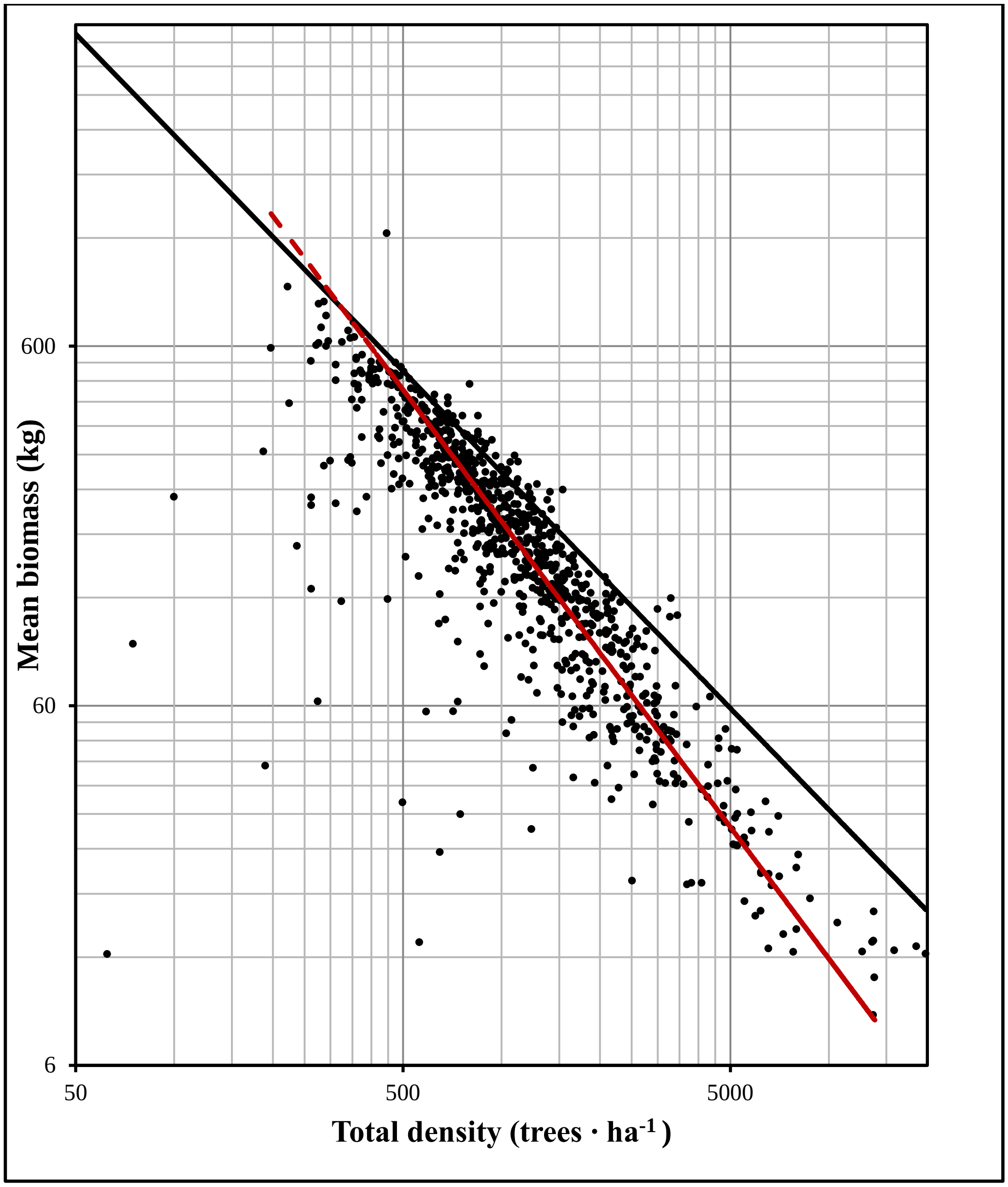
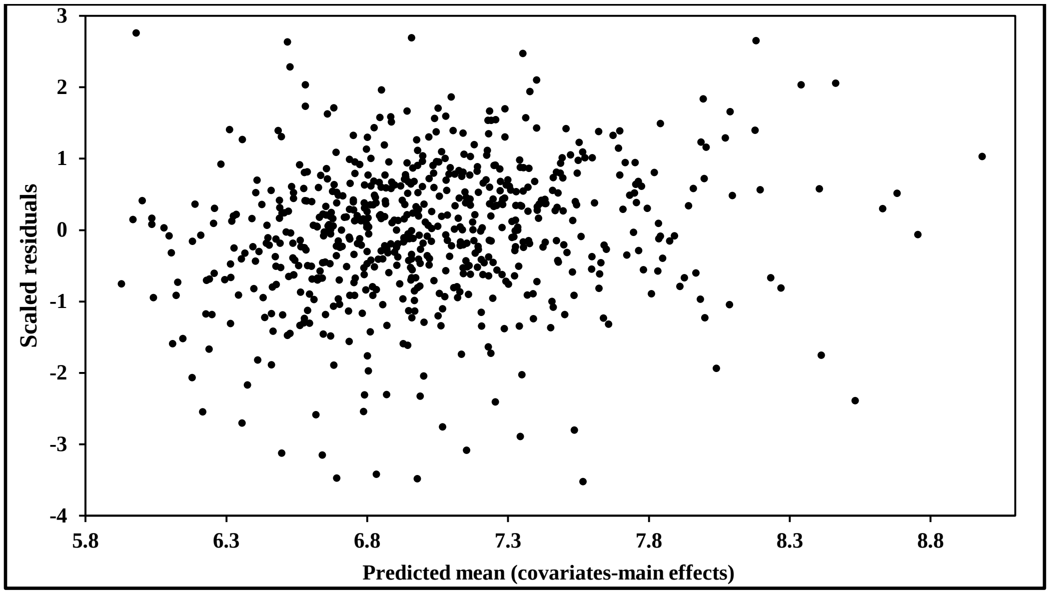
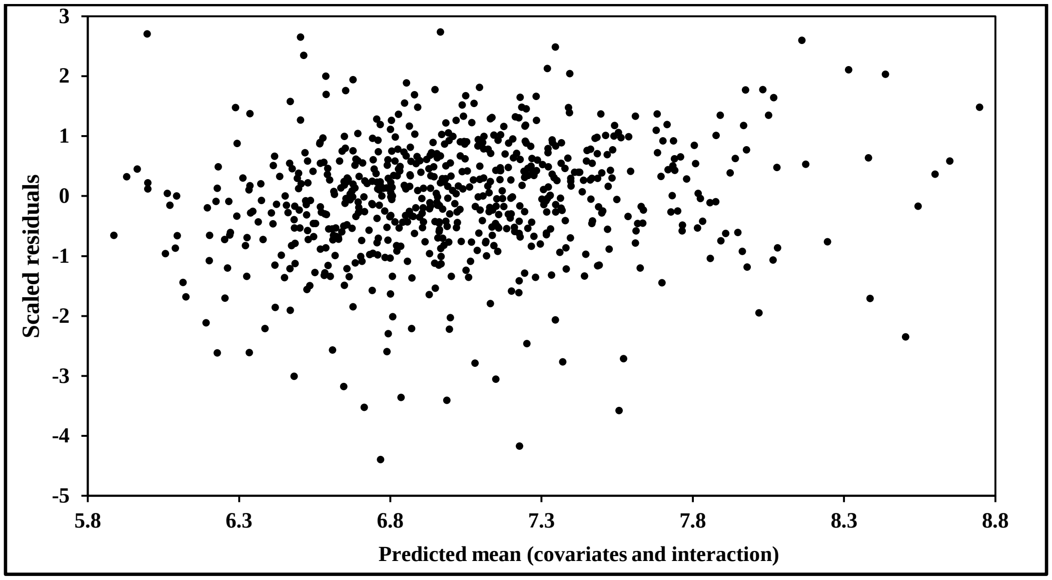


Figure 2.4 Maximum mean tree biomass-density relationships for boreal mixed stands of *Populus tremuloides* Michx. (Trembling aspen) and *Picea glauca* (Moench) Voss. (White spruce) in western Canada. The static limit (continuous line) is given by equation 2.8- model with no covariates. The dynamic line (red dotted line) was obtained with equation 2.11- model with no covariates. The black dots are observations used to fit the static upper limit.



(a)



(b)

Figure 2.5 Scatter plots of residuals versus predicted means for the mixed-effects model (equation 2.10) for estimating MSDR dynamic thinning line based on Reineke's equation; (a) equation with covariates- main effects only, and (b) equation with covariates- main effects and interactions.

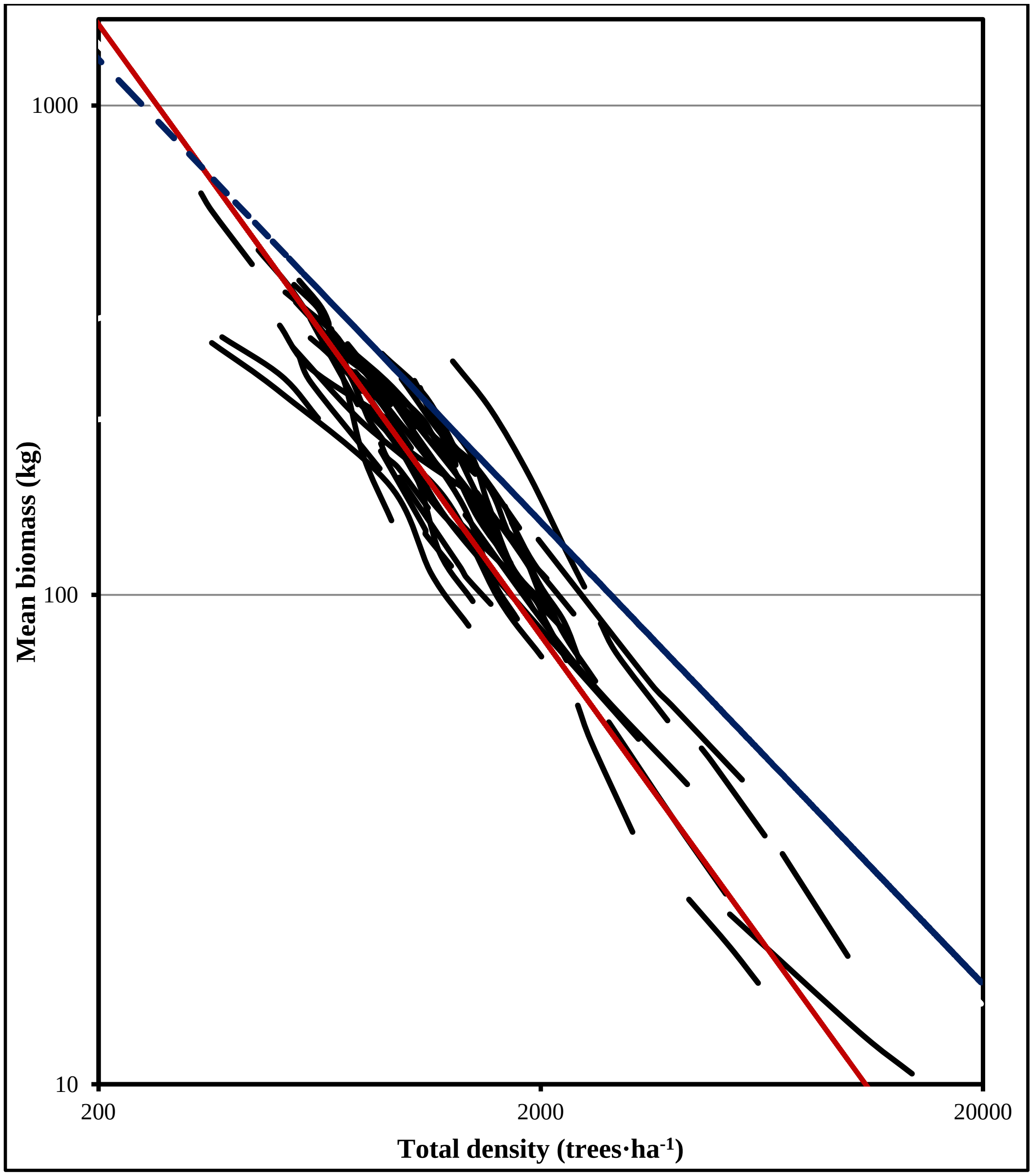
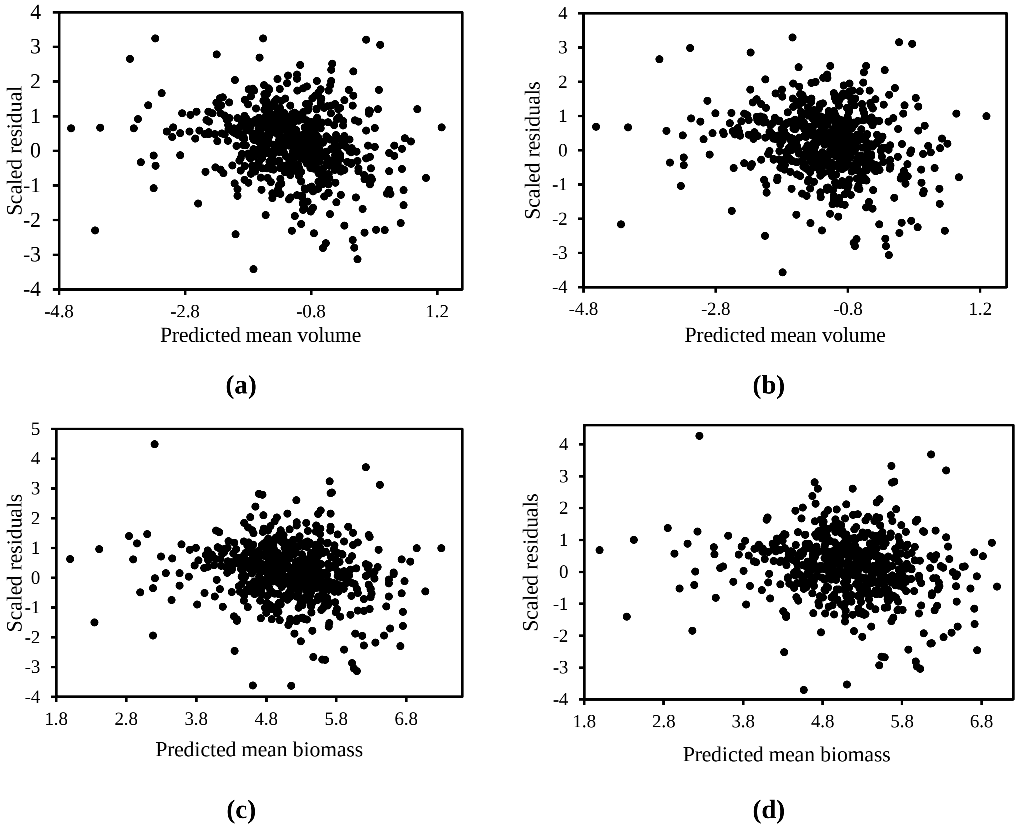


Figure 2.6 Illustration of maximum biomass-density lines with respect to self-thinning boreal mixed stands of trembling aspen and white spruce in western Canada. The static thinning line (blue line) was obtained with equation 2.8 with covariates and interactions (see Table 2.3 for parameter estimates). The dynamic thinning line (red line) was obtained with equation 2.11 with covariates (see Table 2.5 for parameter estimates).



(a) **(b)**

(c) **(d)**

Figure 2.7 Residuals for predicted mean tree size-density relationships as obtained with mixed models for equation 2.11. Mean volume model with no covariates (a), model with covariates (b); mean biomass model with no covariates (c), and model with covariates (d).

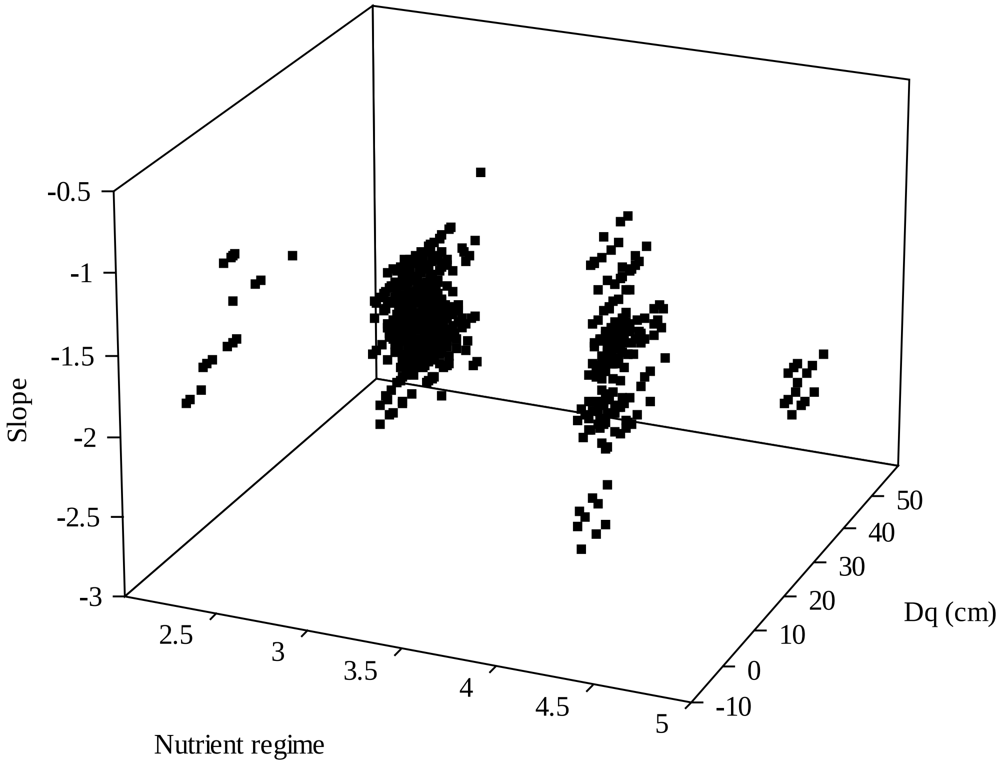


Figure 2.8 Illustration of the variation on individual plot slope values with changes in nutrient regime and quadratic mean diameter (D_q, cm) according to results of model 2.9 fit with mixed models (density-diameter relationship).

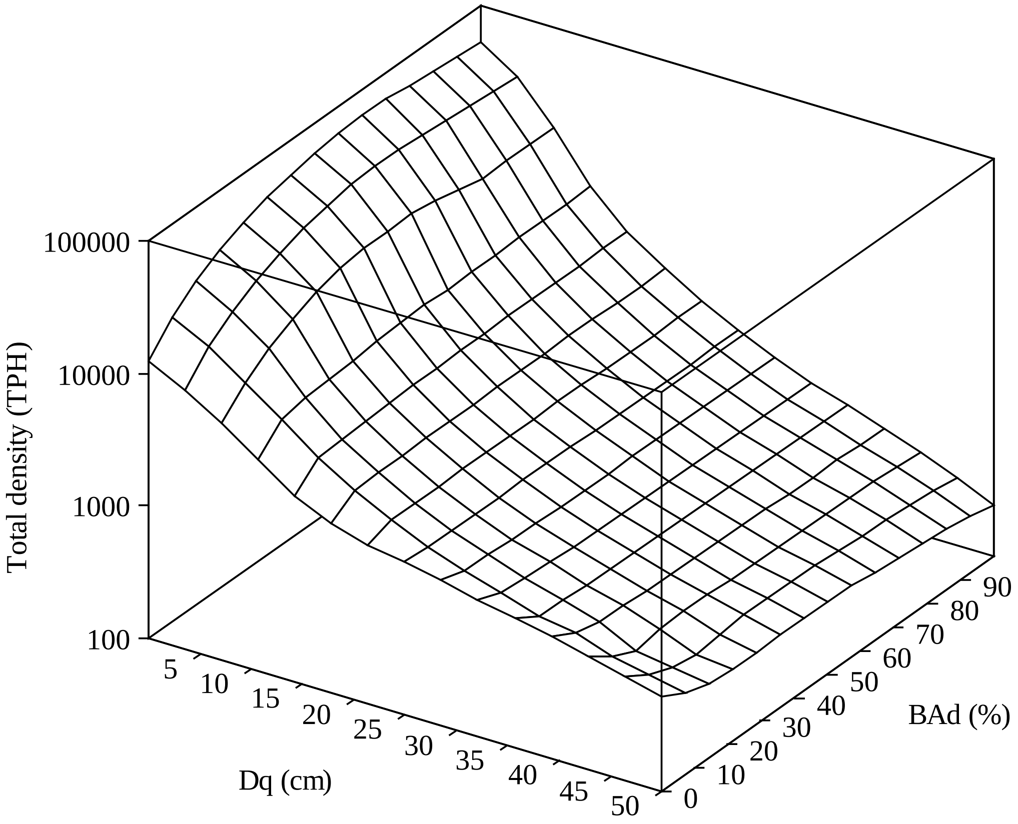


Figure 2.9 Three dimensional graph of the static line for maximum total density (trees per hectare) over quadratic mean diameter (D_q) and percent of basal area in deciduous species (BAd) as obtained with SFF regression for model 2.**7** with covariates. See Table 2.2 for parameter estimates.

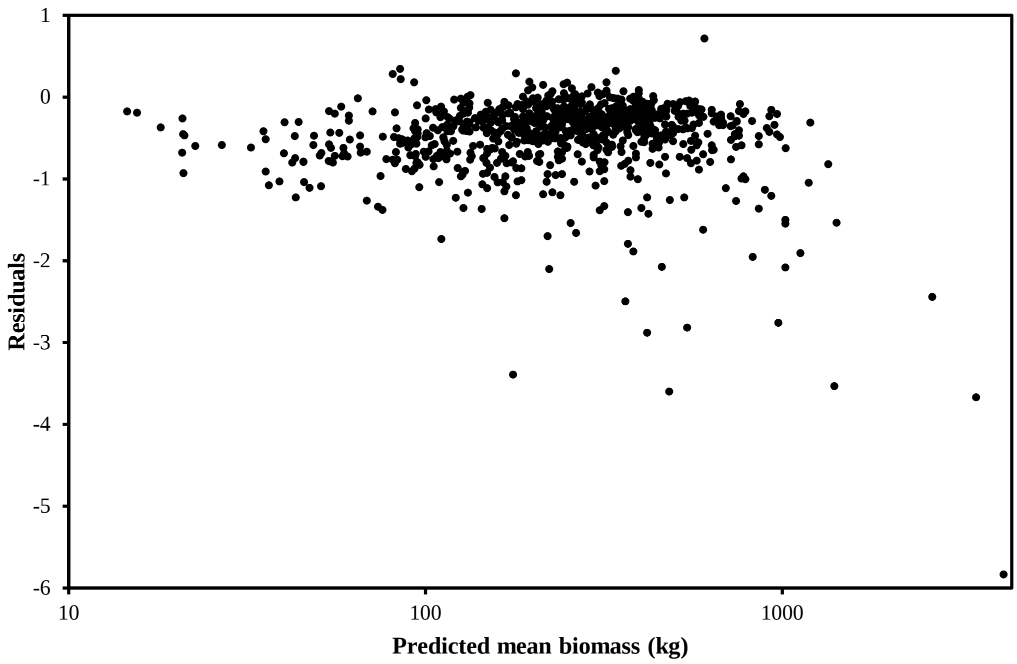


Figure 2.10 Scatter plot of residuals versus predicted mean for the stochastic frontier function regression (equation 2.8-main effects only) used to estimate the mean biomass-density static thinning line for boreal mixed stands of *Populus tremuloides* Michx. (trembling aspen) and *Picea glauca* (Moench) Voss. (white spruce) in western Canada.

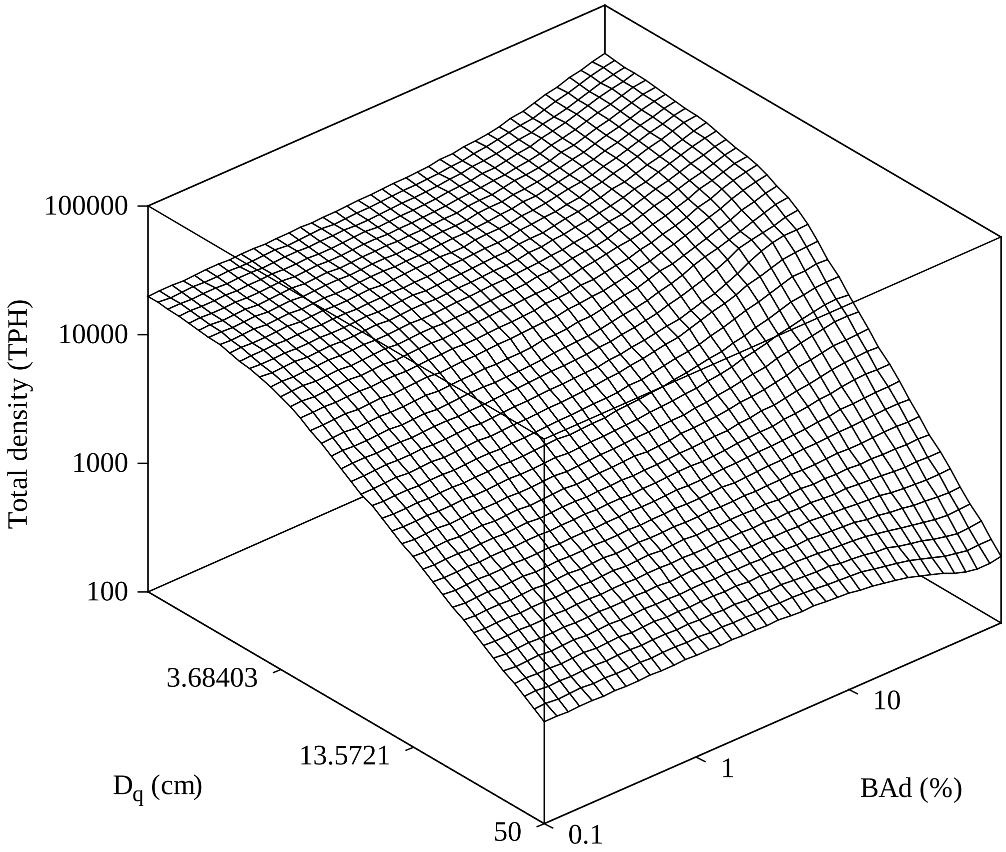


Figure 2.11 Estimated diameter-density surface for pure and mixed stands of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.) in western Canada based on results for equation 2.7 fit with stochastic frontier function regression. See table 2,2 for parameter estimates

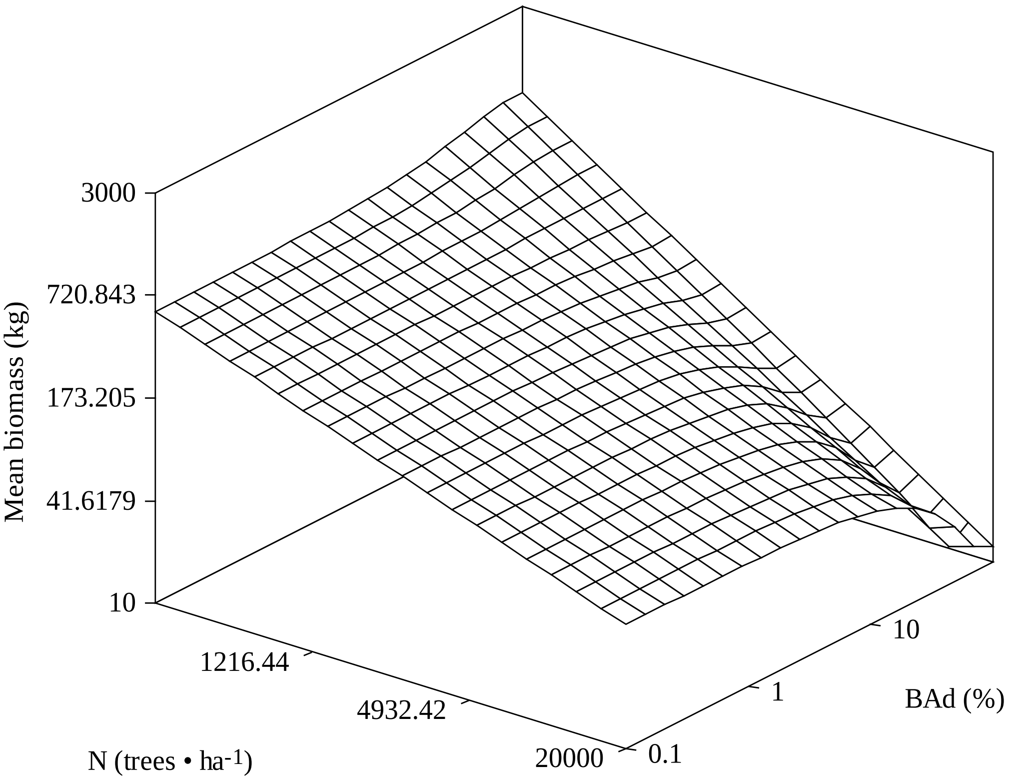


Figure 2.12 Estimated mean tree biomass-density surface for boreal trembling aspen and white spruce mixed forests in western Canada growing in a medium soil nutrient regime, as obtained for the static thinning line by stochastic frontier function regression, equation 2.8 with covariates and interactions. See Table 2.3 for parameter estimates.

Chapter 3 Understory light in boreal mixedwoods in relation to stand structure and composition

3.1 Introduction

Canopy structure and species composition have a significant influence on availability of important resources in the understory. The supply of water and soil nutrients is regulated to some extent by the dominant overstory trees and shrubs (Bartemucci *et* al., 2006). Overstory canopy composition also has a significant role on the interception of solar radiation (Hardy *et* al., 2004), on litter composition and on leaf morphology (Hart and Chen, 2006). Light levels in the understory are strongly affected by overstory cover and species composition (Lieffers and Stadt 1994; Hart and Chen 2006), thus affecting understory plant communities (Bartemucci *et* al. 2006; Hart and Chen 2006). These effects on environmental conditions have major effects on establishment and growth of tree regeneration (Hart, 1988). Although air temperature, soil moisture, air humidity, and other characteristics of the understory microclimate are also influenced by canopy structure and composition (Sharpe *et* al., 1996), these are strongly correlated with light regimes (Barkman, 1992), and variation in understory light is commonly used to explain changes in microclimate in understory environments (Barbier *et* al., 2008).

Intensity and direction of light in forests change through time (diurnally and seasonally) due to earth's movements in relation to the position of the sun, and additional changes and variation in cloud cover result in variation in light reaching the upper canopy of forest stands. Phenological changes in leaf area index (most notably in deciduous stands) add further to seasonal variation in understory light levels (Lieffers *et* al., 1999). Photosynthetically active radiation (PAR) is the light essential for plant photosynthesis, with wavelengths between 380-710 nanometers (nm) (Canham *et* al. 1990; Messier *et* al. 1998). The amount of light that actually penetrates the canopy and reaches the forest floor, mostly diffuse light, is further affected by trees and other vegetation due to variation in sizes, crown depth and leaf area (Lieffers *et* al. 1999).

Light levels in the understory can be influenced through manipulation of trees and other vegetation that absorbs or reflects the incoming sunlight (Lieffers *et* al., 1999). Even though sunlight might be considered an unlimited resource in an open environment, it is one of the most limiting resources for development and growth of understory trees and other plants (Jennings *et* al., 1999). Hence, indicators of density, canopy composition, and light interception are usually the most used stand characteristics to explain and/or to predict the establishment and development of tree regeneration (Canham *et* al. 1994; Nyland 2002; Smith *et* al. 1997).

Trembling aspen is a pioneer species which quickly re-occupies boreal sites after major disturbances (*i.e.* fire, clearcutting), due to its abundant regeneration by root suckering and its rapid early height growth (Chen and Popadiouk, 2002). A pure aspen stand without silvicultural intervention can achieve densities of over 200,000 individuals per hectare sprouting from root suckers, dropping to less than 25,000 stems/ha by age 6 because of self-thinning and to less than 10,000 by age 10 (Peterson and Peterson, 1995). Along with the high tree densities, there is also a rapid increase of leaf area in young aspen stands (DesRochers and Lieffers, 2001). Leaf area is perhaps the most important variable that affects light transmission, and one-sided leaf area index (LAI) values of 4 $m^2 \cdot m^2$ or even higher (6 $m^2 \cdot m^2$) have been estimated for 9-year old aspen stands (Pinno *et* al. 2001). Stands that show LAI of this magnitude transmit approximately 5 % or less of above canopy light (Lieffers *et* al., 2002), which could be problematic for seedlings of species such as spruce since their mortality is expected when light transmitted to the understory is less than 10 % (Lieffers and Stadt 1994; Wright *et* al. 1998).

In boreal mixed stands, competition for light is thought to be one of the most important ways by which deciduous species such as trembling aspen compete and influence survival and growth of understory conifers, mainly white spruce (Burton 1993; Comeau *et* al. 2003; Filipescu and Comeau 2007b). However, as a consequence of the decline in aspen density with stand age, more variation in leaf area is anticipated with reductions in aspen basal area (Pinno *et* al., 2001), which will be beneficial for understory spruce and other shade tolerant species. Mixtures of trembling aspen and white spruce will tend to develop a stratified canopy as stands develop, even if both species regenerate at the same time (Pritchard, 2003).

It is also suggested that light is perhaps one of the key driving factors of self-thinning, with its effects being reflected in either the position or the slope of the self-thinning line (Hutchings and Budd 1981; Westoby and Howell 1981;

Lonsdale and Watkinson 1982; Hutchinson 1983), although other causes are also considered to be important (Burkhart, 2013). In single species stands, mortality of individuals is primarily determined by their size with respect to their neighbours (Westoby 1984; Weiner 1990), and density-dependent mortality can result from carbon starvation due to a lack of sufficient light for smaller trees to maintain a positive carbon balance (Weiner, 1990). However, in a two-species mixture, survival of individuals may be more strongly influenced by traits of the species (*e.g.* shade tolerance) the individual belongs to rather than to its size with respect to others (Westoby, 1984). Differences in physiological and morphological characteristics could lead to differences in self-thinning patterns, particularly if a mixture is composed of species that contrast in key characteristics, such as shade tolerance (Westoby, 1984). These differences enable shade tolerant species to have a net carbon gain and survive in shaded environments (Niinemets and Valladares, 2006), notwithstanding their smaller size relative to individuals of the other species.

A number of studies assessing the competitive effects of overstory aspen and other deciduous species on understory regeneration of conifers have demonstrated that certain stand attributes and simple distance-independent competition indices are useful for explaining and predicting understory light (MacIsaac and Navratil, 1996); in particular, stand basal area and total density have been shown to be as effective as other more complicated indices in predicting understory light in boreal forests (Comeau *et* al. 2003, 2006; Filipescu and Comeau 2007a; Stadt *et* al. 2007). Vales and Bunnell (1988) showed that

Reineke's stand density index (SDI) (Reineke, 1933) and sum of tree diameters are more effective and better predictors of transmittance than the number of trees and basal area for conifer forests in British Columbia. Other studies have also shown the usefulness of basal area, SDI and/or relative density measures in predicting understory light in forest ecosystems (Messier *et* al. 1998; Pinno *et* al. 2001; Hale 2003; DeLong *et* al. 2005; Hale *et* al. 2009). Stadt and Lieffers (2005) indicated that PAR transmission through the understorey can be simply modeled in boreal forest using Beer's Law and one empirical coefficient linked to either leaf area index (LAI) or vegetation cover; these models appeared to be more effective than other more complex distance-dependent models.

Filipescu and Comeau (2007a) evaluated the effectiveness of a number of competition indices for predicting understory light in mixedwood stands of Alberta and Saskatchewan, Canada ranging from 13 to 54 years old. They demonstrated that distance-independent competition indices based only on diameter or basal area can be equally or even more effective than other more complicated competition indices (*i.e.* distance-dependent indices). There is no information on whether Reineke's SDI, alone and in combination with competitor's identity, is as effective as these distance independent indices for predicting light in boreal mixedwoods.

In this Chapter, I examine light availability in mid-rotation and mature boreal pure and mixed natural unmanaged stands, comprised mainly of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) in Alberta, Canada. I evaluate the usefulness of several selected stand attributes, including SDI, for predicting understory light in these stands, including examining whether composition and identity of overtopping competitors (deciduous *vs* conifer) are important in explaining variation in understory light regimes. Stand attributes evaluated include basal area, total density and density by species, as well as stand density index (SDI) calculated based on the dynamic maximum size-density relationships developed for these stands (Reyes-Hernandez *et* al., 2013).

3.2. Methods

3.2.1 Study sites and plot selection

This study was conducted on selected permanent sample plots (PSPs) established in pure aspen, pure white spruce and mixed stands of both species in the Boreal Forest Natural Region of Alberta, Canada. The Central, the Dry, and the Northern Mixedwood ecological sub-regions were included (Beckingham and Archibald 1996; Forest Management Branch 2005). PSP establishment and re-measurement followed rigorous standards, although PSP size, establishment date, and remeasurement intervals are variable (Forest Management Branch, 2005). The majority of PSPs are 0.10 ha in size, with all three species taller than 1.3 m or larger than 2.5 cm in diameter at breast height tagged and measured at time intervals between 3 to 10 years. Data from these PSPs were compiled to calculate several stand attributes as described in Chapter 2 of this Dissertation. A group of approximately one hundred plots was pre-selected from the whole dataset for collection of relevant additional data (see sections 3.2.2 and 3.2.3), based on the following considerations:

1) Composition: pure stands were considered as those sites with 80% or more of total basal area comprised by the leading species (either trembling aspen or white spruce); for mixed stands, any percent combination of basal area for the two species of interest was allowed but plots with more than 10% of basal area in species other than aspen and white spruce were removed.

2) Only plots that had been remeasured within the last 5 to 8 years of the planned field data collection season (years 2007-2008). And

3) Only sites with good summer access were utilised.

The initial goal was to locate and measure 50 stands over the full range of a density-size-stand composition matrix for mature stands. The final set of plots sampled was comprised of 55 PSPs, including 19 pure aspen, 22 mixed and 14 pure spruce stands. A summary of the attributes for the selected plots is presented in Table 3.1. These PSPs were visited during the summers of 2007 and 2008, and additional data (hemispherical photography and LAI-2000 readings) were collected to determine plant area index (PAI) (as a surrogate of leaf area index, LAI), light absorption/transmittance (DIFN), and other stand variables as described in 3.2.2 and 3.2.3.

3.2.2. LAI-2000 plant canopy analyzer (instantaneous DIFN and PAI)

Estimations of transmittance (diffuse non-interceptance - DIFN) reaching a given point in the forest and plant area index (PAI) were obtained by processing field measurements taken with LAI-2000 plant canopy analyzers (Li-COR Inc., Lincoln, Nebraska).The LAI-2000 optical sensors measure the attenuation of diffuse sky radiation at five zenith angles (0-13°, 16-28°, 32-43°, 47-58°, and 61-74°); typically, five numbers from below canopy readings are paired with readings taken in the open, and five values of canopy transmittance are calculated (LI-COR, Inc.). LAI-2000 sensors provide reliable estimates of light transmittance through the growing season (Gendron *et* al., 1998). Indeed, strong correlations have been reported between DIFN and the total light transmitted through the growing season in forest canopies (Lieffers *et* al. 1999; Voicu and Comeau 2006).

Below canopy measurements were taken at 5 points inside each PSP with a LAI-2000 unit by using a 180$^{\mathrm{o}}$ view restrictor and orientating the sensor in two directions (west in the morning and east in the afternoon), ensuring that recording of readings was opposite to the sun’s position and that no direct sunlight reached the sensor. Four out of five of these points were located 5 m away from the plot center, each in one of the 4 cardinal points (north, east, west and south) with the fifth point at plot center. These below canopy readings were obtained with the sensor located at 1.7 m above the ground at each point. A second LAI-2000 device was synchronized with the below canopy unit and mounted on a tripod in a nearby open site to collect measurements every 30 seconds. A view restrictor

(180°) was also used placed on the open sky sensor, and the orientation of both sensors was matched for each set of readings (west in the morning and east in the afternoon). Calibration of both sensors was done at the beginning of the field season, with weekly checking performed to ensure that the sensors were properly cross-calibrated. All readings were processed using the FV-2000 software ® publicly available online. The portion of the sky belonging to the fifth ring of the sensor was ignored (below 31.9° above the horizon) and only values from the first four rings were used for further calculations. Averages of the ten DIFN and ten PAI values calculated for each PSP (*i.e.* five points in two directions) were used in further analysis.

3.2.3 Hemispherical photography

Hemispherical photographs were taken during July and August 2008 at each of the five points described in 3.2.2, using a Nikon Coolpix 990 camera equipped with a Nikorr 8 mm f/2.8 fisheye lens. The top of the camera was oriented to the north after being mounted on a tripod at approximately 170 cm above the forest floor and levelled, and photographs were taken at this point. Hemispherical photographs were taken under completely overcast conditions or when the sun was below the horizon to help reducing glare from direct sunlight, and to improve contrast between sky and foliage (Canham, 1998). Although literature often suggests slight overexposure for film cameras, the best images were obtained for this study using automatic settings (no adjustment to over or underexposure) on the Coolpix (Comeau, P.G.; personal communication).

The SLIM software (Comeau *et* al., 1998) (http://www.ualberta.ca/~pcomeau/Light_Modelling/Lite_and_slim_intro.html) was used to process the hemispherical photographs. Batch processing was performed with SLIM applying the automatic Ridler clustering method (Ridler and Calvard 1978; Jonckheere *et* al. 2005) to set a threshold for each hemiphoto. Open sky PPFD measurements can be utilized in SLIM in place of model estimates. Light intensity (PAR) smart sensors (S-LIA-M003) attached to HOBO® weather station data loggers (Onset Computer Corporation, 2001-2011) were installed in openings at five locations across the geographic range of stands in which hemispherical photographs were taken. These smart sensors have a measurement range of 0 to 2500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ over wavelengths from 400 to 700 nm (Onset Computer Corporation, 2001-2011). Hourly average PAR values recorded for each sensor were used to provide open sky PAR values used for processing of hemispherical photos to calculate below canopy light. Below canopy light (beam, diffuse and total transmittance) and gap fraction were calculated with SLIM and utilised in further analyses.

3.2.4 Data analysis

Scatter plots and other graphs were constructed using Microsoft Excel® 2013 and TableCurve 3D ver. 4.0. All statistical analyses were completed using SAS® ver. 9.2 for windows (SAS Institute, 2010). Analysis of correlation was first used in order to discriminate among the entire set of potential descriptor variables. Logarithmic transformation of transmittance (DIFN) and below total light data was performed before the final regression analyses. Stand attributes such as density, quadratic mean diameter, basal area, sum of diameters, composition (% of basal area in deciduous species), Reineke's SDI, and average height, were calculated from plot data and tested as independent variables to explain the variation in transmittance (DIFN) and in below total light. Table 3.1 summarizes attributes of the plots used in this study.

Linear regression was used to assess relationships between DIFN and below total light (dependent variables) and the various stand attributes described in Table 3.1. Models were compared using adjusted R^2 and distribution of residuals. Combinations of stand variables including those detailed in Table 3.1 (and in Table 3.3) were assessed in the models for DIFN and below total light. One of the objectives was to test for effects of competitor identity on understory light. Therefore, all explanatory variables were tested both as a single total stand value and as separate deciduous and conifer components.

Some of the independent variables showed significant linear relationships among them; hence the inclusion of each of them was assessed through variance inflation factor analysis (VIF). VIF analysis measures the amount of the variance of the estimated regression coefficients that is inflated as compared to when the predictor variables do not have a linear relationship (*i.e.* collinearity) (Kutner *et* al., 2005). When a group of independent variables showed a VIF in excess of 10 it was taken as an indication that multicollinearity was overly influencing the least squares estimates (Kutner *et* al., 2005). Then, the least significant variable (based on partial adjusted R^2 coefficient) was removed from the set of independent variables in the model under evaluation, although it was still considered for assessment in other models.

The final candidate models were ranked according to adjusted R^2 values and mean square of residuals. Graphs of residuals *vs* predicted values were also constructed for the best two models explaining understory light.

3.3 Results

3.3.1 Understory light (DIFN) and plant area index (PAI)

Values of understory light availability (diffuse non-interceptance, DIFN) and plant area index (PAI) calculated from LAI-2000 readings are presented in Table 3.2. Average DIFN at 1.7 m height from the forest floor ranged from 3 to 59 %, with an overall average of 22 % (S.D. = 11.1). Plant area index ranged from 1.0 to 5.8 $m^2 \cdot m^2$, with an average of 2.7 $m^2 \cdot m^2$ and standard deviation of 0.86 (Table 3.2). A number of stand attributes showed significant correlations with DIFN and PAI (Table 3.3). Scatter diagrams were constructed to show the variability of both characteristics as related to relevant independent variables (Figures 3.1 and 3.2); these variables were tested for in alternative regression models seeking to explain variation in diffuse non-interceptance and results are shown in section 3.3.3.

In general, light availability increases as deciduous basal area increases (in % and in m^2/ha) (Fig 3.1a, 3.1c), and decreases as the sum of diameters of spruce and total density of the stand increase (Fig 3.1b, 3.1d); low values of DIFN are observed in dense stands (Fig 3.1d), with its lowest value registered in a stand with total density over 4800 stems per hectare. The lowest transmittance is observed in a pure spruce stand (about 0.01% of basal area in deciduous) with less than 5% of light available at 1.7 m height from the forest floor; higher values of DIFN are observed for pure aspen stands (from 10- 50% of light available) than for pure spruce stands. The highest DIFN values are observed in two mixed plots (38 % and 80 % of basal area in deciduous), with availability of understory light of 50 and 59 %, respectively. The apparent outlier in Figures 3.1d and 3.2d was subject of evaluation in the regressions where it appeared to be influential. Regression models were found to be unaffected by including or not this plot and was included in the final analyses.

Decreases in plant area index (PAI, $m^2 \cdot m^2$) are observed for stands with large quadratic mean diameters and with high occurrence of deciduous species (percentage of basal area) (Figure 3.2a, 3.2c). In general, lower PAI values are observed in pure deciduous than in pure spruce stands, whereas higher values of PAI are recorded in mixtures close to 50 % spruce -50 % deciduous (Figure 3.2c). Mixed stands show higher PAI values than pure deciduous and pure white spruce stands, although an unexpected high PAI value is observed for a pure spruce plot (PAI = 5.82 $m^2 \cdot m^2$). PAI increases with increases in total density and as the sum of diameters of spruce increases (Figs. 3.2b, 3.2d, respectively).

3.3.2 Below canopy light and gap fraction (from hemispherical photography)

Below canopy PPFD levels were variable among the stands sampled (Table 3.2). A maximum of 28.4 % out of the total amount of direct light that hits above canopy reaches the understory, with average of 6.1 % and minimum of 0.2 %; between 21.5 to 54.9 % of the total diffuse light hitting above canopy actually reaches the understory at 1.7 m above ground level, with an average of 33.36 %. Some stand attributes showed a significant correlation with below diffuse and below total light (Table 3.3.). Scatter diagrams for below total light in relation to the most relevant stand attributes are presented in Figure 3.3. Logarithmic transformation of light data was necessary before the regression analysis between below light and stand attributes was performed (section 3.3.3).

The estimated below total light increases as the percentage of deciduous basal area, deciduous basal area, or deciduous SDI increase (Figs 3.3a, 3.3b and 3.3c, respectively). A reduction in total light below canopy is observed as the sum of diameters of white spruce increases (Fig 3.3d). When separating below canopy light into diffuse and direct components, a positive relationship with stand composition is observed for both components (Figs. 3.4a and 3.4b). Direct light appears to be more variable than diffuse light for pure or almost pure aspen stands (Fig 3.4a, 3.4b). A negative correlation is evident for below diffuse and below direct light with sum of diameters of spruce (Figs 3.4c and 3.4d). In addition, a steeper decrease in diffuse light than in direct light is observed with increasing sum of diameters of spruce.

Gap fraction also showed significant correlations with various stand attributes (Table 3.3; Figure 3.5). Higher gap fractions are observed as the percentage of deciduous basal area and as deciduous SDI increase (Fig 3.5a, 3.5b); whereas a negative correlation between gap fraction and both spruce density and the sum of diameters of spruce is observed (Fig 3.5c, 3.5d). Gap fraction also has a significant positive correlation with below diffuse and below total light (r=0.89, p<0.0001 for below total light with GFR; r=0.95, p<0.0001 for below diffuse with GFR), and with stand composition (Table 3.3).

The different indicators of understory light availability also show strong correlations with gap fraction (Figure 3.6), with all of them being positive. High correlations were found between gap fraction and below diffuse light (r=0.95, p<0.001), below total light (r=0.89, p<0.001), or DIFN (r=0.66, p<0.0001). The weakest but still significant correlation was recorded between gap fraction and below direct light (r=0.32, p<0.015). Scatter plots for these correlations are shown in Figure 3.6. Significant positive correlations were also observed for DIFN with below diffuse light (r=0.68, p<0.0001), below total light (r=0.68, p<0.0001), and below direct light (r=0.41, p<0.003) (Figure 3.7).

3.3.3 Models to predict understory light

Significant relationships (p<0.05) were found between understory light (transmittance –DIFN and below total light) and total density, sum of diameters of spruce, quadratic mean diameter, percentage basal area deciduous, SDI spruce, and spruce density. Significant models for explaining DIFN as a function of these stand attributes are presented in Table 3.4; significant models for below total light as a function of stand characteristics are presented in Table 3.5. Distribution of residuals *vs* predicted values for the two best models explaining DIFN are shown in Figure 3.8, whereas Figure 3.9 shows the distribution of residuals *vs* predicted values of below total light for the two models with best fit. The performance of the best models in explaining understory light is illustrated in Figure 3.10. The best model for explaining variation in DIFN is shown in Figure 3.10a, whereas Figure 3.10b shows how below total light model behaves. Both surfaces were built with the sum of spruce diameters and total stand density as independent variables.

It is noteworthy that none of the independent variables tested and finally selected was able to explain either more than 26 % of the total variation in transmittance (Table 3.4), or more than 28% of the variation in below total light (Table 3.5) found in these plots. Although some studies have shown that average stand height or sum of heights can be good predictors of light availability (Messier *et* al. 1998; Lochhead and Comeau 2012), both spruce and aspen average height showed poor performance as explanatory variables in the regression models for DIFN and below total light, either alone or in combination with other stand attributes (Tables 3.4 and 3.5). Results indicate that sum of diameters of spruce and total stand density (number of trees per hectare) are the best independent variables for estimating light levels in these stands.

3.4 Discussion

Results presented in this study are consistent with previous observations in similar ecosystems (Lieffers and Stadt 1994; Messier and Puttonen 1995; Constabel and Lieffers 1996; Messier *et* al. 1998): understory light regimes are highly variable in boreal forests. Variation in understory light has been found to be the result of structural and stocking differences related to the successional status of the stands (Canham *et* al., 1994). This is suggested by the effects of stand density, stand composition and tree size (quadratic mean diameter and sum of diameters of white spruce) on the understory light regimes of these plots.

The majority of natural mixedwood stands in northern Alberta have originated after fire (Rowe and Scotter, 1973). Although this may lead to a variety of successional pathways (Lieffers *et* al., 1996a), the initial stages of fire-origin boreal mixedwoods are characterized by an abrupt decline in understory light regimes due to a steep increase in leaf area as a result of high aspen densities (Pinno *et* al. 2001). After canopy closure is achieved, understory light regimes increase as a stand ages and aspen leaf area index declines (Lieffers and Stadt 1994; Constabel and Lieffers 1996). This decline in aspen leaf area as well as the development of crown shyness (Long and Smith, 1992) result in an increase of light transmission, with a resulting reduction in competition from aspen to understory trees as the stand develops (Lieffers *et* al., 2002).

Intermediate stages in boreal mixedwoods may be characterized by a gradual increase of white spruce in the middle and upper canopy and by a reduction of deciduous species in the previously aspen-dominated stand (Lieffers *et* al., 1996b). In these mid- and late-successional boreal stands, decreases in understory light transmission values have been previously reported along with a decrease in the percentage composition of trembling aspen and an increase in the amount of white spruce (Lieffers and Stadt 1994; Constabel and Lieffers 1996). Understory light transmission in white spruce-dominated stands can be between one half to one-tenth that of aspen dominated sites of similar size (Constabel, 1995).

It is surprising that neither total stand basal area nor aspen basal area were amongst the best predictors of understory light in the regression models that were tested. Indeed, both attributes were among the independent variables that showed the poorest explanatory power (Tables 3.4 and 3.5). A number of studies performed in boreal mixed stands have shown that either stand basal area or aspen basal area are as good or better predictors of understory light than other more complex indices or than distance-dependent indices (MacIsaac and Navratil 1996; Filipescu and Comeau 2007a). Indeed, aspen basal area is suggested as a reliable predictor of understory light transmission at a site level, being more desirable as a general predictor since it incorporates both diameter and density, and may be applicable to a wide variety of mixedwood sites (Filipescu and Comeau, 2007a). However, these previous studies in western Canada boreal forests were focussed in much younger stands (1-15 years old), where trembling aspen was still vigorous and had not culminated its growth. Pure and mixed stands that were included in my study are mostly mature and old, most likely with mature and old trembling aspen trees that, according to my results, are having much less influence on understory light.

It is also unanticipated that, although a positive correlation was found between DIFN and below total light with average aspen height (Table 3.3), this correlation was not significant and inclusion of aspen height in the models did not represent any improvement in performance (Tables 3.4 and 3.5). Positive effects of dominant tree height on understory light levels have been previously reported for boreal mixed stands in eastern Canada (Messier *et* al. 1998). This occurs when greater average stand height leads to reduction in gap fraction (Pritchard, 2003) and associated reductions in understory light levels. This might be the case for stands with a higher proportion of white spruce, as it appears to be indicated by a significant negative correlation between average spruce height and below total light (Table 3.3.).

A portion of the variability in understory light may result from measurement errors due to heterogeneous conditions frequently found in mixed or complex stands (Lochhead and Comeau, 2012). However, it is likely that the fairly low coefficients of determination of the models obtained in this study (*i.e.* low adjusted R^2) are also due to other reasons. The lack of information of the spatial distribution of trees (Canham *et* al. 1994; Courbaud *et* al. 2003; Gersonde *et* al. 2004) and a failure to consider leaf area distribution in the tree canopies (Franklin and Van Pelt, 2004) are two of the most common reasons for failing to explain variation in understory light in stands of trees.

Under clear-sky conditions, short-wave radiation from the sun hits the earth either as direct beam radiation or as indirect scattered or diffuse radiation from the sky. A fraction of each of these two types of radiation is reflected and lost to the sky and other portion is absorbed by a vegetative canopy when it is reached. The final quantity of light that reaches the forest understory is then comprised of the direct beam light (*i.e.* ‘sun-flecks’), the scattered direct light, the indirect or diffuse light from the sky, and the indirect or diffuse light reflected by stems and other elements (Reifsnyder *et* al., 1971). The patterns of spaces free of vegetation in the canopy or gaps, as well as the luminosity of the sky are the decisive factors affecting the amount of light that reaches the forest floor (Reifsnyder *et* al., 1971). In fact, the existence of gaps and clumping, which might be fairly common in mixed species stands of this age, increases the spatial variation in forest structure (Courbaud *et* al. 2003; Maguire *et* al. 2007) and will have significant influence on the amounts of diffuse and direct light ratios (Canham *et* al., 1994), as well as on the variability of understory transmitted light (Canham *et* al. 1994; Coates *et* al. 2003).

The use of basal area in models seeking to explain understory light originates from the rationale of using basal area as an approximation of leaf area. In fact, sapwood basal area, which is theoretically described with the “pipe model theory” using basal area (Shinozaki *et* al., 1964), is suggested to be closely related to leaf area. However, in mid-rotation and old boreal forests, such as many of the stands included in this study, a decline in aspen vigor would be anticipated, likely with a high incidence of aspen stem decay and other problems (Peterson and

Peterson, 1995). Consequently, as aspen grows the relationship between sapwood basal area and total basal area becomes weak, with a resulting disconnection between simple measurements of size and density with leaf area and light interception. Given the variability in vigor, health, and crown characteristics of aspen that are more than 90 years old, it is not surprising that there is a 'decoupling' of the leaf area-basal area relationship in these older stands. Consequently, relationships between simple external measures (*i.e.* diameter) and leaf area are probably not as effective as when the stands were younger, since changes in these allometric scaling relationships as the stands develop might be left unaccounted (Tobin *et* al., 2006).

Leaf area and/or leaf mass do not remain constant during stand development of forest communities, especially in natural forests (Kashian *et* al. 2005; Coomes and Allen 2007). Accordingly, changes in availability of understory light have been linked to variations in leaf area or leaf mass as previously stated (Lieffers and Stadt 1994; Constabel and Lieffers 1996; Lieffers *et* al. 2002). Shade-intolerant species such as trembling aspen transmit more light than shade-tolerant species due in part to their thinner crowns (Canham *et* al. 1994; Messier *et* al. 1998) and to other morphological differences with shade-tolerant species (Valladares and Niinemets, 2008). Mixtures of trembling aspen and white spruce might tend to develop a stratified canopy as stands grow even if the two species regenerate at the same time (Pritchard, 2003), and an increase in vertical stratification enables an increase of light penetration (Kitajima *et* al., 2005) during these later stages of stand development. As a consequence, increased variability in understory light might be expected with stand development in boreal mixedwood stands.

Low levels of understory light have been reported for boreal aspen stands even after most of trembling aspen leaves have fallen, that is, at the beginning or during the aspen leaf-off period, suggesting a strong effect of stem and branches on the variability of transmitted light (Constabel and Lieffers 1996; Comeau *et* al. 2009), especially in aspen dominated stands. Comeau *et* al. (2009) report understory light levels below 35 % in a 40 year old aspen stand during the leafless period. In my study, it would be difficult to determine what proportion of the understory light reduction is due only to leaves and what proportion is due to the shading from stem and branches. However, it is likely that a significant proportion of the variability of understory light is due to the effects of woody perennial tissue, and not only due to leaves. Estimation of understory light levels for these stands during aspen senescence would be helpful to clarify this matter.

From the applicability perspective, this makes it difficult to use simple stand measures (such as breast height diameter or basal area) as a reliable tool for estimating below canopy light in mid-rotation and older aspen or mixedwood stands such as those included in this study. The use of spatial information of trees and crowns, along with simple stand and aspen measurements, might help to increase the power and predictive ability of models in explaining understory light for these stands. The use of crown sizes and their distribution might provide more relevant biological information related to competition, for example the magnitude of the interception of light by subject trees (Filipescu and Comeau, 2007b), as well as the use of other resources.

The significant effects of species identity (*i.e.* the sum of white spruce diameters, white spruce density, and percentage of basal area in deciduous are significant, while aspen basal area and related variables are largely non-significant), suggest a small effect from trembling aspen and a larger effect of white spruce on understory light levels in these stands. The inclusion of stand density index-SDI (either separate for deciduous and spruce components or together) as an independent variable in the models did not provide a significant improvement in light models performance (DIFN, Table 3.4; below total light, Table 3.5). Given the poor performance of SDI in the models tested, the linkage between understory light and size-density relationships appears to be fairly weak for these stands.

3.5 Conclusions

Total stand density and competitor identity are important and significant independent variables for explaining and predicting understory light regimes of mid-successional and mature boreal mixedwood stands. Although SDI showed significant correlations with understory light, its use did not represent any improvement in model performance. Basal area was amongst the poorest predictors of understory light, either as a unique value (*i.e.* stand) or as separate components (deciduous and conifers) in these stands. Despite the significance of variables such as sum of spruce diameters and total stand density, the stand attributes explain less than 30 % of the variation in understory light. Given this variability it is not surprising that linkages to size-density relationships are weak. Perhaps the inclusion of spatial distribution of trees and crowns would be beneficial, as an attempt to increase the explanatory power of models seeking to explain below canopy light in these mid-rotation and mature boreal mixed stands. Also, estimation of light during the aspen leaf-off period would be helpful to clarify the effect of woody tissues on understory light availability. Also, further studies are needed to explore how relationships between leaf area of aspen and diameter change with age, vigor and other factors, and how this influences understory light levels in these stands.

3.6 References

Barbier, S.; Gosseling, F.; and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved- A critical review for temperate and boreal forests. For. Ecol. Manage. 254:1-15

Barkman, J. J. 1992. Canopies and microclimate of tree species mixtures. In: Cannell, M G.R.; Malcolm, D. C.; Robertson, P. A. (Eds). The ecology of mixed-species stands of trees. Blackwell Scientific Publications. Oxford, U.K. pp: 181-188

Bartemucci, P.; Messier, C.; and Canham, C. D. 2006. Overstory influences on light attenuation patterns and understory plan community diversity and composition in southern boreal forests of Quebec. Can. J. For. Res. 36:2065-2079

Beckingham, J.D.; and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Special Report No 5. Natural Resources Canada. Canadian Forest Service-Northern forestry Centre. Edmonton, AB.

Burkhart, H. E. 2013. Comparison of maximum size-density relationships based on alternate stand attributes for predicting tree numbers and stand growth. For. Ecol. Manage. 289: 404-408. doi:10.1016/j.foreco.2012.10.041

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

Canham, C.D. 1998. An index for understory light levels in and around canopy gaps. Ecology 69 (5):1634-1638.

Canham, C.D.; Finzi, A.C.; Pacala, S.W.; and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For Res. 24:337-349

Canham, C.D.; Denslow, J.S.; Platt, W.J.; Runkle, J.R.; Spies, T.A.; and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20:620-631

Chen, H, Y.H.; and Popadiouk, R. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. 10:137-166.

Coates, K.D.; Canham, C.D.; Beaudet, M.; Sachs, D.L.; and Messier, C. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. 186: 297-310.

Comeau, P.G.; Filipescu, C.N.; Kabzems, R. DeLong, C. 2009. Corrigendum to: Growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern B.C.-10 year results. For. Ecol. Manage. 257: 1629-1636.

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

Comeau, P. G.; Wang, J.R.; and Letchford, T. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine-fir following spacing. Can. J. For. Res. 33:1962-1973. doi:10.1139/x03-117

Comeau, P. G.; Macdonald, R.; Bryce, R.; and Groves, B. 1998. Lite: a model for estimating light interception and transmission through forest canopies.

User's manual and program documentation. Res. Br., Min. For., Victoria, B.C. Work. Paper 35/1998.

Constabel, A.J. 1995. Light transmission through boreal mixedwood stands. M.Sc. Thesis. University of Alberta. Edmonton, AB.

Constabel, A.J.; and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26:1008-1014.

Coomes, D.A.; and Allen, R.B. 2007. Mortality and tree-size distributions in natural mixed-aged forests. Journal of Ecology. 95:27-40.

Courbaud, B.; De Coligny, F.; and Cordonnier, T. 2003. Simulating radiation distribution in a heterogeneous Norway spruce forest on a slope. Agric. For. Met. 116:1-18.

DeLong, D.L.; Simard, S.W.; Comeau, P.G.; Dykstra, P.R.; and Mitchell, S.J. 2005. Survival and growth response of seedlings in root disease infected partial cuts in the interior cedar hemlock zone of southeastern British Columbia. For. Ecol. Manage. 206: 365–379.

DesRochers, A.; and Lieffers, V.J. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. Can. J. For. Res. 31:1012-1018

Filipescu, C.N.; and Comeau P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.N.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Forest Management Branch. 2005. Permanent Sample plot (PSP) field procedures manual. Alberta Sustainable Resource Development. Public Lands and Forest Division. Edmonton, AB.

Franklin, J.F.; and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. J. For. 102:22-28.

Gendron, F.; Messier, C.; and Comeau, P. G. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agric. For. Meteor. 92:55-70

Gersonde, R.; Battles, J.J.; and O'Hara, K.L. 2004. Characterizing the light environment in Sierra Nevada mixed conifer forests using a spatially explicit light model. Can. J. For. Res. 34:1332-1342.

Hale, S.E.; Edwards, C.; Mason, W.L.; Price, M.; and Peace, A. 2009. Relationships between canopy transmittance and stand parameters in Sitka spruce and Scots pine stands in Britain. Forestry 82: 503-513

Hale, S.E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. For. Ecol. Manage. 179:341-349.

Hardy, J.P.; Melloh, R.; Koenig, G.; Marks, D.; Winstral, A.; Pomeroy, J.W.; and Link, T. 2004. Solar radiation transmission through conifer canopies. Agric. For. Meteor. 126:257-270.

Hart, S.A.; and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. Plant Sci. 25:381-397.

Hart, J.W. 1988. Light and plant growth. In: M. Black and J. Chapman (Eds.): Topics in plant physiology I. Unwin Hyman. 204 pp.

Hutchings, M.J.; and Budd, C.S.J. 1981. Plant competition and its course through time. Bioscience 31(9):640-645.

Hutchinson, M. 1983. Ecology's law in search of a theory. New Scientist. 98:765-767.

Jennings, S.B.; Brown, N.D.; and Shell, D. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover, and other measures. Forestry 72:59-73.

Jonckheere, I.; Nackaerts, K.; Muys, B.; Coppin, P. 2005. Assessment of automatic gap fraction estimation of forests from digital hemispherical photography. Agric. For. Meteor. 132: 96-114.

Kashian, D.M.; Turner, M.G.; and Romme, W.H. 2005. Variability in leaf area and stemwood increment along a 300-year lodgepole sapling pine chronosequence. Ecosystems. 8:48-61.

Kitajima, K.; Mulkey, S.S. and Wright, S.J. 2005. Variation in crown light utilization characteristics among tropical canopy trees. Annals of Bot. 95:535-547.

Kutner, M.H.; Nachtsheim, C.J.; Neter, J.; and Li, W. 2005. Applied linear statistical models. Fifth edition. McGraw Hill. International edition. New York, USA. 1396 pp.

Lieffers, V.J.; Pinno, B.D.; and Stadt, K.J. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. For. Chron. 78(1):137-145

Lieffers, V.J.; Messier, C.; Stadt, K.J.; Gendron, F.; and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29:796-811.

Lieffers, V.J.; Macmillan, R.B.; MacPherson, D.; Branter, K.; and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72(3):286-292.

Lieffers, V.J.; Stadt, K.J.; and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26:1002-1007

Lieffers, V.J.; and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis Canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198

Lochhead, K.D.; and Comeau, P.G. 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. For. Ecol. Manage. 284: 12-22. doi:10.1016/j.foreco.2012.07.029

Long, J.N.; and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. For. Ecol. Manage. 53: 53-64.

Lonsdale, W.M.; and Watkinson, A.R. 1982. Light and self-thinning. New Phytologist. 90 (3):431- 445

MacIsacc, D.A.; and Navratil, S. 1996. Competition dynamics in juvenile boreal hardwood-conifer mixtures. In: Silviculture of temperate and boreal broadleaf-conifer mixtures. P. G. Comeau, and K. D. Thomas (Eds.). B. C. Ministry of Forests. For. Land Manage. Handbook pp:23-34

Maguire, D.A.; Halpern, C.B.; and Phillips, D.L. 2007. Changes in forest structure following variable-retention harvests: target and non-target effects. For. Ecol. Manage. 242, 708–726.

Messier, C.; Parent, S.; and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9:511-520.

Messier, C.; and Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Can. J. For. Res. 25:343-354.

Niinemets, U.; and Valladares, F. 2006. Tolerance to shade, drought, and water logging of temperate Northern Hemisphere of trees and shrubs. Ecol. Monographs. 76: 521-547.

Nyland, R.D. 2002. Silviculture: concepts and applications. Waveland Press, Inc. Illinois, USA. 682 pp.

Peterson, E.B.; and Peterson, N.M. 1995. Aspen manager's handbook for British Columbia, Canada. British Columbia Partnership Agreement. FRDA II. FRDA Report #230. Victoria, B.C. 121 pp.

Pinno, B.D.; Lieffers, V.J.; and Stadt, K.J., 2001. Measuring and modeling the crown and light transmission characteristics of juvenile aspen. Can. J. For. Res. 31: 1930– 1939.

Pritchard, J.M. 2003. The effect of opening size on light, temperature and the growth of white spruce under a trembling aspen canopy. Master of Science Thesis. University of Alberta. Edmonton, AB. 145 p.

Reifsnyder, W.E.; Furnival, G.M.; and Horowitz, J.L. 1971. Spatial and temporal distribution of solar radiation beneath forest canopies. Agric. Meteorol. 9:21-37.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Reyes-Hernandez, V.; Comeau, P.G.; and Bokalo, M. 2013. Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. For. Ecol. Manage. 289:300-311.

Ridler, W.; and Calvard, S. 1978. Picture thresholding using an iterative selection method. IEEE. Trans. Syst. Man, Cyber. 8 (8): 630-632.

Rowe, J.S.; and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. 3:444-464.

SAS. 2010. Statistical Analysis System for windows, V 9.2. SAS-Institute, Inc. Cary, N.C. USA.

Sharpe, F.; Shaw, D.C.; Rose, C.L.; Sillet, S.C.; and Carey, A.B. 1996. The biologically significant attributes of forest canopies to small birds. North West Sci. 70:86-93

Shinozaki, K.; Yoda, K.; Hozumi, K.; and Kira, T. 1964. A quantitative analysis of plant form- the pipe model theory I. Basic analysis. Japan. J. Ecol. 14: 97–105.

Smith, D.M.; Larson, B.C.; Kelty, M.J.; and Ashton, P.M.S. 1997. The practice of silviculture: applied forest ecology. John Wiley and Sons, Inc. New York, USA. 537 p.

Stadt, K.J.; Huston, C.; Coates, K.D; Feng, Z.; Dale, M.R.T.; and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth n mature boreal mixed forests. Ann. For. Sci. 64:477-490

Stadt, K.; and Lieffers, V.J. 2005. Comparing PAR transmission models for forest understorey vegetation. App. Veg. Sci. 8: 65-76.

Tobin, B.; Black, K.; Osborne, B.; Reidy, B.; Bolger, T.; and Nieuwenhuis, M. 2006. Assessment of allometric algorithms for estimating leaf biomass, leaf area index and litter fall in different-aged Sitka spruce forests. Forestry. 79:453-465

Vales, D.J.; and Bunnell, F.L. 1988. Relationships between transmission of solar radiation and coniferous forest stand characteristics. Agri. For. Mete. 43: 201–223.

Valladares, F.; and Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. Ann. Rev. Ecol. Evol. Syst. 39:237-257.

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

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecol. and Evol. 5: 360-364.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167-225.

Westoby, M.; and Howell J. 1981. Self-thinning: the effect of shading on glasshouse populations of silver beet (*Beta vulgaris*). J. Ecol. 69:359-365.

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

Table 3.1 Summary of attributes of the permanent sample plots in which light measurements were recorded

Stand attribute	**Mean**	**SD**	**Min**	**Max**
Total density (trees·ha^{-1})	1069	692	280	4863
Total basal area (m^{2}·ha^{-1})	40.2	11.8	14.8	66.9
Basal area deciduous (m^{2}·ha^{-1})	19.7	15.6	0.0	49.3
Basal area spruce (m^{2}·ha^{-1})	18.7	18.6	0.0	64.8
Quadratic mean diameter (D_q, cm)	24.2	4.9	14.6	36.7
Aspen height (m)	20.9	7.8	0.0	30.2
Spruce height (m)	14.1	7.8	0.0	26.7
Deciduous basal area (%)	52.4	38.7	0.01	100.0
D_q deciduous (cm)	26.0	8.0	0	44.2
D_q Spruce (cm)	18.7	10.3	0	37.6
SDI total	736	217	292	1183
SDI deciduous	377	306	0	966
SDI spruce	359	353	0	1134
Plot age (years)	105	31.8	25	171
Volume (m^{3}· ha^{-1})	371.4	133.1	118.2	630.2
Biomass (kg·ha^{-1})	191058	53887	75432	276929
Deciduous biomass (kg·ha^{-1})	103387	83153	0	267639
Spruce biomass (kg·ha^{-1})	80182	77420	0	248897

n=55plots

Table 3.2 Understory light availability in plots sampled as obtained with LAI-2000 readings and hemispherical photography

Variable	Mean	SD	Minimum	Maximum
DIFN	21.7	11.1	3.0	59
PAI ($m^2 \cdot m^2$)	2.7	0.86	1.0	5.8
GFR	41.3	9.3	27.3	67.9
Below diffuse	252,914	61,824	155,759	394,928
Below direct	15,103	17,014	528	77,014
Below total	268,016	72,067	158,012	471,942
% diffuse	33.4	8.0	21.5	54.9
% direct	6.1	6.5	0.2	28.4
% total	26.8	6.9	16.5	43.8

n=51for DIFN and PAI; n=55 for other variables; DIFN= %; below light (diffuse, direct and total) =$\mu mol \cdot m^2$, Gap Fraction=%.

Table 3.3 Correlation coefficients for the indicated variables and stand attributes

Stand attribute	Variable					
	DIFN	PAI	GFR	Below diffuse	Below direct	Below total
Basal area deciduous (m^{2}·ha^{-1})	0.28 0.05	-0.38 0.006	0.43 0.001	0.42 0.001	0.28 0.042	0.43 0.001
Basal area spruce (m^{2}·ha^{-1})	-0.25 0.075	0.29 0.037	-0.47 0.0003	-0.46 0.001	-0.14 0.303	-0.42 0.001
Total basal area (m^{2}·ha^{-1})	-0.09 0.54	0.08 0.57	-0.23 0.09	-0.22 0.113	0.09 0.54	-0.17 0.228
Density deciduous (trees·ha^{-1})	0.10 0.48	-0.24 0.09	0.38 0.005	0.32 0.020	0.15 0.281	0.31 0.025
Density spruce (trees·ha^{-1})	-0.30 0.031	0.41 0.003	-0.46 0.001	-0.44 0.001	-0.17 0.224	-0.42 0.002
Total density (trees·ha^{-1})	-0.36 0.01	0.55 0.0001	-0.31 0.02	-0.31 0.03	-0.15 0.29	-0.30 0.03
Sum diameters spruce	-0.34 0.014	0.39 0.005	-0.51 <0.0001	-0.53 <0.0001	-0.23 0.090	-0.51 <0.0001
Sum diameters deciduous	0.213 0.13	-0.323 0.021	0.359 0.008	0.327 0.02	0.133 0.33	0.312 0.02
Total sum of diameters	-0.13 0.38	0.05 0.74	-0.11 0.42	-0.17 0.22	-0.17 0.22	-0.17 0.23
Aspen height (m)	0.17 0.25	-0.28 0.05	0.15 0.27	0.13 0.36	0.10 0.48	0.13 0.34
Spruce height (m)	-0.18 0.20	0.21 0.13	-0.30 0.03	-0.32 0.02	-0.16 0.24	-0.32 0.02
Basal area deciduous (%)	0.30 0.04	-0.39 0.004	0.45 0.001	0.44 0.001	0.25 0.07	0.44 0.001
SDI deciduous (dynamic)	0.28 0.05	-0.38 0.006	0.44 0.001	0.43 0.001	0.30 0.03	0.44 0.001
SDI spruce (dynamic)	-0.26 0.07	0.30 0.03	-0.46 0.001	-0.45 0.001	-0.14 0.31	-0.42 0.002
SDI total (dynamic)	-0.03 0.86	-0.04 0.77	-0.14 0.33	-0.12 0.40	0.19 0.18	-0.06 0.69
D$_q$ – deciduous (cm)	0.22 0.12	-0.29 0.04	0.04 0.75	0.07 0.60	0.20 0.14	0.11 0.43
D$_q$ - Spruce	-0.13 0.35	0.18 0.22	-0.17 0.21	-0.19 0.16	-0.19 0.17	-0.21 0.13
Total D$_q$ (cm)	0.40 0.003	-0.42 0.002	0.26 0.06	0.32 0.02	0.26 0.06	0.34 0.01
Total biomass (kg· ha^{-1})	0.08 0.59	-0.12 0.40	-0.05 0.73	-0.02 0.90	0.21 0.14	0.03 0.81
Total volume (m^{3} · ha^{-1})	0.08 0.60	-0.17 0.25	-0.03 0.83	-0.01 0.95	0.23 0.10	0.05 0.74

D$_q$= quadratic mean diameter (centimeters); n = 51 for DIFN and PAI; n= 55 for other variables; Pearson correlation coefficients significance: α=0.05; plot age did not show significant correlation with any of the variables of interest

Table 3.4 linear regression models for transmittance (DIFN) as a function of stand attributes

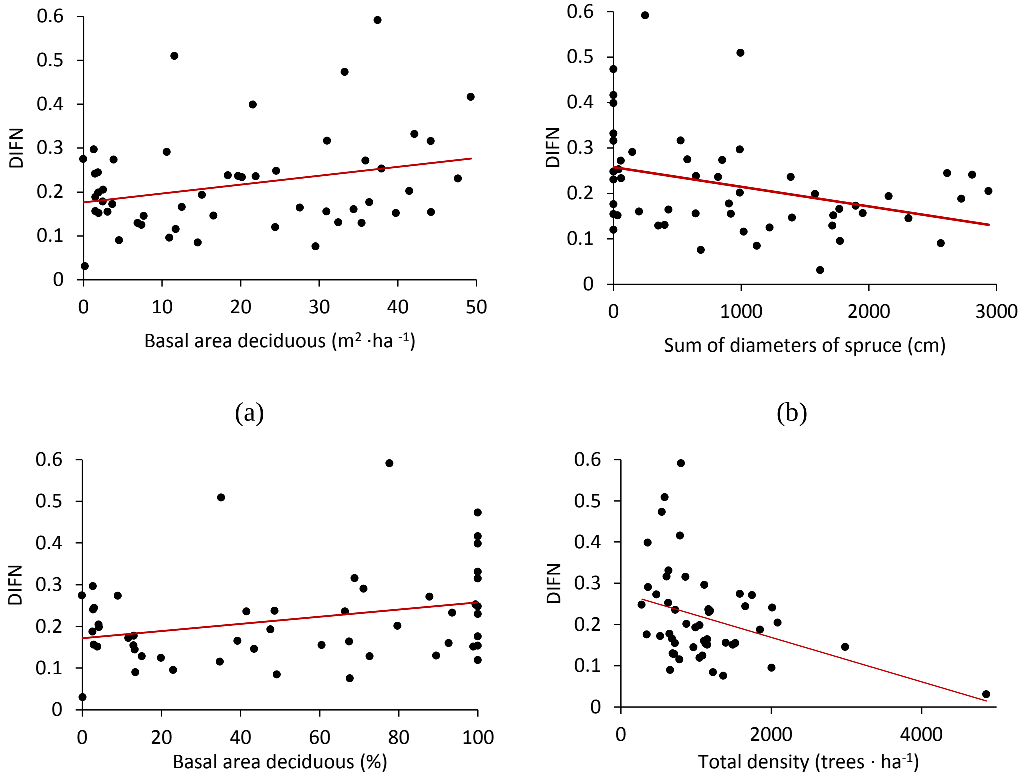
MODEL		R^2_{adj}	MS_{res}	Parameter		
				β_0	β_1	β_2
1	$\ln DIFN = \beta_0 + \beta_1(\sum D_{Sw}) + \beta_2(TPH_{tot})$	0.26	0.449	3.396 (0.119)	-0.00009 (0.00008)	-0.00031 (0.00009)
2	$\ln DIFN = \beta_0 + \beta_1(TPH_{tot})$	0.25	0.452	3.351 (0.114)	-0.00036 (0.00008)	
3	$\ln DIFN = \beta_0 + \beta_1(TPH_{tot}) + \beta_2(D_q)$	0.25	0.453	2.931 (0.481)	-0.00039 (0.0001)	0.0148 (0.016)
4	$\ln DIFN = \beta_0 + \beta_1(TPH_{tot}) + \beta_2(HT_{aw})$	0.24	0.455	3.526 (0.281)	-0.00039 (0.0001)	**-0.0065*** **(0.009)**
5	$\ln DIFN = \beta_0 + \beta_1(D_q)$	0.14	0.483	1.922 (0.339)	0.043 (0.014)	
6	$\ln DIFN = \beta_0 + \beta_1(TPH_{sw})$	0.09	0.500	3.11 (0.094)	-0.0003 (0.0001)	
7	$\ln DIFN = \beta_0 + \beta_1(TPH_{sw}) + \beta_2(\sum D_{sw})$	0.08	0.499	3.139 (0.103)	**-0.00017*** **(0.00019)**	**-0.00010*** **(0.00013)**
8	$\ln DIFN = \beta_0 + \beta_1(TPH_{dec}) + \beta_2(TPH_{sw})$	0.08	0.503	3.21 (0.169)	**-0.00014** **(0.0002)**	-0.0003 (0.0001)
9	$\ln DIFN = \beta_0 + \beta_1(BAH_{tot)} + \beta_2(TPH_{sw})$	0.07	0.502	3.024 (0.259)	**0.0023*** **(0.007)**	-0.00031 (0.0001)
10	$\ln DIFN = \beta_0 + \beta_1(\sum D_{sw}) + \beta_2(\sum D_{aw})$	0.07	0.503	3.09 (0.188)	-0.0002 (0.0001)	**0.00003** **(0.00009)**
11	$\ln DIFN = \beta_0 + \beta_1(BAH_{dec})$	0.06	0.507	2.765 (0.114)	0.0094 (0.0046)	
12	$\ln DIFN = \beta_0 + \beta_1(BAH_{dec}) + \beta_2(BAH_{sw})$	0.04	0.511	2.81 (0.27)	**0.008** **(0.007)**	**-0.0012** **(0.006)**
13	$\ln DIFN = \beta_0 + \beta_1(SDI_{dec}) + \beta_2(SDI_{sw})$	0.04	0.511	2.86 (0.26)	**0.00035** **(0.0004)**	**-0.00012** **(0.0003)**
14	$\ln DIFN = \beta_0 + \beta_1(BAH_{sw})$	0.04	0.512	3.076 (0.102)	-0.0066 (0.0038)	

Parameters' standard errors are in parentheses. TPH_{tot}= total density; D_q = quadratic mean diameter; $\sum D_{Sw}$=Sum of diameters of spruce; HT_{aw}=Average aspen height; D_{qd}=quadratic mean diameter of deciduous; TPH_{sw} = Density of spruce (trees per hectare); BAH_{tot}= total basal area per hectare; BAH_{dec}=Deciduous basal area per hectare; BAH_{sw}=spruce basal area per hectare; * bolded parameters are not significant.

Table 3.5 linear regression models for below total light (BeT) as a function of stand attributes

MODEL		R^2_{adj}	MS_{res}	Parameter			
				β_0	β_1	β_2	β_3
1	$lnBeT= \beta_0+\beta_1(\sum D_{sw})+ \beta_2(TPH_{tot})$	0.28	0.222	12.67 (0.057)	-0.00013 (0.00003)	-0.00007 (0.00005)	
2	$lnBeT= \beta_0+\beta_1(\sum D_{sw)}$	0.25	0.226	12.61 (0.045)	-0.00015 (0.00004)		
3	$lnBeT= \beta_0+\beta_1(TPH_{tot})+ \beta_2(\sum D_{sw})+ \beta_3(SDI_{sw})$	0.28	0.221	12.67 (0.057)	-0.00009 (0.00005)	-0.0002 (0.00008)	**0.0002*** **(0.0002)**
4	$lnBeT= \beta_0+\beta_1(\sum D_{sw})+ \beta_2(TPH_{tot)}+ \beta_3(HT_{aw})$	0.27	0.224	12.72 (0.136)	-0.000130 (0.00004)	**-0.00008*** **(0.00005)**	**-0.002*** **(0.005)**
5	$lnBeT= \beta_0+\beta_1(\sum D_{sw})+ \beta_2(TPH_{sw})$	0.25	0.227	12.61 (0.045)	-0.0001 (0.00005)	-0.00007 (0.00008)	
6	$lnBeT= \beta_0+\beta_1(\sum D_{sw})+ \beta_2(HT_{aw})$	0.24	0.228	12.57 (0.101)	-0.00015 (0.00004)	**0.0017*** **(0.004)**	
7	$lnBeT= \beta_0+\beta_1(\sum D_{sw})+ \beta_2(SDI_{aw})$	0.23	0.228	12.59 (0.08)	-0.00015 (0.00004)	**0.000006** **(0.00004)**	
8	$lnBeT= \beta_0+\beta_1(D_q)+ \beta_2(PBA_{dec})$	0.22	0.247	12.00 (0.160)	0.014 (0.007)	0.0025 (0.00085)	
9	$lnBeT= \beta_0+\beta_1(TPH_{tot})+ \beta_2(D_q)+ \beta_3(PBA_{dec})$	0.21	0.232	12.16 (0.244)	**-0.00005*** **(0.00006)**	**0.010*** **(0.008)**	0.0022 (0.0009)
10	$lnBeT= \beta_0+\beta_1(TPH_{sw})$	0.20	0.233	12.58 (0.04)	-0.00021 (0.00005)		
11	$lnBeT= \beta_0+\beta_1(TPH_{tot})+ \beta_2(BAH_{sw})$	0.20	0.235	12.64 (0.059)	-0.00008 (0.00004)	-0.0046 (0.0019)	
12	$lnBeT= \beta_0+\beta_1(TPH_{dec})+ \beta_2(TPH_{sw})$	0.19	0.235	12.55 (0.08)	**0.00004** **(0.00009)**	-0.0002 (0.00006)	
13	$lnBeT= \beta_0+\beta_1(SDI_{sw})+ \beta_2(SDI_{dec})$	0.17	0.238	12.43 (0.118)	**-0.0002** **(0.002)**	**0.00023** **(0.0002)**	
14	$lnBeT= \beta_0+\beta_1(BAHdec)+ \beta_2(BAH_{sw})$	0.17	0.238	12.45 (0.120)	**0.004** **(0.003)**	**-0.004** **(0.003)**	
15	$lnBeT= \beta_0+\beta_1(Dq_{sw})+ \beta_2(Dq_{dec})+ \beta_3(PBA_{dec})$	0.16	0.239	12.15 (0.147)	**0.004** **(0.004)**	**0.003** **(0.004)**	0.003 (0.001)

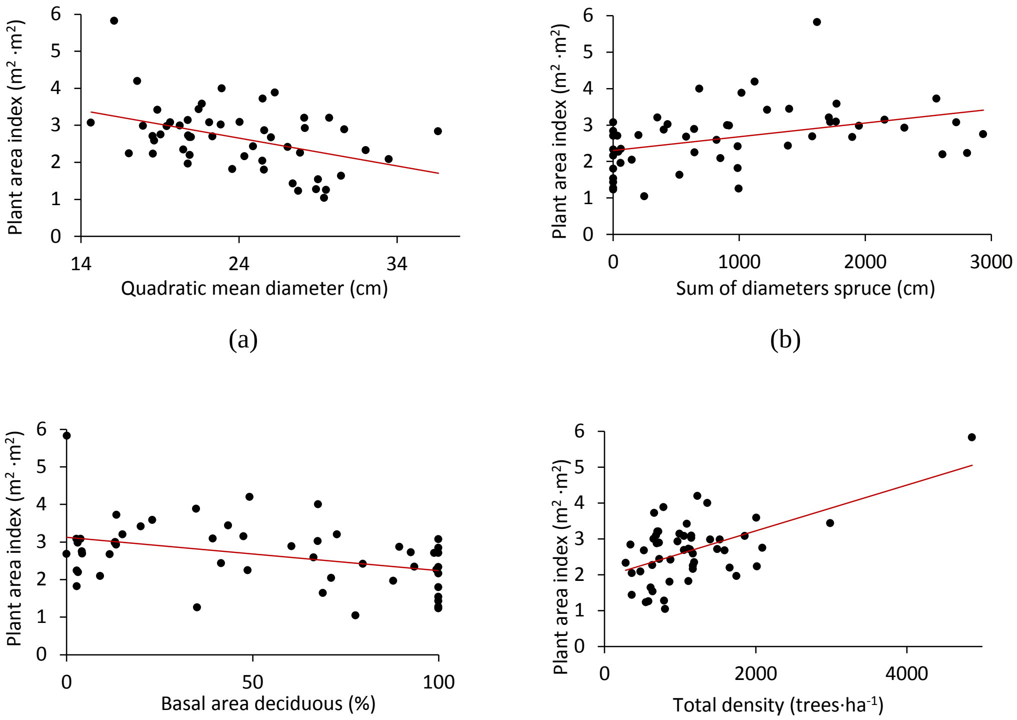
Parameters' standard errors are in parentheses. TPH_{tot}= total density; D_q = quadratic mean diameter; $\sum D_{Sw}$=Sum of diameters of spruce; HT_{aw}= average aspen height; TPH_{sw} = Density of spruce (trees per hectare); SDI_{sw}=Stand Density Index for spruce based on dynamic maximum size-density relationships model (Chapter 2); BAH_{sw}=spruce basal area per hectare; PBA_{dec}= percentage of basal area in deciduous; bolded parameters are not significant.



(a) (b)

(c) (d)

Figure 3.1 Scatter plots of light transmittance (DIFN) calculated with LAI-2000 measurements as related to (a) basal area in deciduous; (b) sum of diameters of spruce; (c) percent of basal area in deciduous; and (d) total density. The red lines show the strongest trend for the data points.



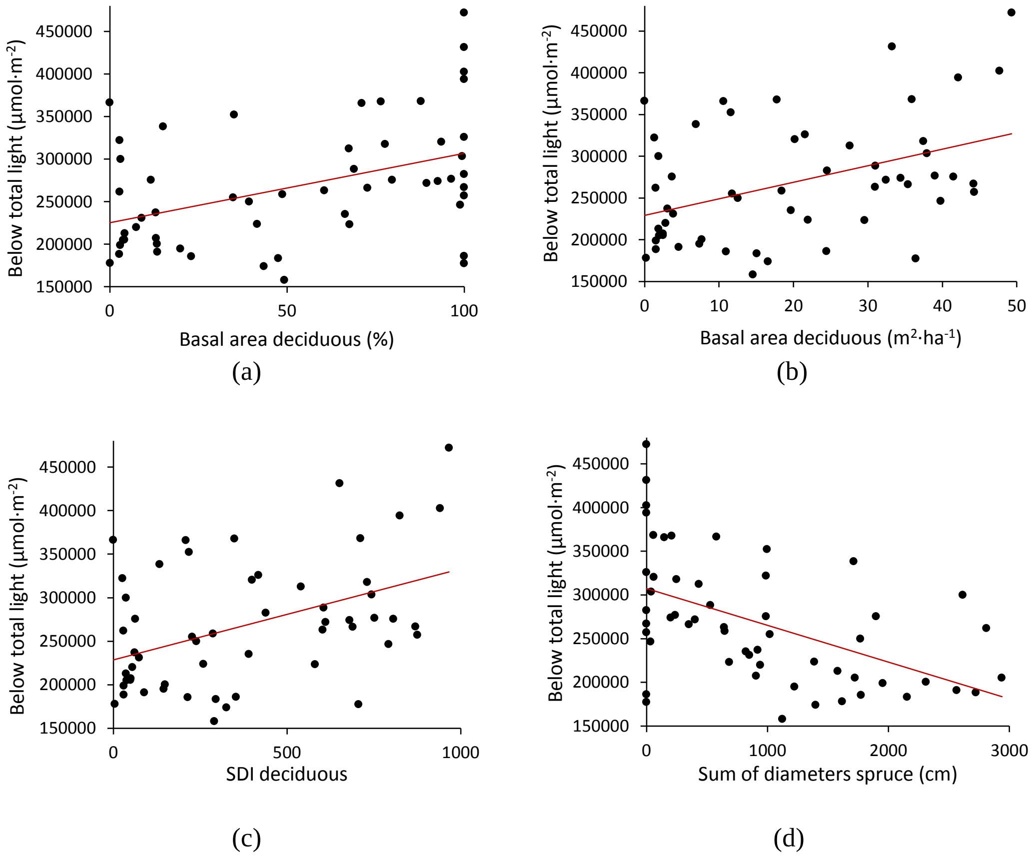
(a)

(b)

(c)

(d)

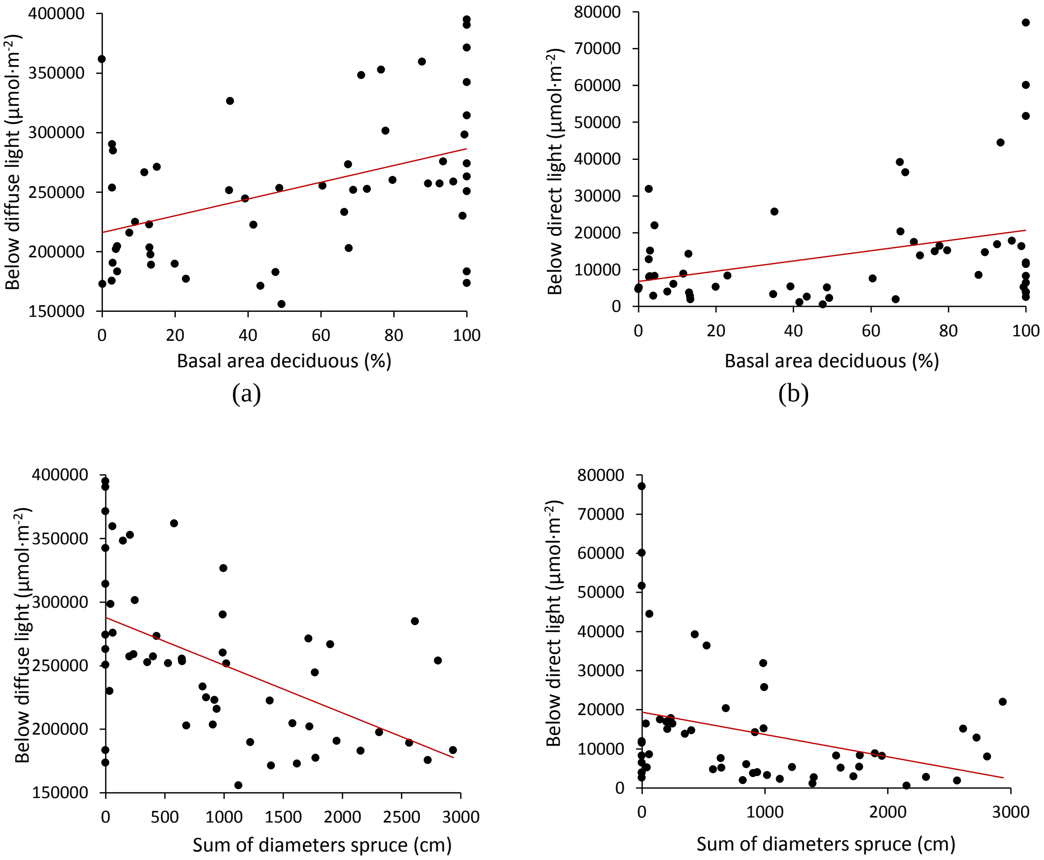
Figure 3.2 Scatter plots of plant area index calculated with LAI-2000 measurements as related to (a) quadratic mean diameter; (b) sum of diameters of spruce; (c) percentage of basal area in deciduous; and (d) total density. The red lines show the strongest trend for the data points.



(a) (b)

(c) (d)

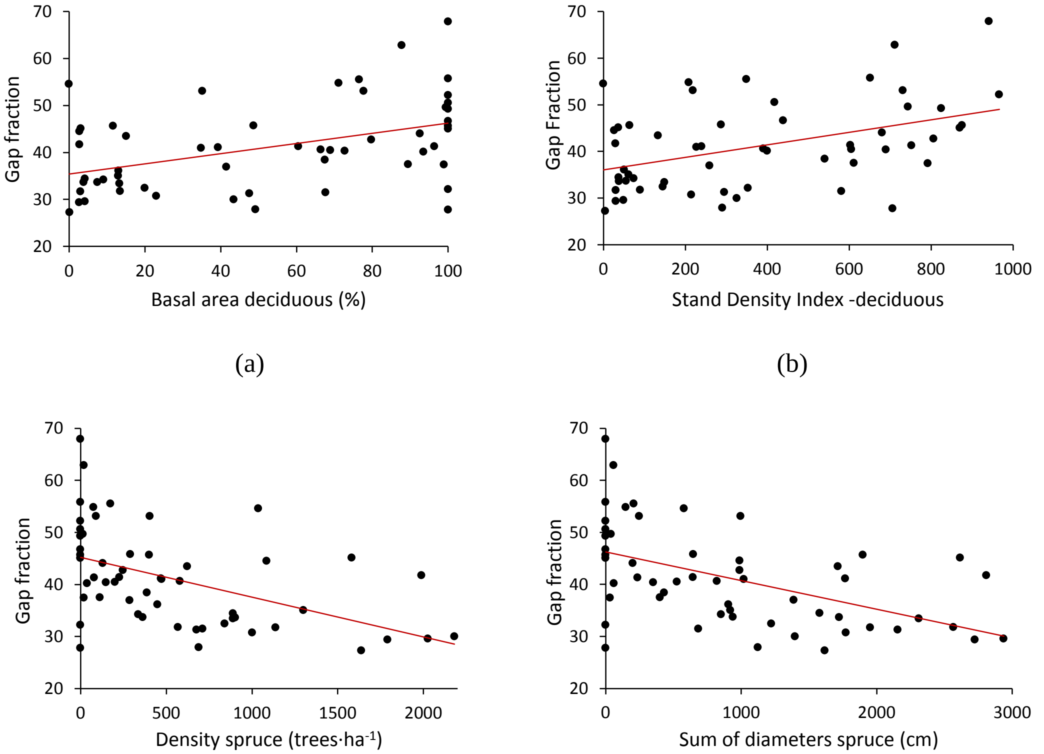
Figure 3.3 Scatter plots of below total light estimated from hemispherical photography as related to (a) basal area deciduous (%) ; (b) deciduous basal area ($m^2 \cdot ha^{-1}$); (c) Stand density index - deciduous; and (d) sum of diameters of spruce. The red lines show the strongest trend for the data points.



(a) (b)

(c) (d)

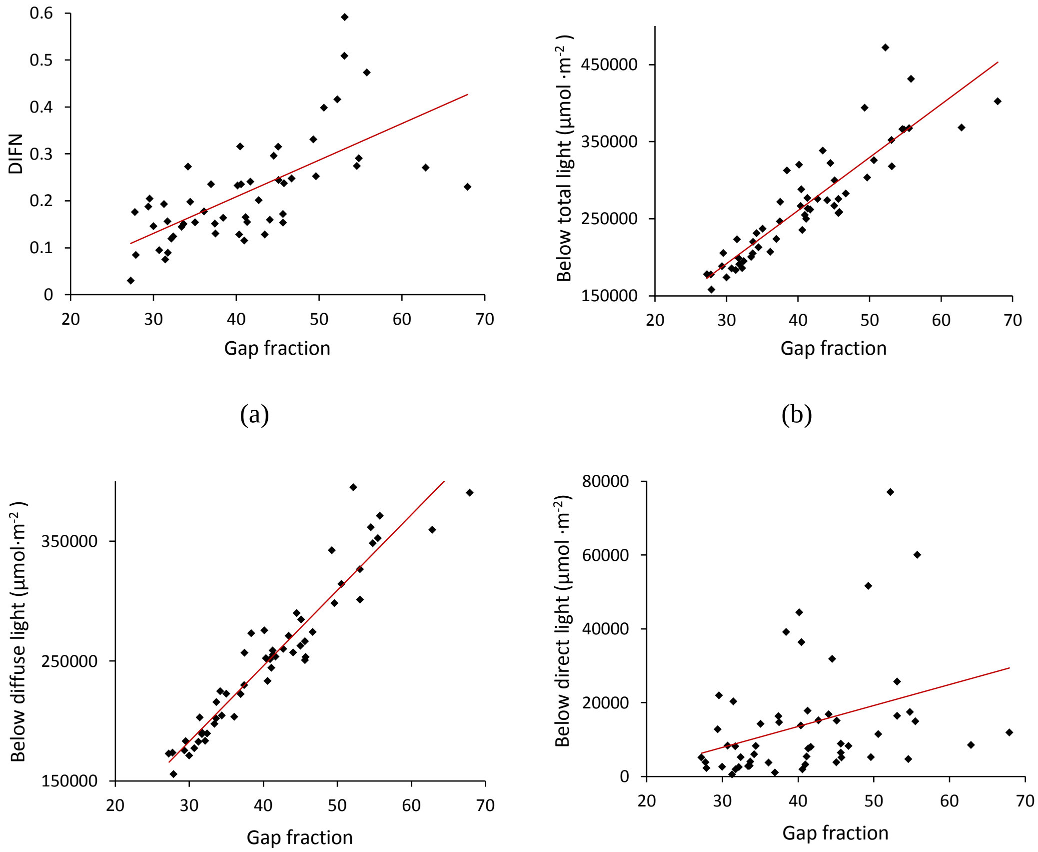
Figure 3.4 Scatter plots for below diffuse light as related to percentage basal area of deciduous (a), and sum of diameters of spruce (c); and below direct light as related to percentage basal area of deciduous (c) and sum of diameters of spruce (d). The red lines show the strongest trend for the data points.



(a) (b)

(c) (d)

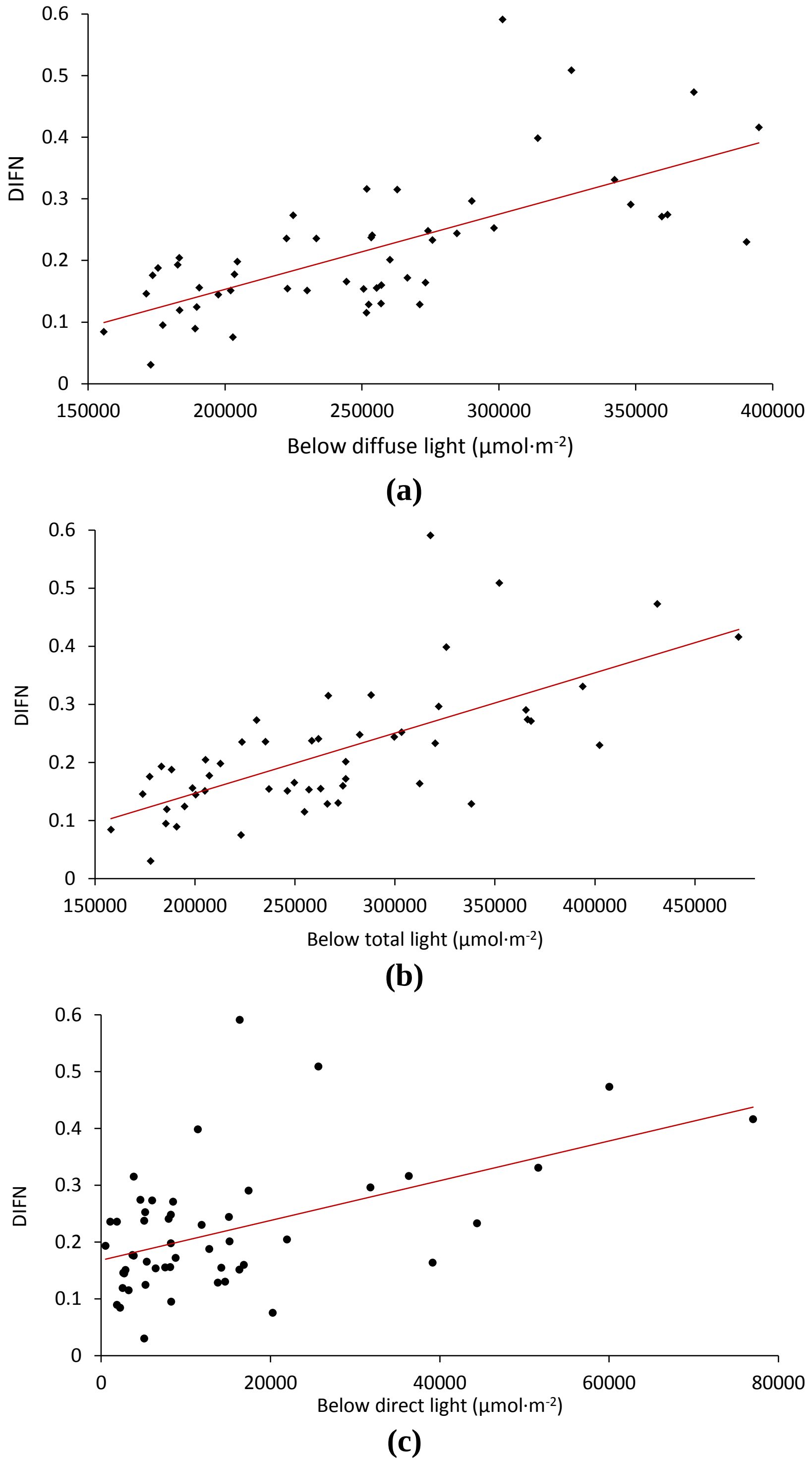
Figure 3.5 Scatter plots of gap fraction calculated from hemispherical photography analysis as related to (a) basal area deciduous (%); (b) Stand Density Index-SDI deciduous; (c) density of spruce; and (d) sum of diameters of spruce. The red lines show the strongest trend for the data points.



(a) (b)

(c) (d)

Figure 3.6 Scatter plots for the different indicators of understory light as related to gap fraction (GFR); (a) DIFN; (b) below total light; (c) below diffuse light; and (d) below direct light. The red lines show the strongest trend for the data points.

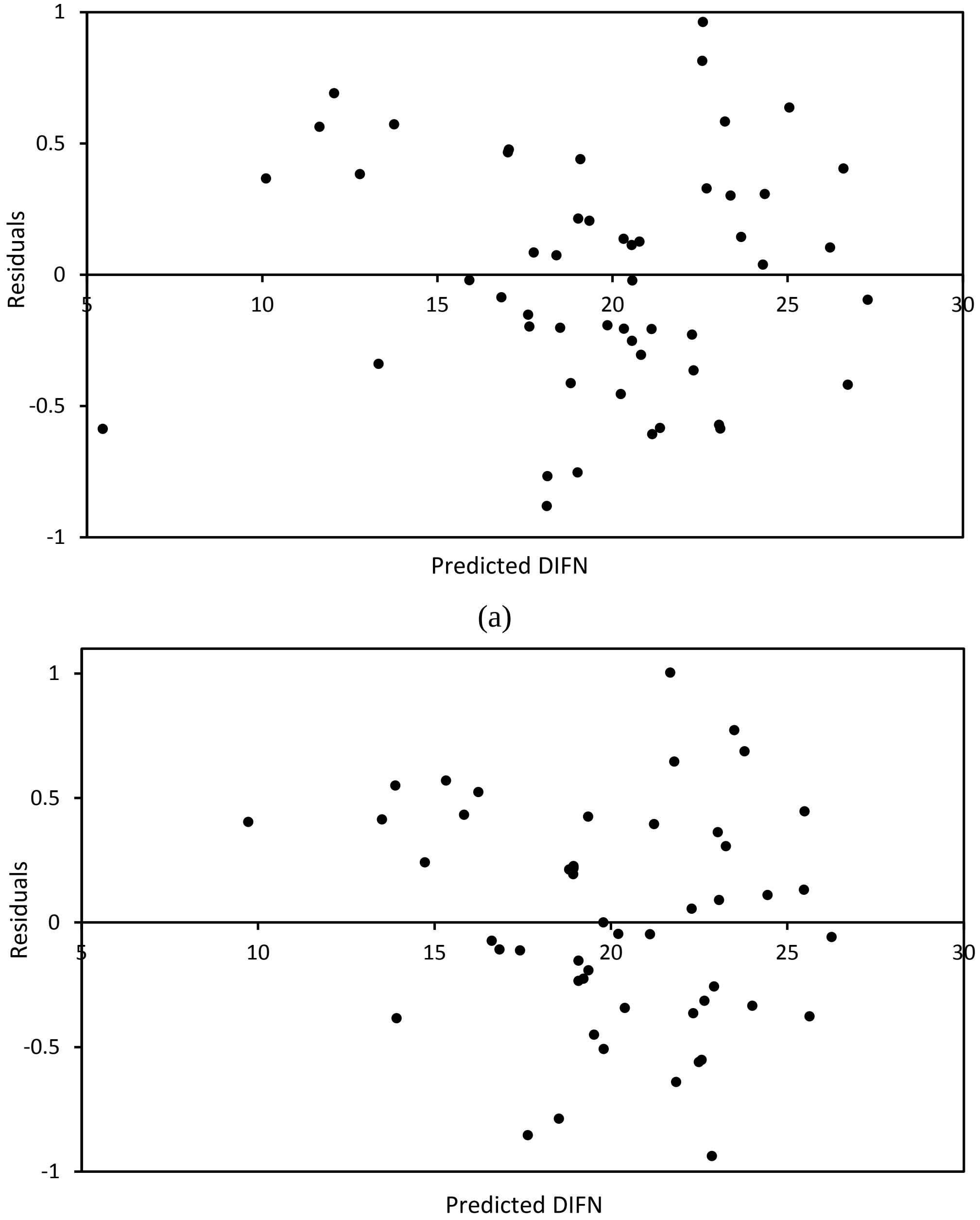


(a)

(b)

(c)

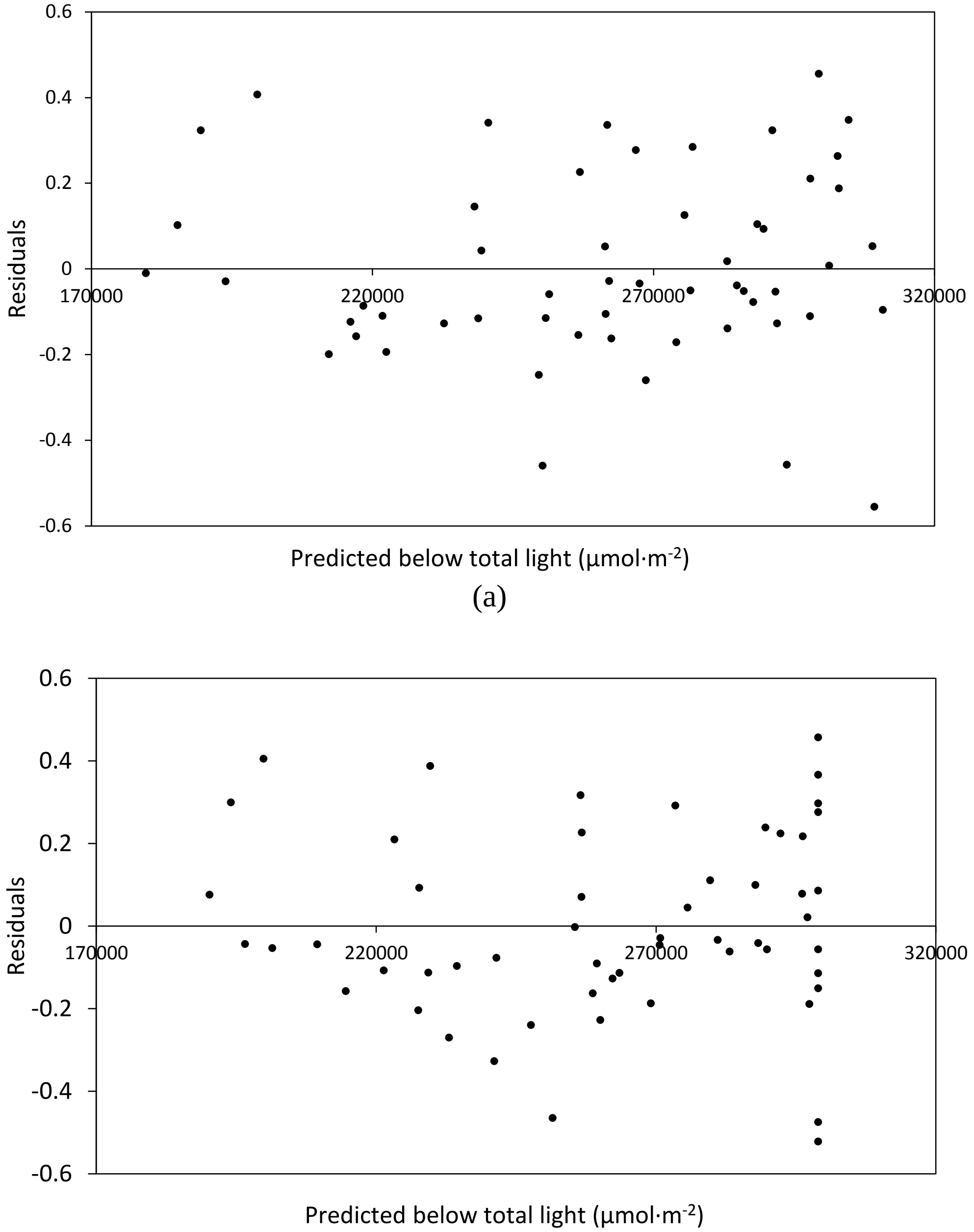
Figure 3.7 Scatter plots of transmittance (DIFN) as related to (a) below diffuse light; (b) below total light; and (c) below direct light. The red lines show the strongest trend for the data points.



(a)

(b)

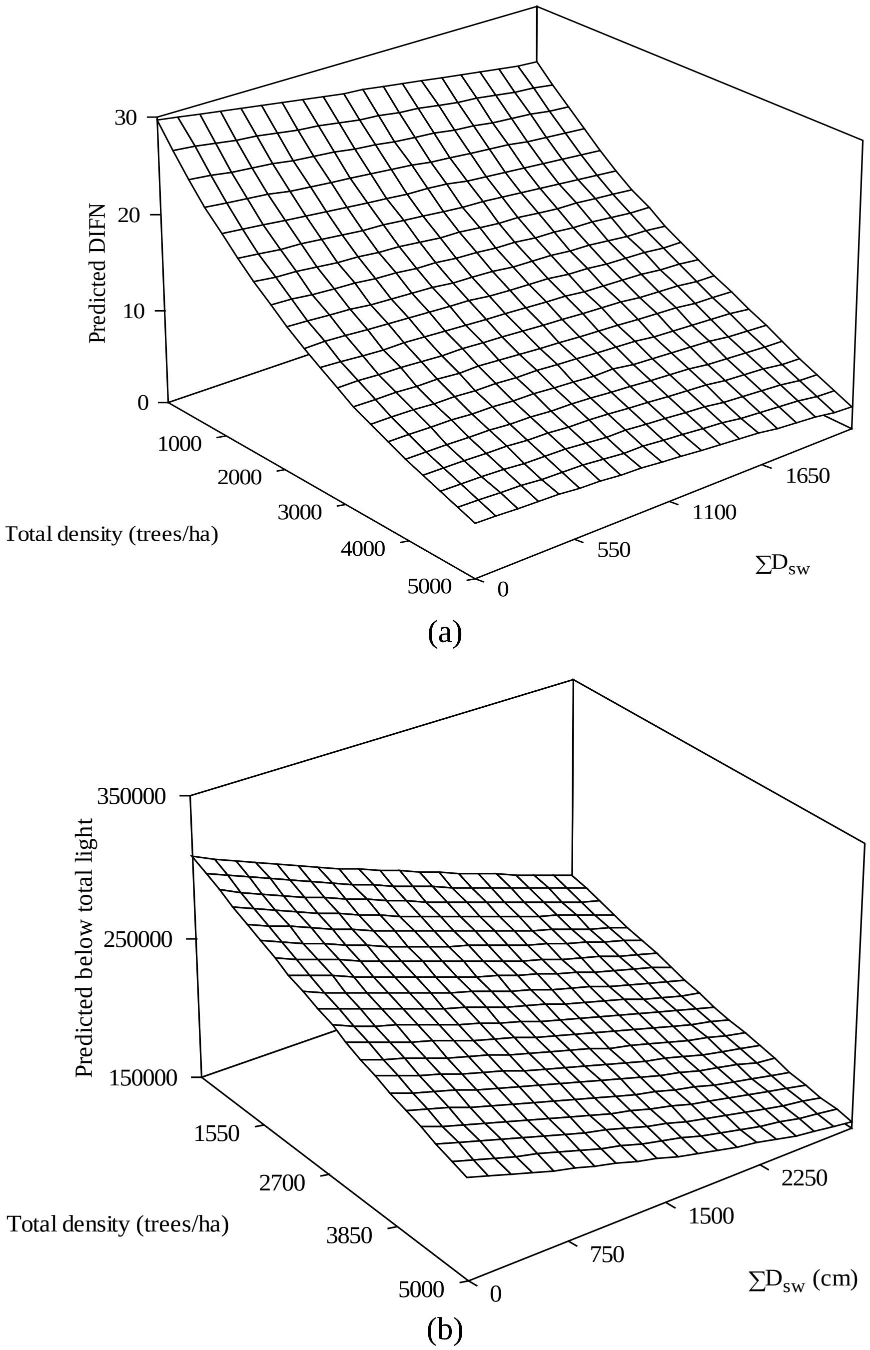
Figure 3.8 Residuals against predicted values for two of the models with best fit to predict transmittance (DIFN) as a function of (a) total density and sum of diameters of white spruce, model 1: $\ln DIFN=3.396-0.00009*\sum D_{Sw}-0.00031*TPH_{tot}$; and (b) total density, model 2: $\ln DIFN=3.351-0.00036*TPH_{tot}$.



(a)

(b)

Figure 3.9 Residuals against predicted values for two of the models with best fit to predict below total light as a function of (a) sum of diameters of spruce and total density, model 1: $\ln BeT=12.67-0.00013*\sum D_{Sw}-0.00007*TPH_{tot}$; and (b) sum of diameters of spruce, model 2: $\ln BeT=12.61-0.00015*\sum D_{Sw}$.



(a)

(b)

Figure 3.10 Relationship between DIFN (a) and below total light ($\mu mol \cdot m^{-2}$) (b) with total density (TPH_{tot}, trees per hectare) and sum of diameters of spruce ($\sum D_{Sw}$, cm) for selected boreal mixedwood stands in Alberta. Models: $DIFN=3.396-0.00009*\sum D_{Sw}-0.00031*TPH_{tot}$; $BET=12.67-0.00013*\sum D_{Sw}-0.00007*TPH_{tot}$ (See Tables 3.4 and 3.5 for statistical information relating to these models).

Chapter 4 Effects of stand density and composition on periodic annual increment of boreal mixedwood stands

4.1 Introduction

Stand density has important effects on growth rates. Understocked stands experience reduced growth rates essentially because individual trees are neither fully occupying the site nor efficiently using the site resources. In contrast, fully stocked stands will achieve full growth potential. As density increases above that required to fully utilizing the site, growth is allocated to more and more stems, and results in smaller individual trees. At maximum attainable densities (*i.e.* maximum stockability), substantial tree mortality induced by competition is experienced. This imposes a constraint beyond which stand growth may not occur (Drew and Flewelling, 1977). At approximately 60% of maximum density both gross and net stand growth will achieve their peak (Nyland, 2002), and beyond this point gross growth remains relatively constant while net growth will show a fairly steady decline; a more abrupt decline in net growth will be recorded with 80 % of relative density and above (Drew and Flewelling, 1977). Stand density representing full stocking, in terms of number of trees per unit area, will vary with tree size (particularly crown size), and consequently also with age.

As stands increase in age both net and gross growth will increase to peak values and then decline (Davis *et* al., 2001), with net growth falling below gross growth at intermediate densities as tree mortality begins to occur and accumulates (Smith *et* al., 1997). Changes in stand density as a result of tree mortality will also affect individual tree sizes (*i.e.* stand structure) and growth rate, as well as stand growth, consequently affecting stand yield. Nevertheless, growth losses as a result of tree mortality are buffered by self-regulating events, with changes in stand structure and resource availability affecting growth rates and tree size and shape, which then lead to further changes in stand structure (Pretzsch, 2009). With reductions in stand density temporary decreases in gross total growth at the stand level may occur. However increases in resource availability to the remaining trees are expected, allowing them to increase their growth and accelerate site occupancy, potentially compensating for the density reduction (Smith *et* al. 1997; Pretzsch 2009). Increases in photosynthetic activity and assimilation will help to reduce the negative effects of density reductions until a new balance in terms of density or a maximum leaf area is again achieved (Pretzsch, 2009).

Stand density estimates, as a function of the number of trees, their size, and their spatial distribution, are widely used in the analysis of forest growth and yield (Davis *et* al. 2001; Pretzsch 2009), as they are useful to explain the degree to which the growing space available for tree growth is utilized (Helms 1998; Davis *et* al. 2001). Density and indicators of relative density, such as Reineke's SDI (Reineke, 1933) and others, provide descriptions of stocking or the degree of crowding expressed by growing space ratios (Helms, 1998). In complex structures like those existing in mixed species stands, estimation of stand occupancy should consider both the total growing space occupancy and how this is allocated among stand components (species, cohorts or canopy strata) (O'Hara and Gersonde, 2004).

A reliable representation of the relationship between species growth rates and characteristics of the growing stock, might be obtained by combining effects of relative density, height, and indicators of site productivity (*i.e.* site index or a surrogate) (Innes *et* al. 2005; Long and Shaw 2010). Indeed, studies have suggested that SDI can be useful as a measure of site utilization and competition between component species in mixed species stands, since it is related to light capture (Vales and Bunnell, 1988), and is suggested to be independent of species composition (Curtis, 1970). However, SDI has not been widely used in mixed species stands and considerable knowledge gaps exist regarding this subject.

Mixed stands are widely thought to be more productive than monocultures when species that differ in key characteristics such as shade tolerance, height growth rate, crown structure, foliar phenology, root depth and phenology, are combined and capture or use site resources more. This results in greater total stand biomass and higher growth rates than would occur in monocultures of the component species (Kelty1992; Man and Lieffers 1999; Kelty 2006). Two ecological concepts of species interactions that may help to explain higher stand productivity of mixtures are competitive reduction and facilitative production (Man and Lieffers, 1999). Reduced inter-specific competition is suggested when competitive reduction takes place, because the species involved show niche differentiation when growing in a mixture (Kelty 1992; Jose *et* al. 2006; Kelty 2006).

A beneficial effect on the growth and/or productivity of one or both component species results when facilitation occurs in a mixture, for example the positive influence of deciduous species in nutrient cycling (Vandermeer 1989; Kelty 1992). Mixtures of species which have reduced competition or improved growth of one or both species are considered to have ‘ecological combining ability’ (Kelty, 1992), and they may show increased productivity when grown in mixtures compared to when they are grown separately (Man and Lieffers, 1999). As a result of ecological combining ability, facilitation, and competition reduction, mixed species stands may also support higher stand densities than single species stands, and this could be associated with mixed stands having higher biomass and increment.

In boreal forests, trembling aspen is a pioneer species that rapidly occupies boreal sites after major disturbances (*i.e.* fire, clearcutting), owing to its profuse regeneration from root suckering and fast early height growth (Peterson and Peterson 1992; Chen and Popadiouk 2002); meanwhile, white spruce can survive and grow under an aspen overstory canopy due to its shade tolerance; white spruce might gradually take over the site, with a resulting stratified canopy as a result. Mixtures between these two species are commonly referred as boreal mixedwoods. Competitive and facilitative interactions might play a significant role over time between these two species (Man and Lieffers 1999; Comeau *et* al. 2005; Filipescu and Comeau 2007a; Filipescu and Comeau 2007b).

Some studies indicate higher productivity for boreal mixed stands than for pure stands of either spruce or aspen (Man and Lieffers 1999; MacPherson *et* al. 2001). Mechanisms that could lead to increased productivity of boreal mixedwoods include: differences in shade tolerance; physical canopy separation;

differences in phenology; changes in availability of and utilization of soil and other resources (Man and Lieffers, 1999); and the fact that mixed stands may support higher densities. The existence of a stratified canopy with two species differing in shade tolerance growing together is expected to improve light capture and utilization over what is found in mono specific stands (Kelty, 1992).

Productivity of mixtures of these two species might be higher, in part because aspen will hold the nutrients within the stand, may improve nutrients cycling owing to its litter properties, and may increase understory light availability (MacDonald 1996; MacPherson *et* al. 2001). Other beneficial effects of aspen on white spruce include reduction of damage by wind and frost, as well as reduction of competition from grasses and other vegetation (Lieffers and Stadt 1994; Constabel and Lieffers 1996; MacDonald 1996; Groot and Carlson 1996; Groot 1999; Comeau *et* al. 2004).

Mixedwoods may also be economically more valuable than monocultures, by providing products from both aspen and spruce simultaneously or consecutively, satisfying more diverse demands and providing more variety of products (Comeau *et* al., 2005). Despite the numerous advantages of trembling aspen-white spruce mixtures compared to pure stands of the same species, mixedwood management is a fairly new silvicultural approach to the western Canadian boreal forest, and further study is needed to support its implementation in a context of more demanding markets and societies.

In this Chapter, I examine white spruce, trembling aspen, and total stand periodic annual increment in stem volume in mid-rotation and mature boreal pure and mixed natural unmanaged stands in Alberta, Canada. Stands comprised primarily by trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) in different proportions and developmental stages are the main focus of study in this Chapter. Based upon the principle that growth of forest stands is primarily a function of site occupancy, site quality, and tree age (Oliver and Larson, 1996), I evaluate the usefulness of selected stand attributes such as tree density, total stand basal area, basal area of deciduous species (mainly trembling aspen), and basal area of white spruce, in explaining white spruce, trembling aspen, and total stand periodic annual increment in volume. These analyses include examination of the effects of stand composition (percent of basal area in deciduous species and percent of basal area of white spruce), as well as the influence of stand density, represented by Reineke's stand density index (SDI) by component species and for the entire stand (Reineke, 1933).

Because boreal trembling aspen and white spruce mixtures might be able to support greater maximum stocking than pure stands of the same species (*i.e.* related to higher maximum size-density relationships) (Reyes-Hernandez *et* al., 2013), this might be an important factor leading mixed stands to have higher productivity than pure stands of the same species. I also test the hypothesis that the presence of a coniferous and deciduous component positively influences total stand growth rates, consistent with observations that the presence of understory spruce does not impact on the productivity of the aspen component (MacPherson *et* al., 2001).

4.2 Methods

4.2.1 Study sites and data

This research was conducted using long-term permanent sample plot (PSP) data, established in pure aspen, pure white spruce and mixed stands of both species in the Boreal Forest Natural Region of Alberta, Canada. The Central, the Dry, and the Northern Mixedwood ecological sub-regions were included in this part of the study (Beckingham and Archibald 1996; Forest Management Branch 2005). Although varying in size, the majority of these PSPs are 0.10 ha in size, with all three species taller than 1.3 m or larger than 2.5 cm in diameter at breast height tagged and measured at time intervals ranging between 3 to 10 years.

Data from these PSPs were compiled to calculate several stand characteristics. These attributes are summarized in Table 4.1. In order for a plot to be taken into account and incorporated in further analysis, the following criteria were applied:

1) The plot was primarily comprised of trembling aspen and white spruce; composition went from almost 0% aspen and 100% spruce, to almost 0% white spruce and almost 100% trembling aspen, including ranges in their proportions with different available combinations.

2) No more than 10% of total stand basal area was comprised of species other than trembling aspen and/or white spruce; any plot containing 10 % or more in basal area of other species than the two species of interest was not included.

Individual tree gross total volume (m^3) was estimated using species specific tree volume equations developed for Alberta tree species (Huang, 1994). Individual periodic annual increment in volume, termed “volume increment” in this Chapter, for spruce (Iv_{sw}), for trembling aspen (Iv_{aw}), and for all species combined in the plot (Iv_{tot}), expressed as $m^3 \cdot ha^{-1} \cdot yr^{-1}$, was calculated by obtaining the difference in net volume values (including ingrowth but excluding mortality) estimated at the beginning and at the end of the measurement period and divided by the number of years. Total periodic annual increment by species and for the plot, as previously indicated, was then calculated by summing individual volume increment for all trees in the plot, and scaled up to a per hectare basis.

Individual tree height was not directly measured in the field for all of the trees but for a sub-sample inside the plot. Consequently, this variable was estimated for all of the remaining trees (*i.e.* those for which height was not measured in the field) using equations previously generated for Alberta tree species (Huang *et* al., 1994). Average tree height values were then obtained by species for each of the plots included in the analysis. Site index by species was also available in the data set. An average site index combined for white spruce and aspen was calculated and tested in the models. Other site quality indicators (*i.e.* soil nutrient and soil moisture regime) were also available in the data set, and represent the availability of essential nutrients and moisture for plant growth on a site (Beckingham and Archibald, 1996). These two indicators of site quality were used as surrogates of site index in model testing. A total of 163 PSPs were available for this study. Table 4.1 provides a summary of the characteristics of the stands that were used in this research.

4.2.2 Data analysis

Analysis was based on the principle that growth is primarily influenced by a combination of site quality, site occupancy, stand composition, and age (Oliver and Larson 1996; Innes *et* al. 2005; Long and Shaw 2010). Under this premise, and due to the fact that a reliable estimation of age of the stands under examination was not available, periodic annual increment in volume of white spruce, trembling aspen, and the total stand was regressed against a number of stand attributes that represent density, site occupancy and site quality. Site occupancy can be characterized by a combination of relative density and height (Long and Shaw, 2010). I used number of trees per hectare, basal area, and a version of Reineke's Stand Density Index-SDI (Reineke, 1933) as measures of stand density.

SDI was calculated separately for each species in all of the stands in the data set, based on maximum size-density relationships previously obtained (dynamic thinning line) (Reyes-Hernandez *et*. al, 2013). The traditional calculation of Reineke's SDI includes the use of quadratic mean diameter of the stand to compute a single stand SDI value (see Chapter 1 of this Dissertation). In this case, a modification in the calculation of SDI was performed and the summation method (Long and Daniel 1990; Shaw 2000) was used for calculating Reineke's SDI, as follows:

$$SDI_{sum} = \sum(TPH_i * (D_i/25)^r \qquad (4.1)$$

Where D_i is the diameter at breast height of the *i_{th}* tree in the plot, TPH_i is the number of trees per hectare^{-1} characterized by the *i_{th}* tree, and ***r*** is the slope of the maximum size-density relationship. The slope obtained for the dynamic thinning line (Reyes-Hernandez *et* al., 2013) was utilized in calculating SDI_{sum} for these stands. SDI_{sum} was estimated for diameter class by species, and summed up to obtain a single value for the stand. It is important to point out that Equation 4.1 represents the general form for calculating SDI_{sum}. In further analyses and for the remaining of this Chapter, SDI_{sum} will be referred to as SDI_{dyt} for total stand dynamic SDI, SDI_{dysw} for white spruce dynamic SDI, and SDI_{dyd} for deciduous species dynamic SDI (mainly trembling aspen).

The general model for the analysis of the relationship between white spruce volume increment, trembling aspen volume increment, and total stand volume increment (*i.e.* growth rates), with selected stand attributes (i.e. growing stock characteristics) including stand composition, takes the following form:

$$Iv = f\ (\text{Density, HT, site quality, } PBA_{dec}) \qquad (4.2)$$

Where Iv is periodic annual increment in volume for spruce (Iv_{sw}), aspen (Iv_{aw}), or total stand (Iv_{tot}) ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); density is represented either by number of trees per hectare, basal area, or SDI_{sum}. HT is the average white spruce (HT_{sw}) or trembling aspen (HT_{aw}) height in meters; site quality is nutrient regime (N_{ur}), moisture regime (M_{or}), or average site index (SI_p); and PBA_{dec} is the percentage of basal area in deciduous species (PBA_{sw} for white spruce).

The three density measures that were used (trees per hectare, basal area and SDI_{sum}), were evaluated either as a total value per stand or further broken down into deciduous and spruce components. Hence, for SDI_{sum}, SDI_{dyd} is deciduous SDI, SDI_{dysw} is white spruce SDI, and SDI_{dyt} is total stand SDI; for basal area ($m^2 \cdot ha^{-1}$), BAH_{dec} is basal area per hectare for deciduous, BAH_{sw} is basal area per hectare for white spruce, and BAH_{tot} is total stand basal area; for density ($trees \cdot ha^{-1}$), TPH_{tot} is total stand density, TPH_{dec} is deciduous density (mainly trembling aspen), and TPH_{sw} is white spruce density;

All statistical analyses were completed using non-linear regression with PROC NLIN of SAS version 9.2 for windows (SAS Institute, 2010). Analyses were performed for three different data sets for volume increment. The first one was completed by using only the most recent calculation of volume increment for white spruce alone, which was obtained from the two most recent measurements in each of the plots. The second analysis included only volume increment for trembling aspen alone, obtained in the same way as that for white spruce. In the third analysis, volume increment for all of the species combined was evaluated.

Model goodness-of-fit was assessed with adjusted R^2 values, whereas estimated parameters were assessed for their significance. The standardized Hougaard’s measure of skewness was used to assess the ‘close-to-linear’ behavior of each parameter estimate associated to the independent variables. The ‘close-to-linear' behavior of a parameter in a non-linear regression model essentially indicates that the parameter has properties similar to those of a linear regression model, that is, that they are close to be unbiased, normally distributed, and with minimum variance (Ratkowski, 1990).

Values of skewness less than 0.1 in absolute value indicate a very close-to-linear behavior; values between 0.1 and 0.25 in absolute value indicate reasonably close-to-linear behavior; and an apparent nonlinear behavior of each parameter is indicated by skewness absolute values above 0.25. Independent variables that showed skewness above these levels were excluded from the model under evaluation, although they were still considered for evaluation in other models. Finally, examination of Studentized residuals against predicted volume increment for each of the models tested was also performed.

4.3 Results

4.3.1 Trembling aspen volume increment

Trembling aspen periodic annual increment ranges from <0.1 to 12.8 $m^3 \cdot ha^{-1} \cdot yr^{-1}$, with an average of 3.3 $m^3 \cdot ha^{-1} \cdot yr^{-1}$. Combinations of selected independent variables were able to explain up to 80 % of the total variation in trembling aspen gross total stem volume periodic annual increment (Table 4.2). Height of deciduous and spruce were among the most consistently significant variables in the models evaluated. Although the final set of selected models show similar goodness-of-fit and performance, the most parsimonious model was obtained when the number of trees of deciduous species was utilized in combination with the average height of both spruce and aspen in the same model. This model explains 80 % of the variation in aspen volume increment and shows the lowest residual sum of squares (SS_{res}=261.7) among the competing models (Table 4.2).

Similar Adjusted R^2 values were obtained when SDI_{dyd} and BAH_{dec} were used in combination with average height of both deciduous and white spruce (Adjusted R^2= 0.76 in both cases). Although SDI_{dysw} and percentage of deciduous species also showed a significant effect, the incorporation of these variables did not contribute significantly to the improvement of model performance (Table 4.2) Based on these considerations, the best model for explaining variation in Iv_{aw} is:

$$Iv_{aw}=0.000000042*TPH_{dec}^{1.02}*HT_{sw}^{0.20}*HT_{aw}^{2.96} \tag{4.3}$$

Where Iv_{aw} is trembling aspen periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); TPH_{dec} is deciduous total density; HT_{sw} is average white spruce height; and HT_{aw} is average aspen height.

Although other models with different combinations of independent variables were also obtained, selection of the best model for explaining aspen increment was based on the significance of the model, residual sum of squares, adjusted R^2 values, significance of model parameters, and the distribution of residuals. Fit statistics for the selected best model (model 4.3) and for other models with similar performance are presented in Table 4.2. Figure 4.1 shows the distribution of studentized residuals for the best and for the second best model as indicated.

4.3.2 White spruce volume increment

White spruce volume increment ranges up to 12.7 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ with an average of 3.5 $m^3 \cdot ha^{-1} \cdot yr^{-1}$. Two density measures for the component species (SDI and basal area) were also among the most significant and consistent independent variables in the models evaluated (Table 4.3). The best model in this case explained 84 % of the total variation in spruce volume increment (Table 4.3), while alternative models explained between 80- 83 % of the total variation in Iv_{sw}.

The percentage of basal area in deciduous (PBA_{dec}) also showed a significant effect on white spruce volume increment. However, its contribution to model performance was rather small, and it has conflicting behavior with other independent variables, as seen in Table 4.3. The two density measures (basal area, and SDI) performed similarly in the models evaluated, as can be seen in Table 4.3. However, the model that includes SDI by component species and average height for each species shows the smallest residual sum of squares. Consequently, the most parsimonious model for explaining white spruce volume PAI is:

$$Iv_{sw}=0.001*SDI_{dyd}^{0.99}*SDI_{dysw}^{0.06}*HT_{sw}^{0.32}*HT_{aw}^{0.15} \qquad (4.4)$$

Where Iv_{sw} is white spruce periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); SDI_{dyd} is deciduous dynamic SDI; SDI_{dysw} is white spruce dynamic SDI; HT_{sw} is average white spruce height; and HT_{aw} is average aspen height. This model explains 84 % of the total variation in spruce volume increment.

Model fit statistics of the most parsimonious model (model 4.4) and for alternative models with similar performance are presented in Table 4.3. Figure 4.2 shows the distribution of studentized residuals for the best and for the second best model as indicated.

4.3.3 Total stand volume increment

Total stand periodic annual increment in volume ranges from 0.01 to 14.7 $m^3 \cdot ha^{-1} \cdot yr^{-1}$, with an average of 6.8 $m^3 \cdot ha^{-1} \cdot yr^{-1}$. Since this data set characterizes a wide range of species composition and proportions of both white spruce and trembling aspen, the effects of stand composition on total stand volume increment (*i.e.* growth rates) was evaluated. Different sets of independent variables were able to explain between 30 and 31 % of the total variation in Iv_{tot} (Table 4.4). Dynamic SDI split by species, basal area per hectare also divided by component species, average height of component species, and percentage of basal area of deciduous were among the most consistent variables in the models evaluated.

Better model performance is achieved when the effects of SDI for deciduous and spruce are used in the same model, separately but in combination with the average height of both components and the percentage of basal area of deciduous, explaining up to 31 % of the total variation in Iv_{tot}. A marginal decrease in residual sums of squares of the model is achieved when SI_p is included in the model, but there is no improvement in adjusted R^2 (R^2=0.30, SS_{res}=535.9).

Other combinations of independent variables, which are not shown in Table 4.4, were able to explain only between 10 and 20 % of the total variation in Iv_{tot}. Including these other variables did not improve adjusted R^2 values, and they necessitated additional parameters. Consequently, for this relationship (*i.e.* total stand volume growth rates, which include the growth of all species in the stand, as a function of stand/site attributes), the most parsimonious model is:

$$Iv_{tot} = 0.222 * SDI_{dysw}^{-0.03} * SDI_{dyd}^{0.99} * HT_{sw}^{0.11} * HT_{aw}^{0.31} * PBA_{dec}^{-0.93} \qquad (4.5)$$

Where Iv_{tot} is total stand periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); SDI_{dysw} is the dynamic spruce SDI; SDI_{dyd} is the dynamic deciduous SDI; HT_{sw} is average spruce height; HT_{aw} is average trembling aspen height; PBA_{dec} is percentage of basal area of deciduous. The adjusted R^2 for this model is 0.31.

Fit statistics for the most parsimonious model (Equation 4.5) and for other different models with similar performance and fit statistics are presented in Table 4.4. The distribution of studentized residuals for the best model and for the second best model is shown in Figure 4.3.

4.4 Discussion

Average biomass periodic annual increment for trembling aspen in boreal mixedwoods has been reported to range from 3.9 $Mg \cdot ha^{-1}$ in mixed stands to 4.8 $Mg \cdot ha^{-1}$ in pure aspen stands, in a 48-105 years of age at breast height range (MacPherson *et* al., 2001) (approximately 9.2 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ to 11.5 $m^3 \cdot ha^{-1} \cdot yr^{-1}$); for white spruce growing in mixed stands and with ages ranging from 4 to 64 years at breast height, reported average biomass periodic annual increment values are around 1.5 $Mg\cdot ha^{-1}$ (MacPherson *et* al., 2001) (approximately 3.3 $m^3\cdot ha^{-1}\cdot yr^{-1}$). Other reports for natural mixed unmanaged stands indicate stem volume periodic increment values of about 2.5 $m^3\cdot ha^{-1}\cdot yr^{-1}$ for white spruce, and also an average of 4.8 $m^3\cdot ha^{-1}\cdot yr^{-1}$ for white spruce growing in stands that have been previously released from deciduous competition, ranging from 15 to 60 years of age (Yang, 1989). The volume increment values that I obtained for trembling aspen, white spruce, and for the whole stand appear to be largely within the range of variation for volume/biomass increment previously reported for this type of forests.

None of the indicators of site productivity for both pure and mixed stands that were available for this study (*i.e.* average site index, moisture regime, and nutrient regime) showed a significant effect on either white spruce or trembling aspen volume increment in the models evaluated. In the case of total stand volume increment, average site index showed significance in one of the models, although its effects were small and did not contribute to better model performance. The lack of site index effects is likely due to the fact that most plots included in this analysis come from circum-mesic sites with Clay-Loam and Silty Clay Loam soils which are moderately-well to imperfectly drained.

However, the general basic relationships proposed for both species (Equations 4.3 for aspen and 4.4 for white spruce) and for the stand as a whole, provide a fairly good characterization of the relationship between volume growth rate of these two species with growing stock for these mid-rotation and mature boreal pure and mixed natural unmanaged stands. This is supported by the model goodness of fit, the significance of parameters and the analysis of their residuals. Additionally, the resulting functions appear to be fairly realistic representations of the relationship between trembling aspen, white spruce, and total stand volume growth, with stand growing stock characteristics.

Results for trembling aspen suggest a positive effect of deciduous density and relative site occupancy on aspen volume increment. Figure 4.4 illustrates changes in volume increment for trembling aspen with changes in deciduous and spruce relative site occupancy (*i.e.* dynamic SDI). While the presence of understory spruce in boreal mixedwoods does not seem to have a negative impact on aspen productivity (MacPherson *et* al., 2001), spruce occupancy in later stages of stand development appears to be negatively influencing trembling aspen volume increment in these mid-rotation boreal mixedwood stands, as suggested by the negative sign of SDI_{dysw} on aspen Iv (Table 4.2). Although significant, this negative effect of spruce on aspen volume increment appears to be rather small.

Results for spruce indicate a significant positive relationship between white spruce volume increment and basal area of both spruce (BAH_{sw}) and trembling aspen (BAH_{dec}) (Table 4.3), although the aspen effect is small. My results also suggest that the presence of aspen in boreal mixed stands could enhance the productivity of white spruce in mid-rotation and mature stands, which also agrees with previous observations for similar forests in the same region (Man and Lieffers 1999; MacPherson *et* al. 2001). Figure 4.5 illustrates the variation in spruce I_v with changes in basal area of both spruce and aspen. The positive sign of the parameters relating to SDI_{dyd} and BAH_{dec} in the models shown (Table 4.3), suggest that the presence of a deciduous component is having a significant positive effect on white spruce volume increment. These results are consistent with Legare *et* al. (2004), who found that 5 to 15% of trembling aspen basal area in mixture with black spruce was beneficial to black spruce volume growth. My models indicate that increases in spruce volume increment are largest when spruce basal area is above 20 $m^2 \cdot ha^{-1}$.

Average aspen height appears to be positively affecting spruce growth (Table 4.3), which appears to be consistent among the models presented. This would indicate that possible competition from tall deciduous trees is not an important factor affecting spruce growth for these stands. The positive exponent for spruce height is consistent with other studies indicating that tree growth typically increases with size (*e.g.* Filipescu and Comeau 2007a; Huang *et* al. 2013). Figure 4.6 illustrates changes in white spruce volume increment as a function of spruce and deciduous dynamic SDI, showing a positive effect of both spruce SDI and deciduous SDI on spruce Iv, although the effect of spruce is smaller than the effect of trembling aspen.

A fairly low proportion of the variation in total stand volume increment could be explained by the model that showed the best performance (R^2=0.31, equation 4.5). The complexity of the interactions between spruce and aspen and the contributions of other factors, limit the ability of these simple models to explain larger amounts of variation in growth (Filipescu and Comeau 2007b; Huang *et* al. 2013). In general, this model suggests a beneficial effect of trembling aspen and a small but negative effect of white spruce on total stand volume growth rates, as suggested by the signs of their respective parameter estimates (negative for SDI_{dysw} and positive for SDI_{dyd}). Average height of both species has a positive effect on stand volume increment. Figure 4.7 illustrates changes in stand volume increment as a function of changes in SDI for both aspen and spruce. It is important to note that total SDI (sum of SDI_{dyd} and SDI_{dysw}) has been constrained to a maximum value of approximately 1300 so that it does not go over the data range registered for the stands. However, individual SDI_{dyd} and SDI_{dysw} are above this value. The nearly planar nature of the surface shown in Figure 4.7 indicates that SDI_{dyd} and SDI_{dysw} are the predominant factors influencing stand volume increment.

Maximum stockability has been suggested to be relatively invariant for tree species, implying that the intercept of maximum mean tree size-density relationships is essentially constant regardless of age, environment, and management conditions (Reineke 1933; Westoby 1984). However, variation in attainable maximum stockability among stands has been proposed as one of the main mechanisms that could significantly impact productivity of forests (DeBell *et* al. 1989; Harms *et* al. 1994). Recent studies for boreal mixedwoods suggested that both the slope and the intercept of the maximum size-density relationship vary with changes in stand composition and site characteristics (Reyes-Hernandez *et* al. 2013), and that a decline in maximum densities (*i.e.* stockability) as the proportion of aspen in the stand decreases could be expected for these boreal mixed stands.

According to my results (Figure 4.7) decreases in SDI of either spruce or aspen, or both, at maximum stocking densities, are associated with a decrease in total stand volume increment. This also indicates that total volume increment is highest when SDI of both species combined is at its maximum possible, suggesting important ecological combining ability. A mixture of spruce and aspen with a combined total dynamic SDI of 1200 (SDI_{dysw}~600 and SDI_{dyd} ~ 600) would be close to full site occupancy, and would imply that the highest total PAI has been achieved (approximately 12 $m^3 \cdot ha^{-1} \cdot yr^{-1}$) for the ranges of SDI of the stands under consideration. This indicates that variation in maximum stockability in boreal mixedwoods is an important factor affecting stand periodic annual increment (Figure 4.7).

Differences in maximum stockability are most likely a result of complex interactions between environmental conditions, stand history, crown architecture, species autoecology, and physiological differences among species (DeBell *et* al. 1989; Harms *et* al. 1994; Harms *et* al. 2000; Comeau *et* al. 2010). High stockabilities for a given species have also been attributed to a complex crown-class structure that allows more efficient site occupancy with more active leaf area (Harms *et* al. 1994).

It has also been documented that leaf structure and photosynthetic capacity are sensitive to the light environment (Kozlowski *et* al., 1991). Therefore, leaf and crown differences among stands and crown structure which occur in response to high solar radiation intensities and high sun angles, could increase penetration of sunlight deep into the canopy (Harms *et* al., 2000). Also, a relatively low incidence of pests, a long growing season, suitable soil conditions (temperature and moisture), and appropriate air temperature could enhance component species growth rates among different sites (Harms *et* al., 1994), and lead to variability in their maximum stockabilities.

4.5 Conclusions

Effects of competition and facilitation are difficult to separate even in very well established experiments (Callaway and Walker, 1997) and especially in natural unmanaged stands of trees, due to variation in sizes, developmental stages, and other factors. Although the data sets that were used in this study include a wide range of variation in sizes, species compositions, and developmental stages, the lack of information of environmental conditions and availability of resources at the local level limits my ability to analyze and interpret the results. Effects of mixtures are indeed further complicated with changes in stands developmental stage, type of mixtures, and site conditions (Holmgren *et* al., 1997), which is also the case for boreal mixedwoods (Filipescu and Comeau, 2007b). However, results presented here indicate increased stocking and productivity at the stand level with increases in SDI of either spruce or aspen or both.

My results, which suggest continuous increment in volume for these stands with increasing maximum stocking densities of either of the two main species, appear to be contradictory with classic works in forest literature that suggest a decline in forest productivity under intense competition (Langsaeter hypothesis) (Langsaeter, 1941). However, there is evidence in this study and other studies (DeBell *et* al. 1989; Harms *et* al. 1994; Harms *et* al. 2000), indicating that maximum stockability might be leading to an increase in forest productivity. My results indicate a need for future discussion and research to clarify and/or support these and similar findings for other tree species.

In mixed species stands, spatial distribution patterns for the component species and changes in these patterns over time might also play a significant role in growth rates, as this might influence the occurrence of particular interactions among the species (Garber and Maguire, 2004) and the productivity of the stand. For example, in a two-species mixture, mixtures of single trees inside patches or groups are expected to experience a much closer niche occupation than trees that are aggregated in groups or clusters of the two species within the stand (Pretzsch *et* al., 2010). Further analysis of the effects of spatial distribution of trees, light capture and utilization, and resource availability and utilization in mixed stands and their influence on growth of component species in mixed and pure boreal stands would be useful in explaining the findings from this study.

4.6 References

Beckingham, J.D.; and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Special Report No 5. Natural Resources Canada. Canadian Forest Service-Northern forestry Centre. Edmonton, AB.

Callaway, R.M.; and Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology. 78:1958-1965.

Chen, H.Y.H.; and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Reviews. 10:137-166.

Comeau, P.G.; White, M.; Kerr, G.; and Hale, S.E. 2010. Maximum density-size relationships for Sitka spruce and coastal Douglas-fir in Britain and Canada. Forestry. 83(5):461-468. doi:10.1093/forestry/cpq028

Comeau, P.G.; Kabzems, R.; McClarnon, J.; and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. For. Chron. 81(4):559-574

Comeau, P.; Filipescu, C.N.; Kabzems, R.; and DeLong, C. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern B.C. Can. J. For. Res. 34:2277-2283.

Constabel, A.J.; and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26:1008-1014.

Curtis, R.O. 1970. Stand density measures: an interpretation. For. Sci.16:403-414.

Davis, L.S.; Johnson, K.N.; Bettinger, P.; and Howard, T.E. 2001. Forest management: to sustain Ecological, Economic, and Social value. 4th Edition. Waveland Press, Inc. Illinois, USA. 804 pp.

DeBell, D.S.; Harms, W.R.; and Whitesel, C.D. 1989. Stockability: a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern United States. For. Sci. 35(3):708-719.

Drew, T.J.; and Flewelling, W. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. 23(4):517-534.

Filipescu, C.; and Comeau, P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Forest Management Branch. 2005. Permanent Sample plot (PSP) field procedures manual. Alberta Sustainable Resource Development. Public Lands and Forest Division. Edmonton, AB.

Garber, S.M.; and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. For. Sci. 50(1):92-105.

Groot, A. 1999. Effects of shelter and competition on the early growth of planted white spruce (*Picea glauca*). Can. J. For. Res. 29:1002-1014.

Groot, A.; and Carlson, D.W. 1996. Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. Can. J. For. Res. 26:1531-1538.

Harms, W.R.; Whitesell, C.D.; and DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126(1):13-24.

Harms, W.R.; DeBell, D.S.; and Whitesell, C.D. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Can. J. For. Res. 24:511-521.

Helms, J.A. (ed). 1998. The dictionary of Forestry. Society of American Foresters. Bethesda, MD. USA. 210 pp.

Holmgren, M.; Scheffer, M.; and Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. Ecology. 78:1966-1975.

Huang, J.G.; Stadt, K.J.; Dawson, A.; and Comeau, P.G. 2013. Modelling growth-competition relationships in trembling aspen and white spruce mixed boreal forests of western Canada. PLos ONE 8(10): e77607. doi:10.1371/journal.pone.0077607

Huang, S. 1994. Individual tree volume estimation procedures for Alberta: methods for formulation and statistical foundations. Forest Resources Information Branch. Land and For. Serv. Technical Report # 1. T/288. Edmonton, AB. 80 pp.

Huang, S.; Titus, S.J.; Lakusta, T.W.; and Held, R.J. 1994. Ecologically based individual tree height-diameter models for major Alberta tree species. Alberta Env. Protection. Land and Forest Services. Forest Management Division. 27 p.

Innes, J.C.; Ducey, M.J.; Gove, H.J.; Leak, W.B.; and Barrett, J.P. 2005. Size-density metrics, leaf area, and productivity in eastern white pine. Can. J. For. Res. 35: 2469-2478.

Jose, S.; Williams, R.; and Zamora, D. 2006. Belowground ecological interactions in mixed-species forest plantations. For. Ecol. Manage. 233: 231-239.

Kelty, M.J. 2006. The role of species mixtures in plantations forestry. For. Ecol. Manage. 233: 195-204

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed species stands. In: M. J. Kelty, B. C. Larson and C. D Oliver (eds). The ecology and silviculture of mixed species forests. pp 125-141. Kluwer Academic Publishers. Dordrecht. 287 p.

Kozlowski, T.T.; Kramer, P.J.; and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press. New York. 657 pp.

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog (About thinning in even-aged stands of spruce, fir and pine), Meddel. f.d. Norske Skogforsoksvesen. 8: 131-216.

Legare, S.; Pare, D.; and Bergeron, Y. 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. Can. J. For. Res. 34:405-416. doi: 10.1139/X03-251

Lieffers, V.J.; and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Long, J.N.; and Shaw, J.D. 2010. The influence of compositional and structural diversity on forest productivity. Forestry. 83(2): 121-128. doi:10.1093/forestry/cpp033

Long, J.N.; and Daniel, T.W. 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For. 5:93-96.

MacDonald, G.B. 1996. The emergence of boreal mixedwood management in Ontario: background and prospects. In: Advancing boreal mixedwood management in Ontario. Ed: C.R. Smith and G.W. Crook. Natural Resources Canada. CFS. Sault Ste. Marie, Ontario. pp 11.

MacPherson, D.M.; Lieffers, V.J.; and Blenis, P.V. 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For. Chron. 77:451-356

Man, R.; and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75(3):505-513.

Nyland, R.D. 2002. Silviculture: concepts and applications. Waveland Press, Inc. Illinois, USA. 682 p.

O'Hara, K.L.; and Gersonde, R.F. 2004. Stocking control concepts in uneven-aged silviculture. Forestry. 77:131-143.

Oliver, C.D.; and Larson, B.C. 1996. Forest stand dynamics. Wiley, New York. 520 pp.

Peterson, E.B.; and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Can. For. Serv. North. Cent. Spec. Rep. 1. 252 pp.

Pretzsch, H. 2009. Forest dynamics, growth and yield: from measurement to model. Springer-Verlag. Berlin Heidelberg. 664 p.

Pretzsch, H.; Block, J.; Dieler, J.; Dong, P.H.; Kohnle, U.; Nagel, J.; Spellman, H.; and Zingg, A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67:712. doi:10.1051/forest/2010037

Ratkowsky, D.A. 1990. Handbook of nonlinear regression. Marcel Dekker, Inc. New York. 241 p.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Reyes-Hernandez, V.; Comeau, P.G.; and Bokalo, M. 2013. Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. For. Ecol. Manage. 289:300-311.

SAS. 2010. Statistical Analysis System for windows, V 9.2. SAS-Institute, Inc. Cary, N.C. USA.

Shaw, J.D. 2000. Application of stand density index to irregularly structured stands. West. J. Appl. For. 15: 40-42.

Smith, D.M.; Larson, B.C.; Kelty, M.J.; and Ashton, P.M.S. 1997. The practice of Silviculture: applied forest ecology. 9th edition. John Wiley & Sons. USA. 537 p.

Vales, D.J.; and Bunnell, F.L. 1988. Relationships between transmission of solar radiation and coniferous forest stand characteristics. Agric. For. Meteor. 43:210-233.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge University Press. Cambridge, MA. 237 pp.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167-225.

Yang, R.C. 1989. Growth response of white spruce to release form trebling aspen. Northern Forestry Centre. Forestry Canada. Information report NOR-X-302. Edmonton, AB. Canada. 24 p.

Table 4.1 Summary of characteristics of the boreal pure and mixed stands included in the analysis of periodic annual increment in volume.

Variable	**N**	**Mean**	**SD**	**Min**	**Max**
Iv_{sw} = white spruce periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$)	163	3.5	2.85	0.01	12.7
Iv_{aw}= trembling aspen periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$)	163	3.4	2.96	0.01	12.8
Iv_{tot}= total stand periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$)	163	6.8	2.42	1.6	14.7
PBA_{sw}= percentage of basal area of white spruce	163	48.1	34.6	0.1	100.0
PBA_{dec}= percentage of basal area of deciduous	163	51.1	34.8	0.1	100.0
BAH_{dec}= deciduous basal area per hectare ($m^2 \cdot ha^{-1}$)	163	20.4	14.0	0.0	58.0
BAH_{sw}= white spruce basal area per hectare ($m^2 \cdot ha^{-1}$)	163	23.6	19.4	0.0	72.3
BAH_{tot}= Total stand basal area per hectare ($m^2 \cdot ha^{-1}$)	163	44.2	10.9	12.8	74.6
HT_{sw}= Average white spruce height (m)	163	16.3	7.2	0.0	28.6
HT_{aw}= Average trembling aspen height (m)	163	19.3	8.8	0.0	30.5
SDI_{dyd}= dynamic SDI deciduous species	163	402	275	0.0	1137
SDI_{dysw}= dynamic SDI white spruce	163	430	346	0.0	1339
SDI_{dyt}= total stand dynamic SDI	163	831	197	255	1306
SI_p= Average site index (m)	163	18.0	2.51	8.1	25.1
N_{ur}=nutrient regime	163	3.0	1.0	2.0	5.0
M_{or}=moisture regime	163	5.0	1.0	4.0	8.0

N= number of plots; SD= standard deviation; Min=minimum value; Max=maximum value.

Table 4.2 Fit statistics and parameter estimates for the final selected model (equation 4.3 in text) and alternative models for trembling aspen volume increment (Iv_{aw}).

Model	SS_{res}	Parameter					Adj R^2
		β_0	β_1	β_2	β_3	β_4	
$Iv_{aw}=\beta_0*TPH_{dec}^{\beta1}*HT_{sw}^{\beta2}*HT_{aw}^{\beta3}$	261.7	4.2E-7 (5.5E-7)	1.02 (0.07)	0.20 (0.11)	2.96 (0.26)		0.80
$Iv_{aw}=\beta_0*SDI_{dyd}^{\beta1}*HT_{sw}^{\beta2}*HT_{aw}^{\beta3}$	297.3	0.0001 (0.0001)	1.27 (0.12)	0.12 (0.11)	0.68 (0.27)		0.76
$Iv_{aw}=\beta_0*BAH_{dec}^{\beta1}*HT_{sw}^{\beta2}*HT_{aw}^{\beta3}$	298.9	0.007 (0.006)	1.26 (0.12)	0.11 (0.11)	0.66 (0.27)		0.76
$Iv_{aw}=\beta_0*SDI_{dysw}^{\beta1}*SDI_{dyd}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}$	296.3	0.0002 (0.0002)	-0.020 (0.032)	1.24 (0.12)	0.17 (0.14)	0.65 (0.27)	0.76

n=163; Iv_{aw} =trembling aspen volume increment ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); TPH_{dec}= deciduous density ($trees \cdot ha^{-1}$); HT_{sw}=Average white spruce height (m); HT_{aw} = average aspen height (m); SDI_{dyd}=dynamic SDI for deciduous species; SDI_{dysw}=dynamic SDI for white spruce; BAH_{dec}=deciduous basal area ($m^2 \cdot ha^{-1}$); SS_{res}=Residual sum of squares; Adj R^2= adjusted R squared; β_0-β_5= parameters estimated; standard errors are shown in parenthesis.

Table 4.3 Fit statistics and parameter estimates for the final selected model (equation 4.4 in text) and alternative models for white spruce volume increment (Iv_{sw}).

Model	SS_{res}	Parameter						Adj R^2
		β_0	β_1	β_2	β_3	β_4	β_5	
$Iv_{sw}=\beta_0*SDI_{dyd}^{\beta1}*SDI_{dysw}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}$	187.7	0.001 (0.001)	0.99 (0.09)	0.06 (0.04)	0.32 (0.18)	0.15 (0.23)		0.84
$Iv_{sw}=\beta_0*BAH_{dec}^{\beta1}*BAH_{sw}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}$	194.6	0.024 (0.17)	0.063 (0.048)	0.94 (0.09)	0.605 (0.177)	0.04 (0.22)		0.83
$Iv_{sw}=\beta_0*BAH_{dec}^{\beta1}*BAH_{sw}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}$	189.2	0.078 (0.07)	0.46 (0.22)	0.77 (0.12)	0.52 (0.18)	0.08 (0.23)	-0.45 (0.24)	0.83
$Iv_{sw}=\beta_0*SDI_{dyd}^{\beta1}*SDI_{dysw}^{\beta2}*HT_{sw}^{\beta3}$	221	0.006 (0.004)	0.14 (0.02)	0.912 (0.08)	0.26 (0.11)			0.80

n=163; Iv_{sw} =white spruce periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot yr^{-1}$); BAH_{dec}=deciduous basal area ($m^2 \cdot ha^{-1}$); BAH_{sw}=spruce basal area ($m^2 \cdot ha^1$); HT_{sw}=Average white spruce height (m); HT_{aw}=average aspen height (m); TPH_{dec}= deciduous density ($trees \cdot ha^{-1}$); TPH_{sw}= white spruce density ($trees \cdot ha^{-1}$); SDI_{dyd}=dynamic SDI for deciduous species; SDI_{dysw}=dynamic SDI for white spruce; PBA_{dec}=percentage of basal area in deciduous; SSE= Residual sum of squares; Adj R^2= adjusted R squared; β_0-β_5= parameters estimated; standard errors are shown in parenthesis.

Table 4.4 Fit statistics and parameter estimates for the final selected model (Model 4.5 in text) and alternative models for total stand volume increment (Iv_{tot}).

Model	SS_{res}	Parameter							Adj R^2
		β_0	β_1	β_2	β_3	β_4	β_5	β_6	
$Iv_{tot}=\beta_0*SDI_{dysw}^{\beta1}*SDI_{dyd}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}$	540.0	0.222 (0.16)	-0.03 (0.03)	0.99 (0.17)	0.11 (0.14)	0.31 (0.21)	-0.93 (0.17)		0.31
$Iv_{tot}=\beta_0*BAH_{dec}^{\beta1}*BAH_{sw}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}$	545.7	4.0 (2.5)	0.95 (0.16)	-0.009 (0.03)	0.04 (0.14)	0.32 (0.21)	-0.88 (0.17)		0.30
$Iv_{tot}=\beta_0*SDI_{dysw}^{\beta1}*HT_{sw}^{\beta2}*SDI_{dyd}^{\beta3}*HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}*SI_p^{\beta6}$	535.9	0.32 (0.28)	-0.03 (0.03)	0.14 (0.14)	1.02 (0.17)	0.35 (0.21)	-0.95 (0.17)	-0.23 (0.25)	0.30

n=163; Iv_{tot}=total stand periodic annual increment in volume ($m^3\cdot ha^{-1}\cdot yr^{-1}$); SDI_{dyd}=dynamic SDI for deciduous species; SDI_{dysw}=dynamic SDI for white spruce; HT_{sw}=average white spruce height (m); HT_{aw}=average aspen height (m); PBA_{dec}=percentage of basal area in deciduous; BAH_{dec}=deciduous basal area ($m^2\cdot ha^{-1}$); BAH_{sw}=spruce basal area ($m^2\cdot ha^1$); SI_p=average site index (spruce and aspen); SS_{res}=residual sum of squares; Adj R^2=adjusted R squared; β_0-β_6= parameters estimated; standard errors are shown in parenthesis.

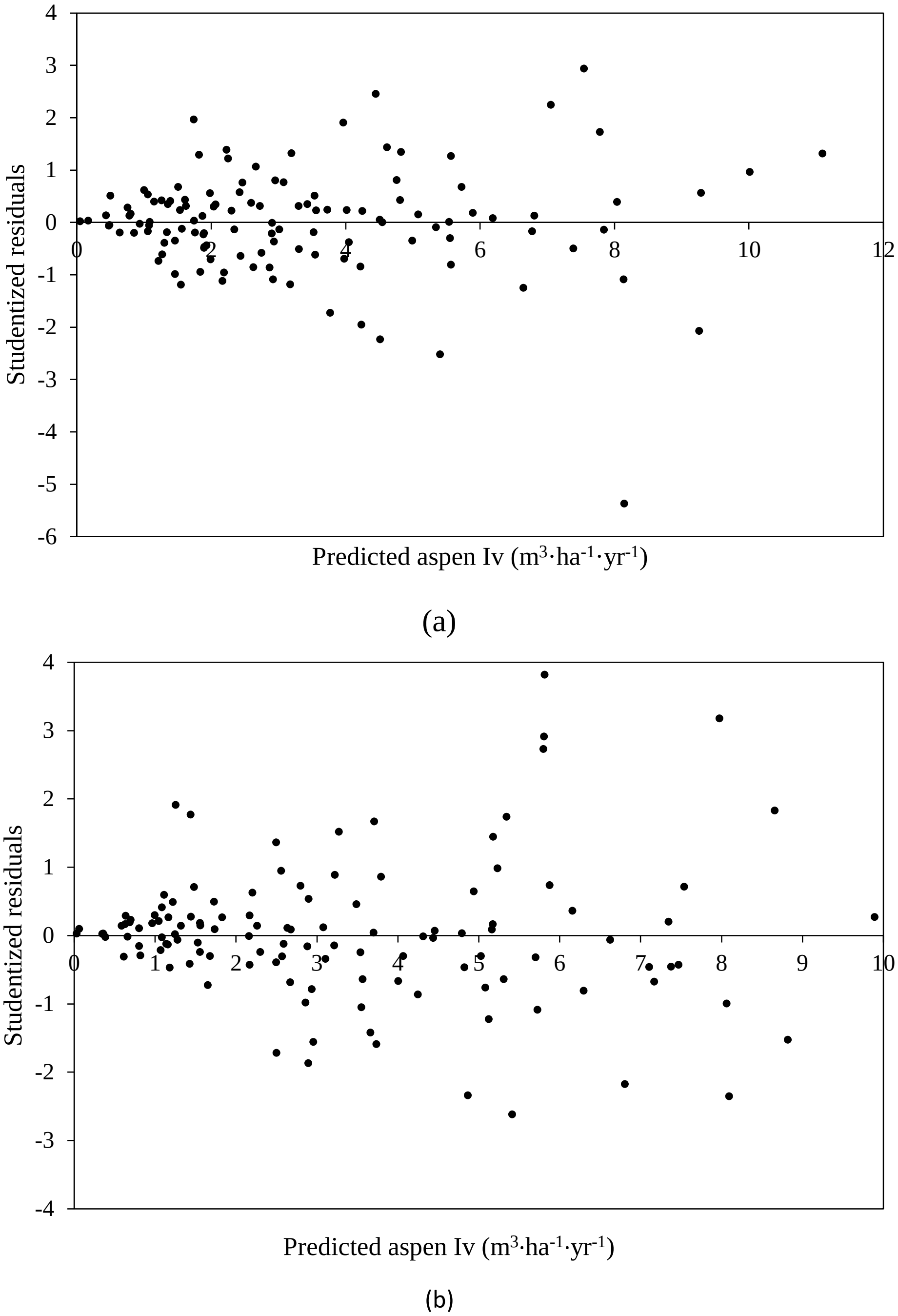
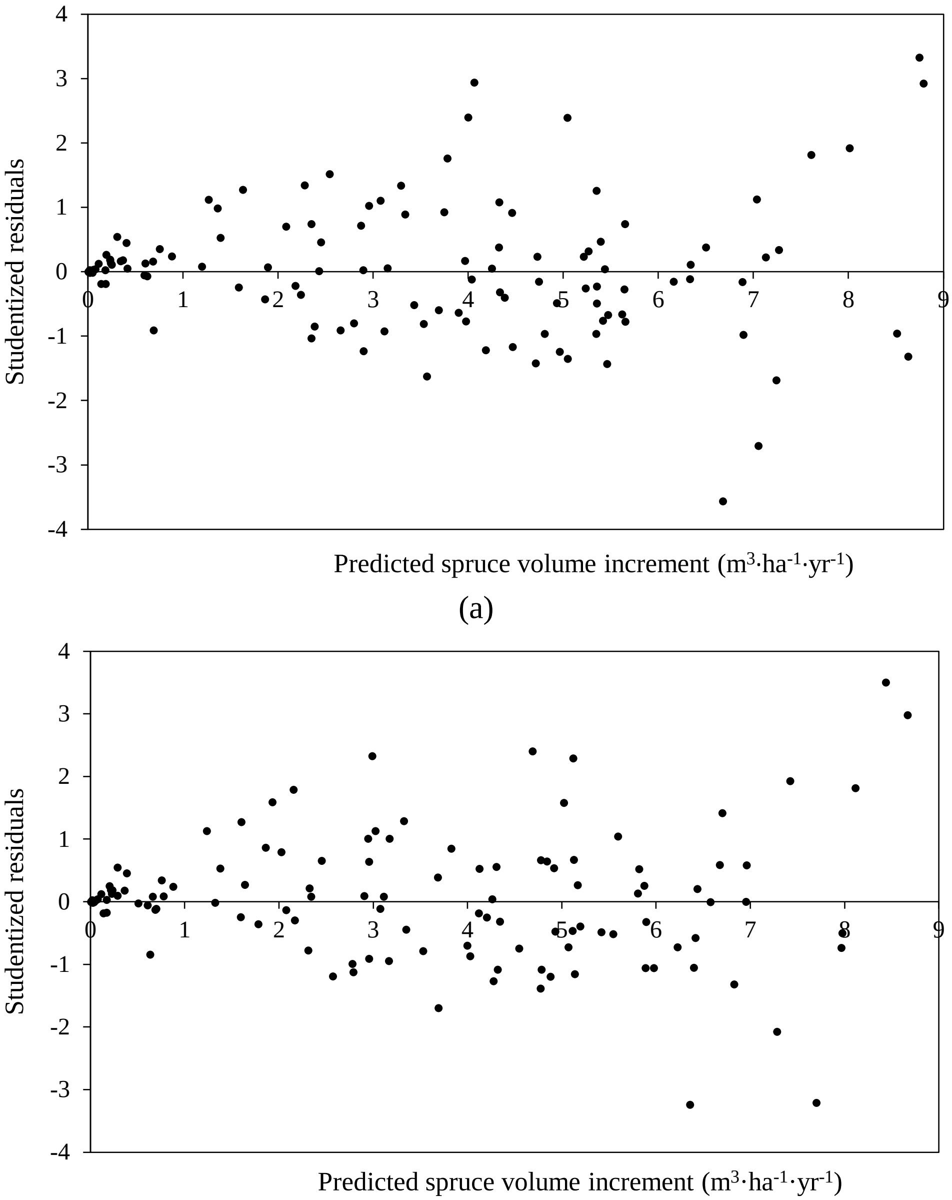


Figure 4.1 Distribution of residuals for the best model (a) and for the second best (b) model for trembling aspen volume increment.

(a): $Iv_{aw}=\beta_0*TPH_{dec}^{\beta1}*HT_{sw}^{\beta2}*HT_{aw}^{\beta3}$; (b): $Iv_{aw}=\beta_0*SDI_{dysw}^{\beta1}*SDI_{dyd}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}$

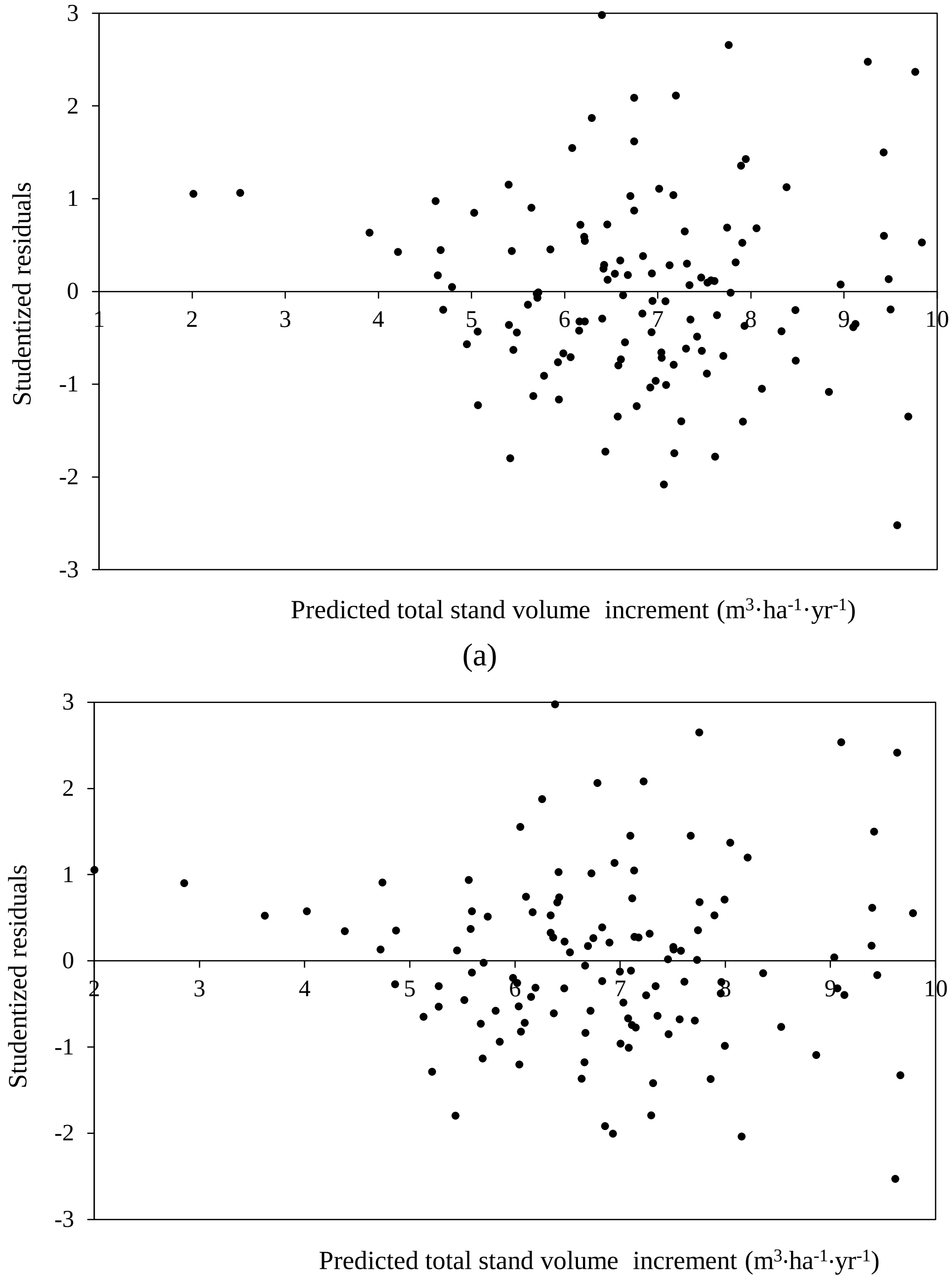


(a)

(b)

Figure 4.2 Distribution of residuals for the best model (a) and for the second best (b) model of spruce volume increment.

(a): $Iv_{sw}=\beta_0*SDI_{dysw}{}^{\beta 1}*SDI_{dyd}{}^{\beta 2}*HT_{sw}{}^{\beta 3}*HT_{aw}{}^{\beta 4}$ (b): $Iv_{sw}=\beta_0*BAH_{dec}{}^{\beta 1}*BAH_{sw}{}^{\beta 2}*HT_{sw}{}^{\beta 3}*HT_{aw}{}^{\beta 4}$



(a)

(b)

Figure 4.3 Distribution of residuals of the best model (a) and for the second best model (b) for total volume increment (Iv_{tot}).

(a): $Iv_{tot}=\beta_0*SDI_{dysw}^{\beta1}*SDI_{dyd}^{\beta2}*HT_{sw}^{\beta3}*$

$HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}$; (b): $Iv_{tot}=\beta_0*BAH_{dec}^{\beta1}*BAH_{sw}^{\beta2}*HT_{sw}^{\beta3}*HT_{aw}^{\beta4}*PBA_{dec}^{\beta5}$

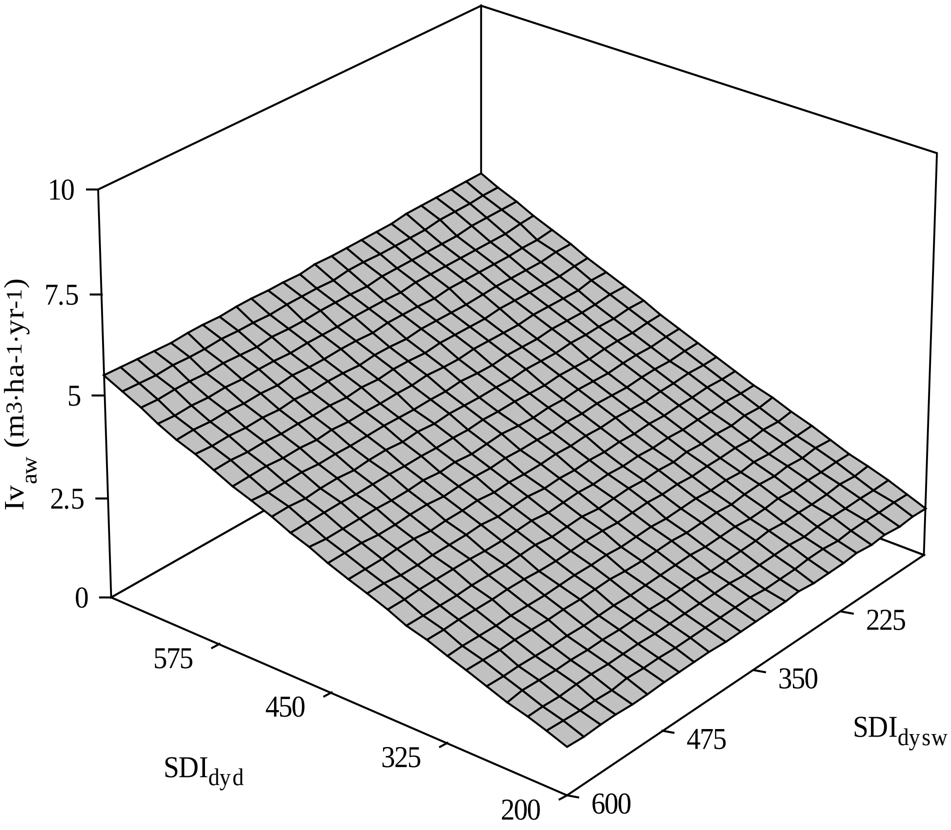


Figure 4.4 Illustration of changes in trembling aspen volume increment (Iv_{aw}) as a function of deciduous dynamic SDI (SDI_{dyd}) and spruce dynamic SDI (SDI_{dysw}) (HT_{sw} and HT_{aw} held constant).

Model: $Iv_{aw}=0.0002*SDI_{dysw}^{-0.020}*SDI_{dyd}^{1.24}*HT_{sw}^{0.17}*HT_{aw}^{0.65}$

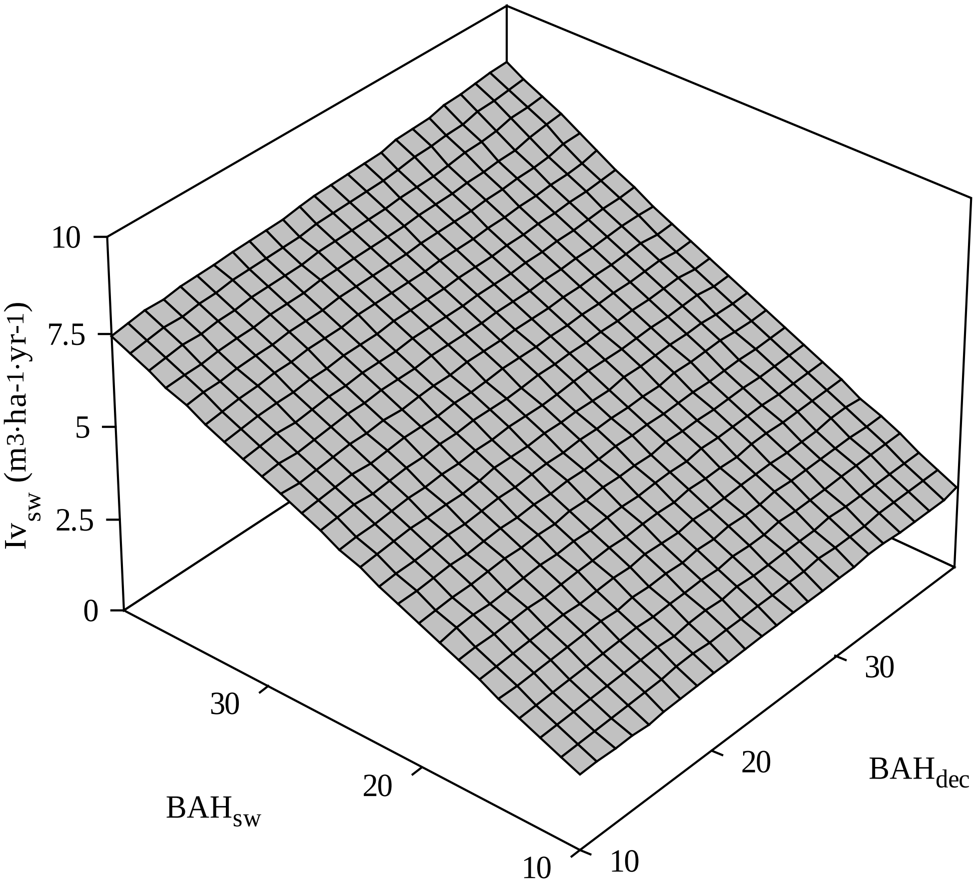


Figure 4.5 Illustration of changes in white spruce volume increment (Iv_{sw}) as a function of basal area per hectare in deciduous (BAH_{dec}) and spruce (BAH_{sw}) (HT_{sw} and HT_{aw} held constant). Model:

$Iv_{sw}=0.024*BAH_{dec}^{0.063}*BAH_{sw}^{0.94}*HT_{sw}^{0.61}*HT_{aw}^{0.04}$

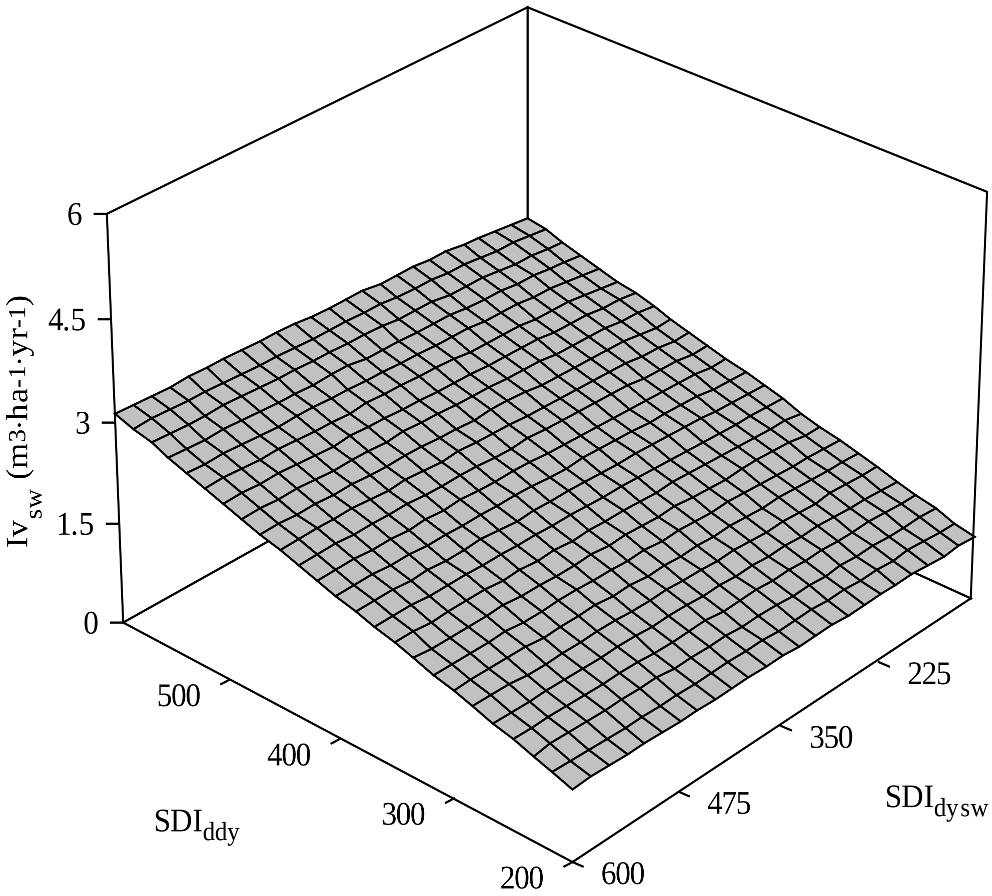


Figure 4.6 Illustration of changes in white spruce volume increment (Iv_{sw}) as a function of deciduous dynamic SDI (SDI_{dyd}) and spruce dynamic SDI (SDI_{dysw}); (HT_{sw} and HT_{aw} held constant). Model: $Iv_{sw}=0.001*SDI_{dysw}^{0.99}*SDI_{dyd}^{0.06}*HT_{sw}^{0.32}*HT_{aw}^{0.15}$

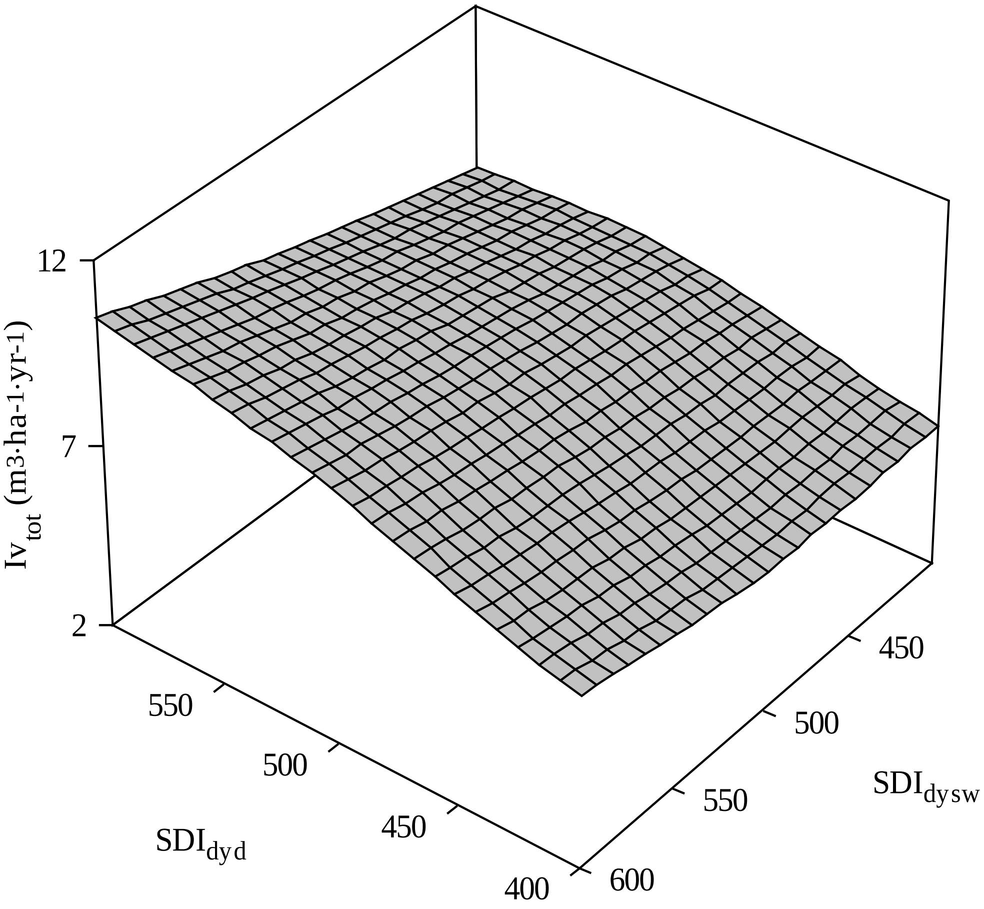


Figure 4.7 Illustration of changes in total volume increment (Iv_{tot}) as a function of dynamic deciduous SDI (SDI_{dyd}) and dynamic spruce SDI (SDI_{dysw}). HT_{sw} and HT_{aw} held constant and PBA_{dec} varying with changes in SDI_{dyd}.

Model: $Iv_{tot}=0.222*SDI_{dysw}{}^{-0.03}*SDI_{dyd}{}^{0.99}*HT_{sw}{}^{0.11}*HT_{aw}{}^{0.31}*PBA_{dec}{}^{-0.93}$

Chapter 5 Survival probability of white spruce and trembling aspen in boreal pure and mixed stands experiencing self-thinning

5.1 Introduction

Tree mortality has long term effects on stand composition, structure, productivity, and dynamics (Caspersen and Kobe, 2001; Mencuccini *et* al. 2005; Chen *et* al. 2008). While large scale disturbances, such as wildfires and insect outbreaks, may act as whole stand replacing events (Turner *et* al., 1997), mortality of individuals results from competition and carbon starvation, and other events (such as root or stem diseases, insects, or snow or wind damage) (Kneeshaw and Bergeron, 1998). Mortality due to these other events has been also called background mortality (Kenkel, 1998). In general, mechanical damage and the inability of trees to defend themselves against diseases are among the most important factors that cause background mortality of trees in forest stands (Luo and Chen, 2011).

Despite the fact that the main causes are known, mortality is not an easy event to model and predict, and as a component of growth and yield estimation models it remains poorly understood (Yang *et* al., 2003). A number of studies have shown that individual tree characteristics and stand level attributes can provide reliable estimates of the probability of mortality (or survival) of individual trees in forest stands (Yang *et* al. 2003; Chen *et* al. 2008).

In the specific case of density-dependent mortality, which is thought to be caused mainly by the inability of trees to maintain a positive carbon balance and then die as a consequence of carbon starvation (Weiner, 1990; Guneralp and Gertner, 2007), it is widely assumed that the relative size of an individual tree as related to its neighbors has a substantial influence on the probability of a tree survival (Westoby 1984; Weiner 1990). The smallest trees in the stand are the most affected by asymmetric competition (i.e. larger individuals affect smaller individuals in their ability of resources acquisition), thus variation in tree mortality can be better explained with measures of tree size, stand density, indicators of competition, and tree growth rate (Hamilton 1986; Chen *et* al. 2008; Yang and Huang 2013). With a limited supply of resources, the smallest size classes are usually the most affected and higher mortality rates of smaller individuals is anticipated (Westoby 1984; Weiner 1990). The relative competitiveness of the species (*i.e.*degree of intraspecific competition), stand composition, tree longevity, and other factors influence the occurrence of this type of mortality (Chen *et* al. 2008; Yang and Huang 2013).

In mixed species stands where species with differences in morphology and physiological characteristics, as well as ecological requirements (such as differences in shade tolerance) are growing together, mortality is more difficult to understand and predict than in even-aged mono-specific stands (Westoby 1984; Yang *et* al. 2003). The capacity of some species to live and photosynthesize in a shaded environment can provide them with certain advantages against competition. For example, in boreal mixedwoods, in which a shade tolerant species such as white spruce is able to grow under the canopy of a shade intolerant species such as trembling aspen, there is generally enough light reaching the understory to allow white spruce to survive and grow (Lieffers and Stadt 1994; Chen and Popadiouk 2002).

The logistic function has been the standard approach for modeling the probability of mortality or survival for a number of tree species (Monserud, 1976; Hamilton 1986; Monserud and Sterba, 1999; Yang *et* al. 2003), and it represents perhaps the best approach for modelling tree mortality behavior (Yang *et* al. 2003; Feng *et* al. 2006; Groom *et* al. 2012). Standard logistic regression analysis works well with data collected in permanent sample plots in which the time interval between consecutive measurements is frequently homogenous (i.e. equal number of years between consecutive measurements). When the time interval is not equal among measurements, adjustments to the traditional logistic model may have to be made (Monserud, 1976).

Models for predicting the probability of individual tree mortality have been developed for boreal tree species in western Canada including white spruce, trembling aspen, and jack pine (Yao *et* al. 2001; Yang *et* al. 2003, Yang and Huang, 2013). In the case of trembling aspen and white spruce in boreal forests of Alberta, Yang *et* al. (2003) found that a number of stand attributes might be powerful predictors of individual tree mortality, including total stand basal area, diameter increment, relative size, and basal area of larger deciduous and conifer trees. These studies, however, did not evaluate whether probability of survival or probability of mortality of individual trees in mixed stands experiencing self-thinning is affected by stand composition.

The objective of this study was to the examine factors influencing the probability of survival of individual trembling aspen and white spruce trees growing in pure and mixed stands in Alberta boreal forests, which were previously identified as experiencing density-dependent mortality (Reyes-Hernandez *et* al., 2013). It is important to note that it is not the purpose of this Chapter to generate new and more powerful models to predict individual tree survival or mortality of the above mentioned species in a more general context (i.e. large scale or not background mortality), since these models have already been generated and validated (Yang *et* al. 2003; Yang and Huang 2013); rather, my objective is to evaluate some of the stand and individual tree characteristics that might be affecting and defining mortality occurring in self-thinning stands only.

In this Chapter, I hypothesize that the probability of survival of individual trees in boreal pure and mixed self-thinning stands comprised by trembling aspen and white spruce, can be modeled and predicted with measures of density and relative density (Reineke’s Stand Density Index-SDI), stand structure and stand composition. I also hypothesize that stand composition (percentage of basal area in deciduous species) has an important effect and influences the probability of survival of individual trees in these stands, because the species of interest have differences in ecological requirements (*i.e.* there is niche separation between these two species). Results from this Chapter will help elucidate whether species, relative size, and competitiveness are important in defining which trees survive and which trees die in self-thinning boreal pure and mixed stands. Also, these analyses will allow for further testing of stand characteristics to determine whether or not one-sided (and not two-sided) competition is one of the key drivers of tree mortality in these stands.

5.2 Methods

5.2.1 Study sites and data

This study was completed using long-term data from permanent sample plots (PSPs) established in pure and mixed stands of trembling aspen and white spruce, located in the Boreal Forest Natural Region of Alberta, Canada. Establishment and re-measurement of these PSPs were made following rigorous standards, albeit their size, establishment date, and re-measurement intervals are variable (Forest Management Branch, 2005). Most of these PSPs are 0.10 ha in size with all trees taller than 1.3 m or larger than 2.5 cm in diameter at breast height tagged and measured at time intervals ranging between 3 to10 years. Data from these plots were compiled and a number of stand attributes were calculated.

Only stands that were previously identified as experiencing density-dependent mortality (Reyes-Hernandez *et* al., 2013) were included in this section. A total of 179 plots were available. From these plots, individual tree observations of white spruce and trembling aspen were separated and used in further analysis. A total of 22,391 individual tree observations from these plots were available for both species; trembling aspen accounted for 11,615 total observations, with 10,176 live trees and 1,439 mortality events (or trees that died during the period of measurement). White spruce accounted for 10,776 individual observations, with 9,379 live trees and 1,397 mortality events registered during the measurement period (Table 5.1). Trees that were recorded as ‘dead’ when the first measurement in the plot was taken (or at plot establishment) were not considered for analysis and were removed from the data set.

Predictor variables included were: a) individual tree characteristics: diameter at breast height (cm), diameter at breast height squared (cm^2), height (m), and individual basal area (m^2); b) stand level characteristics: total density (number of trees per hectare), stand basal area ($m^2 \cdot ha^{-1}$), stand composition (percentage of basal area in deciduous), Reineke’s Stand Density Index (Reineke, 1933) calculated based on maximum size-density relationships previously obtained (dynamic thinning line) (Reyes-Hernandez *et*. al, 2013), quadratic mean diameter (cm), and mean height (m).

In order to test whether or not one-sided competition influences the probability of survival of the two species of interest, basal area of larger trees ($m^2 \cdot ha^{-1}$) was also calculated and tested in the models. Basal area of trees larger than the subject tree has been one of the most frequently used variables to assess the effects of one-sided competition (Monserud and Sterba, 1999). The effects of inter- and intra-specific competition were also assessed by partitioning the effects of basal area of larger trees into conifer and deciduous components (Yang *et* al., 2003). Table 5.1 summarizes the individual characteristics and these stands attributes.

5.2.2 Data analysis and model

A logistic regression function was used to model the probability of survival of individual white spruce and trembling aspen trees. The general equation has the following form:

$$\mathbf{P_S} = 1 / [1 + e^{(-X\beta)}] \qquad \mathbf{(5.1)}$$

Where $\mathbf{P_S}$ is probability of survival of an individual tree, β is the vector of unknown parameters (*i.e.* to be estimated); and X is the matrix of predictor variables.

All variables summarized in Table 5.1 were considered as potential predictors for fitting equation 5.1. The full data set was used for the analyses, which allowed testing for the effects of stand composition (*i.e.* percentage of basal area of deciduous species) on $\mathbf{P_s}$ for each species, in both pure and mixed stands at the same time. Separate models were developed for P_s of white spruce and P_s of trembling aspen

A generalized logistic regression analysis was performed with PROC GENMOD of SAS® ver. 9.2 to fit model 5.1. This SAS procedure allows modeling of autocorrelated data, which is highly probable for data collected through time in permanent sample plots, using a REPEATED statement. The estimation methodology is referred to as a Generalized Estimation Equation (GEE) (SAS, 2010). Since many alternative functions with different combinations of independent variables were fitted, the best model for each species was selected based on goodness-of-fit statistics and a minimal correlation between independent variables, as explained in section 5.3.

The Akaike Information Criterion (AIC) was used to discriminate between the alternative models. Receiver Operating Characteristic Curves (ROC curves), which are a graphical representation of the proportion of 'true positives' (events predicted to be actual events) versus the proportion of 'false positives' (nonevents predicted to be events), were generated and used to evaluate and compare the performance and fit of alternative models (SAS, 2010). Finally, a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2000) was performed. This test divides the entire data set in ten groups of approximately the same size (*i.e.* with similar number of individual observations, trees in this case), based on the percentiles of their estimated probabilities. The differences between the observed and the expected number of observations within each group are summarized by a Pearson chi-square statistic and then compared to a Chi-square distribution with '*t*' degrees of freedom, where '*t*' is the number of groups minus '*n*' (default n=2).

5.3 Results

Occurrence of mortality events was evident during the whole period in which the stands experienced self-thinning. Mortality of white spruce was mainly concentrated in the 5, 10, and 15 cm diameter classes (from 2.5-7.5 cm, 7.6-12.5 cm, and from 12.6-17.5 cm, respectively), whereas trembling aspen mortality was concentrated in the 10, 15, and 20 cm diameter classes (from 7.6-12.5 cm, from

12.6-17.5 m, and from 12.6-17.5 cm, respectively) (Figure 5.1, Table 5.2); there were also some mortality events in larger diameter classes for both species (diameter classes larger than 45 cm) (Figure 5.1, Table 5.2).

Figure 5.2 shows the ROC curves for the best models for explaining the probability of survival of trembling aspen (a) and white spruce (b). The area under an ROC curve essentially measures discrimination among the events, that is, the ability of the model to accurately categorize individuals that have the characteristic of interest from those who do not have it (Hanley and McNeil, 1982), in this case, dead individuals from live individuals. An ROC curve value close to 1 indicates that the model is excellent at discriminating the events (live *vs*. dead trees). ROC curves values for the best models of both species show in general a regular fit of each of the selected models (Table 5.3, ROC=0.70 for trembling aspen and ROC=0.6 for white spruce). With base on ROC curve values, the model for trembling aspen showed a better fit than that for white spruce.

Based on AIC and ROC curve values the best survival probability functions for each species are presented below.

For trembling aspen:

$$\mathbf{P_s}=1 / [1+\exp(-(\beta_0+\beta_1 * DBH-\beta_2 * BAHLT_{aw}-\beta_3 * BAHLT_{sw}))] \qquad \mathbf{(5.2)}$$

For white spruce:

$$\mathbf{P_s}=1 / [1+\exp(-(\beta_0+\beta_1 * DBH-\beta_2 * BAHLT_{aw}-\beta_3 * BAHLT_{sw}))] \qquad \mathbf{(5.3)}$$

Where $\mathbf{P}_s$ is the survival probability of an individual tree; β_0-β_4 are the model parameters estimated; DBH=diameter at breast height; $BAHLT_{aw}$ =basal area of larger aspen trees; $BAHLT_{sw}$ =basal area of larger white spruce trees.

Other different combinations of independent variables than the ones presented in models 5.2 and 5.3, that showed statistical significance were also obtained. However, the following criteria were applied to discriminate between alternative models in order to provide a parsimonious model. Because some explanatory variables recorded a significant correlation with each other, and in order to avoid the inclusion of highly correlated variables in the same model, these were discriminated based on the significance of their correlation coefficient. The amount of variation that each variable explained in the model was taken into account. This was evaluated through changes in AIC and ROC values with and without the highly correlated variables under examination.

For example, individual height and diameter at breast height showed similar explanatory performance in some models; however, height values were not measured directly in the field but estimated from equations previously generated for Alberta tree species (Huang *et* al., 1994); these two variables showed a highly significant correlation with each other and their effects were inconsistent when included in the same model. In general, diameter at breast height performed better than height when fitting the models. For this reason, and because diameter was directly measured in the field (and not estimated), it was selected for use in the models. In addition, goodness-of-fit was poor for models with other variables.

Significant effects of diameter at breast height, the square of diameter at breast height, basal area of larger trembling aspen trees, and basal area of larger white spruce trees on the probability of survival of trembling aspen are observed (Table 5.3). A small but significant improvement in the P_s function performance is observed for the model selected for trembling aspen when separate values of basal area of larger trees for both the deciduous and the conifer components, and when the square of DBH were included (Function 1 for aspen, Table 5.3). However, performance (*i.e.* fit) differences between the model that includes DBH^2 from the one that does not include this variable are minimal, and because of the correlation between DBH and squared DBH, function 1 for aspen is preferred.

Significant effects of diameter at breast height, basal area of larger aspen trees, and basal area of larger spruce trees, on the probability of survival of white spruce are observed (Table 5.3). Finally, the Hosmer-Lemeshow test for the best survival probability model is presented, for trembling aspen (Table 5.4), and for white spruce (Table 5.5). These tables are useful to compare the differences between the observed and the expected number of trees that were calculated with the selected models, for each species within each of the ten groups formed according to tree status (dead and live) as indicated.

Several previous studies suggest a strong link between tree growth and P_s of trees (Hamilton 1986; Kobe and Coates 1997; Yang *et* al. 2003; Chen *et* al. 2008; Yang and Huang 2013). Periodic annual increment in diameter (PAI_d) for each individual tree was used and incorporated in the best models already obtained for each species. When individual PAI_d is included in the models the number of observations is reduced. Incorporating PAI_d for trembling aspen reduces the dataset from 11615 individual observations initially available to 9587 observations, whereas for white spruce the reduction causes a loss of 1645 observations.

The incorporation of PAI_d in the P_s functions produced a strong reduction in the significance of many of the independent variables previously used (i.e. stand characteristics) and that were included in the original models. Both AIC and ROC values did not show any improvement when these variables were used together with PAI_d. This and the fact that many of these stand variables showed a highly significant correlation with PAI_d were the main reasons to remove most of these variables in these models. Models that incorporate PAI_d as explanatory variable were developed using PROC Logistic in SAS, and results are shown in Table 5.6. The P_s functions for trembling aspen and white spruce are presented below.

For trembling aspen:

$$\mathbf{P_s}=1/ [1+\exp (-(-0.251+0.022*DBH+21.39*PAId))] \quad \mathbf{(5.4)}$$

For white spruce:

$$\mathbf{P_s}=1/ [1+\exp (-(0.965+0.005*DBH+22.87*PAId))] \quad \mathbf{(5.5)}$$

Where $\mathbf{P_s}$ is the survival probability of an individual tree; DBH=diameter at breast height; PAI_d=individual periodic annual increment in diameter.

Both PAI_d and DBH showed a significant positive effect on the probability of survival for both species. The contribution of DBH to the P_s function for white spruce appears to be smaller than the contribution for trembling aspen P_s function. Also, a larger influence of PAI_d on the P_s function is observed for white spruce than that for trembling aspen.

5.4 Discussion

These results show that the absolute size of individual trees appears to be one of the strongest explanatory variables for the probability of survival for both trembling and white spruce in the stands analyzed (significant positive effect of diameter at breast height). This shows that mortality for both trembling aspen and white spruce is higher for small than for large diameter classes, and that their probability of survival increases as the absolute size of the trees increases, regardless of species. This appears to be consistent with what could be expected regarding density-dependent mortality patterns in self-thinning stands (Westoby 1984; Newton 2006) resulting from one-sided competition. That is, competition from neighbors limits the supply of essential resources for the smallest size classes which are the most affected, and higher mortality rates of small individuals would be anticipated (Chen *et* al. 2008; Kunstler *et* al. 2009). The diameter term in this case is the variable defining the trend for small trees and saplings, which is indicated by its larger coefficient in contrast to the coefficient for DBH squared.

These results also suggest that probability of survival for trembling aspen will decrease for large diameter trees, as indicated by the significant negative effect of the square of DBH (DBH^2) for this species. Although reliable estimates of age for these stands were not available, it is likely that some of the pure aspen and mixed species stands included in the data set are mature and old-aged, containing a few old aspen trees with reduced vigor. It is well documented that aspen trees are susceptible to decay (Peterson and Peterson 1992), and that their vigor generally declines with age after age 60. However, it should be noted that the number of dead large aspen trees seems to be rather small (Table 5.2), overall for diameter classes above 40 cm.

Previous studies for temperate tree species (Dwyer *et* al., 2010) and for *Pinus banksiana*, *Populus tremuloides*, and *Picea mariana* in the eastern Canadian boreal forests (Luo and Chen, 2011) have suggested that crowding, represented by total stand basal area, might have a significant negative effect on tree survival. In this study, some of the tested models suggested that total stand basal area might have an important effect on the probability of survival of both species, and that two-sided competition could be an important factor for both trembling aspen and white spruce mortality. However, total stand basal area was not among the most powerful explanatory variables of survival either for trembling aspen or for white spruce, and due to its conflicting behavior with both basal area of larger aspen and basal area of larger spruce trees, total stand basal area was removed and not included in the final models.

Some authors have also suggested a decrease in mortality for paper birch (*Betula papyrifera*) in boreal stands of Eastern Canada as the total basal area of the stand increases. An increase in birch mortality due to intensive browsing from mammals in less crowded than in highly crowded stands has been suggested as a possible explanation for this effect (Danell *et* al., 1985); a less crowded stand might facilitate mobility of large mammals that feed on small shrubs and saplings, causing damage and an increase in mortality of birch saplings (Luo and Chen, 2011). It has also recently been reported that moose and other large mammals feed on the bark of hardwood trees (especially trembling aspen) in western Canada, even if there is a good supply of edible shrubs (Rea and Booth, 2011).

Similar to the case of birch, a less crowded aspen stand might facilitate access and mobility for large mammals such as moose, enabling an increase in browsing leading to mechanical damage to small aspen trees and saplings, negatively affecting their survival. In this study, however, it was not possible to detect any positive effect of total stand basal area on aspen survival. Further exploration of this probable association might be needed, since lower basal area could also be associated with poorer sites, wet sites, snow breakage, and lower vigor, and with a highest incidence of diseases, history of early browsing and other affecting tree survival.

One-sided inter and intra-specific competition influences the probability of survival of both species, as indicated by the significant effects of basal area of larger spruce and larger aspen trees on P_s of both species (Table 5.3). Trembling aspen survival is negatively affected by spruce and by aspen competition, but the effect of spruce is larger than the effect of aspen ($BAHL_{sw}$ coefficient larger than $BAHLT_{aw}$), indicating that white spruce competition on trembling aspen appears to be stronger than the aspen-to-aspen competition(Table 5.3, function for aspen). The behavior of the probability of survival function for trembling aspen with changes in basal areas of larger aspen and larger spruce trees is shown in Figure 5.3.

On the other hand, white spruce survival appears to be more strongly affected by trembling aspen than for white spruce one-sided competition, although both effects appear to be small (Table 5.3, function for white spruce). These results are not expected and are not consistent with previous findings reported in relevant literature. Although negative effects of increasing basal area of larger trembling aspen on white spruce survival have been previously reported (Yang *et* al., 2003), recent research reports that spruce survival is more strongly affected by spruce than by aspen competition, owing in part to the shade tolerance of white spruce and their ability to survive under aspen canopies (Lieffers and Stadt 1994; Pinno *et* al. 2001; Feng *et* al. 2006). Discrepancies between my results and these previous findings are unexpected, and might necessitate further exploration for clarification. Nevertheless, the behavior of the best equation for spruce survival as a function of basal area of larger aspen and larger spruce trees is shown in Figure 5.4.

Yao *et* al. (2001) suggested a greater probability of mortality for trembling aspen with an increasing white spruce composition, whereas survival of white spruce did not differ between pure and mixed stands. My results suggest that survival of both white spruce and trembling aspen are negatively affected by increasing basal area of the other species; that is, P_s of trembling aspen is negatively affected by basal area of white spruce and *vice versa*, although the effect of white spruce on aspen is larger than the effect of aspen on white spruce. Although the negative effects of mixtures on survival of trembling aspen reported by (Yao *et* al., 2001) might be attributed to less suitable growing conditions for this species in mixed than in pure aspen stands, it is also suggested that interactions among tree species and their growing environment can show a large variation (Partel *et* al. 2007; Yachi and Loreau 2007).

Trembling aspen can be a strong competitor and reduce the development of white spruce in their early stages, but aspen can also have positive effects on young white spruce (Man and Lieffers 1999; Comeau *et* al. 2005; Filipescu and Comeau 2007a). Indeed, it has been suggested that competitive and facilitative interactions between these two species vary with stand age, site and other factors (Filipescu and Comeau, 2007a), which might lead to a dynamic relationship between growth of white spruce and competition from aspen (Filipescu and Comeau, 2007b). A positive effect of PBA_{dec} has been suggested for maximum size-density relationships in boreal mixed stands, which implies that higher maximum densities might be achieved as the amount of deciduous species increases in a boreal stand (Reyes-Hernandez *et* al., 2013). Hence, it might be possible that a significant positive effect of stand composition (PBA_{dec}) on white spruce survival occurs, which could be partly due to the existence of a trade-off between competitive and facilitative effects of aspen on white spruce, due partly to the temporal niche-separation between these two species, as has been suggested for jack pine and trembling aspen in eastern Canada boreal mixedwoods (Chen *et* al. 2008).

It is remarkable that a highly significant reduction in AIC as well as an outstanding increase in ROC curves values are attained when individual PAI_d is incorporated to the P_s models for both species (Table 5.7). It is also noteworthy that the effect of PAI_d is large when compared to the effects of stand attributes and individual tree size (DBH). This highlights the importance of individual growth rates in defining the probability of mortality or survival of individuals in forest stands, as previously suggested in studies for tree species growing in similar or in different ecosystems (Hamilton 1986; Kobe and Coates 1997; Yang *et* al. 2003; Chen *et* al. 2008; Yang and Huang 2013).

Diameter increment (*i.e.* tree radial growth rate) is a strong indicator of tree vigor (Yang *et* al. 2003), indicating as well a positive carbon balance of a sapling or a tree growing in a certain environment (Kobe and Coates, 1997). Leaves and roots are of primary importance for carbon allocation after the costs of respiration have been satisfied, with stem increment usually of secondary importance (Waring, 1987). Therefore, the positive effect of PAI_d indicates that faster growing trees will be less likely to die, regardless of species. The behavior of the P_s models as a function of diameter at breast height and PAI_d are shown in Figure 5.7 for trembling aspen and in Figure 5.8 for white spruce, respectively. A dramatic decrease in the probability of survival for both species is observed when PAI_d decreases and approaches zero; this decrease appears to be sharper for smaller diameter classes for trembling aspen than for the same diameter classes in white spruce

Microsite characteristics, genetics, and climate are also suggested as factors that, besides growth rates and stand characteristics, influence the probability of survival of trees (Caspersen and Kobe 2001; Yang and Huang 2013). Soil moisture, drought, availability of nitrogen, and species differences in rooting depth may also influence the probability of survival of tree species (Caspersen and Kobe, 2001). Likewise, root and stem diseases, and insects' outbreaks, could negatively influence the survival probability of tree species. Although tree mortality might not be the direct consequence of defoliation caused by insects, and/or damage by foliage diseases, their continuous occurrence might cause a substantial and sustained reduction in leaf area, live-crown volume, and diameter annual increment (Hodson 1981; Cooke and Roland 2007), which will reduce their growth rate and probability of survival.

For example, defoliation of trembling aspen caused by forest tent caterpillar in Canada has been identified as the main source of variation that affects tree ring width of aspen, and that could show periodicity at many time scales (Cooke and Roland, 2007). When trembling aspen trees are not able to withstand continuous defoliation by insects (i.e. forest tent caterpillar) they may not be able to recuperate their vigor and the stand might decline shortly thereafter (Cooke *et* al. 2011). Aspen shoot blight is also another disease which, after repeated infections, might affect growth of aspen trees, causing significant losses in intensively managed boreal stands (Blenis, 2007). It is also documented that periodic spruce budworm outbreaks have caused substantial mortality of both white spruce and balsam fir in Canada (Bouchard *et* al., 2007).

Similar to forest tent caterpillar on trembling aspen, spruce budworm attacks might cause considerable defoliation, consequently affecting tree growth, and depending upon their periodicity, increasing the probability of mortality of white spruce trees. From this perspective, there are other factors that due to either the lack of reliable data or the lack of sufficient observations were not included in these analyses that could be influencing these results. These data are needed to support development of mechanistic models and would also contribute to our understanding of tree mortality.

Although the methodology that I used is useful to deal with autocorrelated data, it might not be the best approach to account for other local (random) factors affecting the survival of the species of interest. Other methodologies, such as mixed effects models might be more appropriate to account for these components. For example, incorporating random effects at the stand level might be useful to account for these and other factors that are not easy to measure (Yang and Huang, 2013), such as slope, aspect, drainage, soil density, soil composition, genetics of growing stock, and other local factors (Fortin *et* al. 2008; Caspersen and Kobe 2001).

However, although mixed modeling might represent a powerful procedure to analyze this phenomenon, it also embodies a challenge in terms of the quality and reliability of the data that are needed. The complex structure of the mixed models needed, in terms of their error terms, would necessitate the existence of more individual tree observations than the actual number of observations available for the plots that were analyzed in this study. Relative paucity of data might compromise the fit and the outcome, making it difficult to obtain consistent results (Groom *et* al, 2012). Also, the lack of reliable information at the local stand level might be a further difficulty for performing these analyses.

5.5 Conclusions

Absolute tree size of individuals appears to be the best independent variable in explaining the variation on the probability of survival for both trembling aspen and white spruce in self-thinning stands in boreal mixedwoods in Alberta. One-sided competition seems to be the primary driving force for competition related mortality of both aspen and white spruce, and basal area of larger trees appears to be effective for representing these effects. The general trend for both aspen and spruce mortality agree with what we would expect in stands experiencing density-dependent mortality; small trees have higher probability of mortality regardless of species, even in mixed stands. Due to the type of stands that were included in this study, the decrease in the probability of survival for large trembling aspen trees appears to be most likely related to a loss of tree vigor due to aging.

Stand occupancy and crowding also have a strong influence on defining which trees die and which trees survive in these stands. Tree growth rate is one of the most important individual characteristics that define the probability of survival of individuals in stands of trees. Slower growth indicates reduced vigor, and consequently higher probability of mortality in the presence of competition for resources and/or mechanical damage, pests or other factors.

5.6 References

Blenis, P. 2007. Impact of simulated aspen shoot blight on trembling aspen. Can. J. For. Res. 37:719-725

Bouchard, M.; Kneeshaw, D.; and Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. Can. J. For. Res. 37:763-772. doi: 10.1139/X06-278

Caspersen, J.P.; and Kobe, R.K. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos. 92:160-168

Chen, H.Y.H.; Fu, S.; Monserud, R.A.; and Gillies, I.C. 2008. Relative size and stand age determine *Pinus banksiana* mortality. For. Ecol. Manage. 255:3980-3984.

Comeau, P. G.; Kabzems, R.; McClarnon, J.; and Heineman, J. L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. For. Chron. 81(4):559-574

Cooke, B.J.; MacQuarrie, C.J.K.; and Lorenzetti, F. 2011. The dynamics of forest tent caterpillar outbreaks across east-central Canada. Ecography. 35:422-435. doi: 10.1111/j.1600-0587.2011.07083.x

Cooke, B.J.; and Roland, J. 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. Can. J. For. Res. 37:1586-1598.

Chen, H, Y.H.; and Popadiouk, R. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. 10:137-166.

Danell, K.; HussDanell, K.; and Bergstrom, R. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology. 66:1867-1878.

Dwyer, J.M.; Fensham, R.J.; Fairfax, R.J.; and Buckley, Y.M. 2010. Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. J. Veget. Science. 21:573-585.

Feng, Z.; Stadt, K.J.; and Lieffers, V.J. 2006. Linking juvenile white spruce density, dispersion, stocking, and mortality to future yield. Canadian Journal of Forest Research. 36:3173-3182. doi:10.1139/X06-192

Filipescu, C. and Comeau, P. G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C. and Comeau, P. G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Forest Management Branch. 2005. Permanent Sample plot (PSP) field procedures manual. Alberta Sustainable Resource Development. Public Lands and Forest Division. Edmonton, AB.

Fortin, M.; Bedard, S.; DeBlois, J.; and Meunier, S. 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in Southern Quebec, Canada. Ann. For. Sci. 65: 205(1-12).

Groom, J. D.; Hann, D.W.; and Temesgen, H. 2012. Evaluation of mixed-effects models for predicting Douglas-fir mortality. Fo. Eocl. Manage. 276:139-145. doi:10.1016/j.foreco.2012.03.029

Guneralp, B.; and Gertner, G. 2007. Feedback loop dominance analysis of two tree mortality models: relationship between behavior. Tree Physiology. 27:269-280.

Hamilton, Jr. D.A. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. For. Sci. 32:989-1000.

Hanley, J.A.; and McNeil, B.J. 1982. The meaning and use of the Area under a Receiver Operating Characteristic (ROC) Curve. Radiology. 143(1):29-36.

Hodson, A.C. 1981. The response of aspen (*Populus tremuloides*) to artificial defoliation. Great Lakes Entomol. 14:167-169.

Hosmer, D.W. Jr.; and Lemeshow, S. 2000. Applied logistic regression. 2nd Edition. New York. John Wiley & Sons. USA. 369 p.

Huang, S.; Titus, S.J.; Lakusta, T.W.; and Held, R.J. 1994. Ecologically based individual tree height-diameter models for major Alberta tree species. Alberta Env. Protection. Land and Forest Services. Forest Management Division. 27 p.

Kenkel, N.C. 1998. Pattern of self-thinning in jack pine-testing the random mortality hypothesis. Ecology. 69:1017-1024.

Kneeshaw, D.D.; and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology. 79:783-794.

Kobe, R.K.; and Coates, K.D. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of Northwestern British Columbia. Can. J. For. Res. 27: 227-236.

Kunstler, G.; Coomes, D.A.; and Canham, C.D. 2009. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. J. Ecol. 97:685-695.

Lieffers, V. J. and Stadt, K. J. 1994. Growth of understory *Picea glauca, Calamagrostis Canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198

Luo, Y.; and Chen, H.Y.H. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. J. of Ecol. 99:1470-1480.

Man, R., and Lieffers, V. J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75(3):505-513.

Mencuccini, M.; Martinez-Vilalta, J.; Vanderklein, D.; Hamid, H.A.; Korakaki, E.; Lee, S.; and Michiels, B. 2005. Size-mediated ageing reduces vigor in trees. Ecol. Letters. 8:1183-1190.

Monserud, R.A. 1976. Simulation of forest tree mortality. For. Sci. 22: 438-444.

Monserud, R.A.; and Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113:109-123.

Newton, P.F. 2006. Asymptotic size-density relationships within self-thinning black spruce and jack pine stand-types: parameter estimation and model reformulation. For. Ecol. Manage. 226: 49-59.

Partel, M.; Laanisto, L.; and Zobel, M. 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. Ecology. 88: 1091-1097.

Peterson, E. B., and Peterson, N. M. 1995. Aspen manager’s handbook for British Columbia, Canada. British Columbia Partnership Agreement. FRDA II. FRDA Report #230. Victoria, B.C. 121 pp.

Peterson, E. B., and Peterson, N. M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Can. For. Serv. North. Cent. Spec. Rep. 1. 252 pp.

Pinno, B.D.; Lieffers, V.J.; and Stadt, K.J., 2001. Measuring and modeling the crown and light transmission characteristics of juvenile aspen. Can. J. For. Res. 31: 1930– 1939.

Rea, R.V.; and Booth, A.L. 2011.Use of trembling aspen bark by moose in a browse-abundant habitat during winter. Wildlife Afield. 8(1):104-107.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Reyes-Hernandez, V.; Comeau, P. G.; and Bokalo, M. 2013. Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. For. Ecol. Manage. 289:300-311.

SAS. 2010. Statistical Analysis System for windows, V 9.2. SAS-Institute, Inc. Cary, N.C. USA.

Turner, M.G.; Romme, W.H.; Gardner, R.H.; and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. 67:411-433.

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience. 37(8):569-574.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecol. and Evol. 5: 360-364.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167-225.

Yachi, S.; and Loreau, M. 2007. Does complementarity resource use enhance ecosystem functioning? A model of light competition in plan communities. Ecology Letters. 10:54-62.

Yang, Y.; and Huang, S. 2013. A generalized mixed logistic model for predicting individual tree survival probability with unequal measurement intervals. For. Sci. 59(2): 177-187.

Yang, Y.; Titus, S. J.; and Huang, S. 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Model. 163:209-222.

Yao, X.; Titus, S.J.; and MacDonald, S.E. 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. Can. J. For. Res. 31(2):283-291.

Table 5.1 Individual-tree and stand attributes by tree status and species used for probability of survival model fit in self-thinning boreal stands.

Variable	**Species**	**Tree status**	**N**	**Mean**	**Standard deviation**	**Minimum**	**Maximum**
DBH	Aspen	Live	10176	23.8	9.1	2.0	58.1
		Dead	1439	18.9	8.8	2.0	56.7
	Spruce	Live	9379	19.6	11.3	2.0	59.8
		Dead	1397	14.8	8.5	2.0	58.9
HT	Aspen	Live	10176	20.7	4.6	2.2	37.2
		Dead	1439	17.9	4.2	4.3	26.1
	Spruce	Live	9379	16.9	7.6	1.4	41.2
		Dead	1397	13.4	5.9	2.5	31.4
BAHT	Aspen	Live	10176	42.49	10.1	18.3	76.1
		Dead	1439	41.4	9.9	21.6	76.1
	Spruce	Live	9379	49.4	9.9	18.3	76.1
		Dead	1397	51.0	10.9	19.4	76.1
L	Aspen	Live	8162	8.9	3.1	3.0	30.0
		Dead	1425	9.8	3.2	3.0	23.0
	Spruce	Live	7738	9.0	3.4	3.0	34.0
		Dead	1393	10.4	3.2	3.0	24.0
QMD	Aspen	Live	10176	24.0	6.5	10.6	50.5
		Dead	1439	24.9	5.8	11.9	48.9
	Spruce	Live	9379	22.5	5.9	5.5	43.1
		Dead	1397	23.2	5.2	11.9	39.9
SDI	Aspen	Live	10176	606.1	228.7	8.4	1094
		Dead	1439	591.9	231.9	101.2	1094
	Spruce	Live	9379	697.5	258.1	1.35	1339
		Dead	1397	684.1	264.1	28.1	1339
PAI$_d$	Aspen	Live	8162	0.158	0.115	-0.47	1.06
		Dead	1425	0.0098	0.077	-0.39	0.820
	Spruce	Live	7738	0.104	0.121	-0.486	1.029
		Dead	1393	-0.019	0.074	-0.41	0.94
BAHLT	Aspen	Live	10176	13.9	11.0	0	57.0
		Dead	1439	17.1	14.1	0	57.0
	Spruce	Live	9379	12.4	10.3	0	49.8
		Dead	1397	13.9	10.9	0	59.7

N= number of trees; DBH=diameter at breast height (cm); HT= height (m); BAHT= Total basal area ($m^2 \cdot ha^{-1}$); L=measurement interval (years); QMD= quadratic mean diameter (cm); SDI=Stand density index (dynamic MSDR); PAI$_d$= periodic annual increment in diameter (cm); BAHLT= Basal area larger trees ($m^2 \cdot ha^{-1}$).

Table 5.2 Distribution of mortality by species and diameter classes.

Diameter class	Frequency of mortality for Trembling aspen	Frequency of mortality for white spruce
5	97	**363**
10	**269**	**308**
15	**380**	**322**
20	**286**	190
25	173	92
30	105	47
35	57	42
40	45	16
45	22	9
50	4	6
55	1	1
60	--	1

Ranges for diameter classes are as follows: 2.5 -7.5 cm (5); 7.6-12.5 cm (10); 12.6-17.5 cm (15); 17.6-22.5 cm (20); 22.6-27.5 cm (25); 27.6-32.5 cm (30); 32.6-37.5 cm (35); 37.6-42.5 cm (40); 42.6-47.5 cm (45); 47.6-52.5 cm (50); 52.6-57.5 cm (55); 57.6-62.5 cm (60).

Table 5.3 Estimated parameters for the best models for predicting the probability of survival of trembling aspen and white spruce in self-thinning boreal mixed stands in Alberta, Canada, as indicated.

Species	**Par**	**Variable**	**Estimate**	**Standard error**	**AIC**	**ROC**
Aspen	β_0	Intercept	-0.17	0.15	8139	0.7
	β_1	DBH	0.19	0.013		
	β_2	DBH^2	-0.003	0.0003		
	β_3	$BAHLT_{aw}$	-0.02	0.003		
	β_4	$BAHLT_{sw}$	-0.07	0.006		
Aspen	β_0	Intercept	0.91	0.10	8214	0.7
	β_1	DBH	0.07	0.005		
	β_2	$BAHLT_{aw}$	-0.02	0.003		
	β_3	$BAHLT_{sw}$	-0.06	0.006		
Spruce	β_0	Intercept	1.34	0.09	8044	0.6
	β_1	DBH	0.04	0.003		
	β_2	$BAHLT_{aw}$	-0.02	0.003		
	β_3	$BAHLT_{sw}$	-0.01	0.003		

β_0-β_4 = model parameters estimated; DBH=individual diameter at breast height (cm); DBH^2=squared DBH; $BALT_{aw}$ = basal area of larger aspen trees (m^2); $BALT_{sw}$=basal area of larger spruce trees (m^2); AIC=Akaike's Information Criterion; ROC=Receiver Operating Characteristic Curve (area under the curve).

Table 5.4 Partition of the Hosmer-Lemeshow test for the best model obtained to evaluate probability of survival of trembling aspen in self-thinning boreal stands.

Group	Total	Status=0 (alive)		Status=1 (dead)	
		Observed	Expected	Observed	Expected
1	1163	836	861	327	302
2	1162	873	935	289	227
3	1163	969	969	194	194
4	1162	1008	994	154	168
5	1162	1049	1018	113	144
6	1162	1072	1039	90	123
7	1162	1096	1060	66	102
8	1162	1106	1080	56	82
9	1162	1092	1101	70	61
10	1155	1075	1120	80	35

Model: P_s=1/[1+exp(-(0.91+(0.07*DBH)-(0.02* $BAHLT_{aw}$)-(0.06* $BAHLT_{sw}$))))]

Table 5.5 Partition for the Hosmer-Lemeshow test for the best model obtained to evaluate probability of survival of white spruce in self-thinning boreal stands.

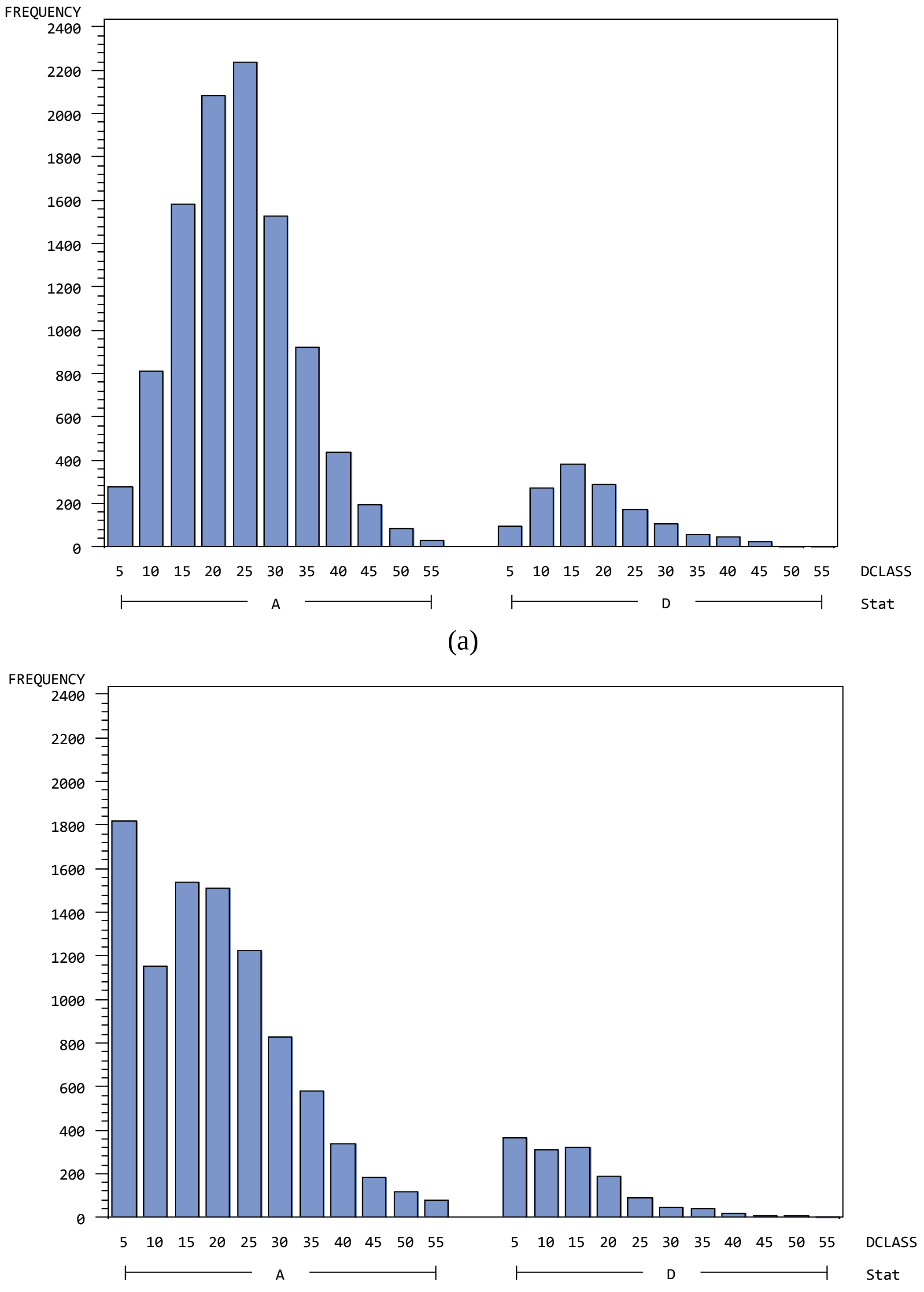
Group	Total	Status=0 (alive)		Status=1 (dead)	
		Observed	Expected	Observed	Expected
1	1078	893	842	185	236
2	1078	898	877	180	201
3	1078	863	896	215	182
4	1079	862	914	217	165
5	1080	890	932	190	148
6	1078	950	946	128	132
7	1078	974	964	104	114
8	1078	1009	982	69	96
9	1078	1016	1003	62	75
10	1071	1024	1025	47	46

Model: P_s=1/[1+exp(-(1.34+(0.04*DBH)-(0.02* $BAHLT_{aw}$)-(0.01* $BAHLT_{sw}$)))].

Table 5.6 Estimated parameters of probability of survival functions for trembling aspen and white spruce in self-thinning boreal stands in Alberta, Canada, with periodic annual increment in diameter as explanatory variable.

Species	**Par**	**Variable**	**Estimate**	**Standard error**	**AIC**	**ROC**
Trembling aspen	β_0	Intercept	-0.251	0.095	5292	0.91
	β_1	DBH	0.022	0.005		
	β_2	PAI_d	21.39	0.634		
White spruce	β_0	Intercept	0.965	0.067	5621	0.89
	β_1	DBH	0.005	0.0004		
	β_2	PAI_d	22.87	0.726		

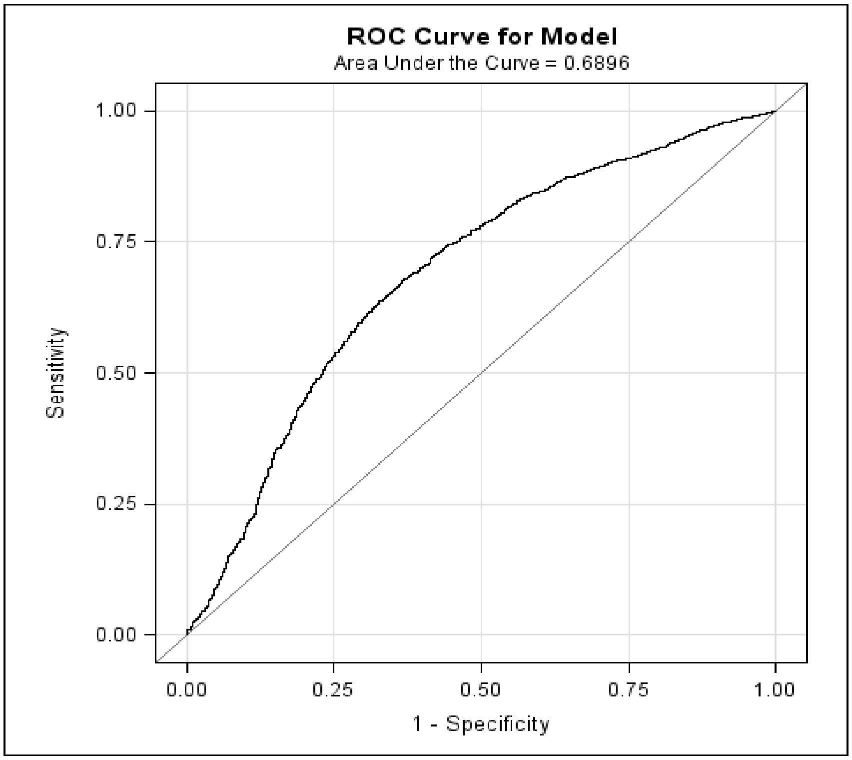
β_0, β_1, β_2= model parameters estimated; DBH=individual diameter at breast height (cm); PAI_d=Individual tree periodic annual increment in diameter (cm); AIC=Akaike's Information Criterion; ROC=Receiver Operating Characteristic Curve (area under the curve). Par= parameter



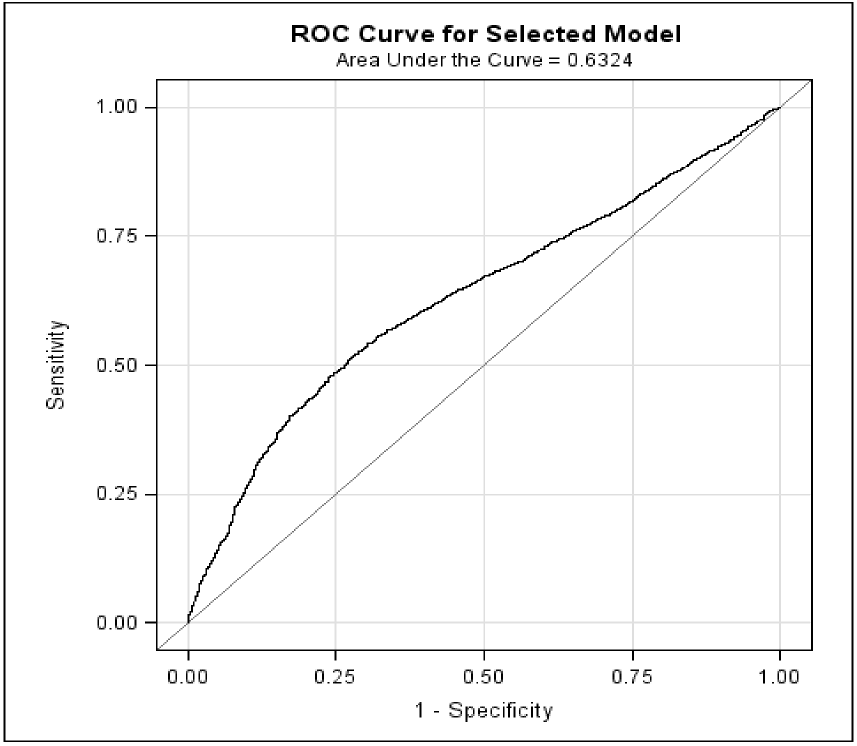
(a)

(b)

Figure 5.1 Distribution of mortality status (live=A; Dead=D) of individual trees of trembling aspen (a), and white spruce (b) by diameter class in boreal self-thinning stands.



(a)



(b)

Figure 5.2 Receiver Operating Characteristic Curve (ROC) for the best models for estimating the probability of survival of trembling aspen (a) and white spruce (b) in boreal self-thinning stands.

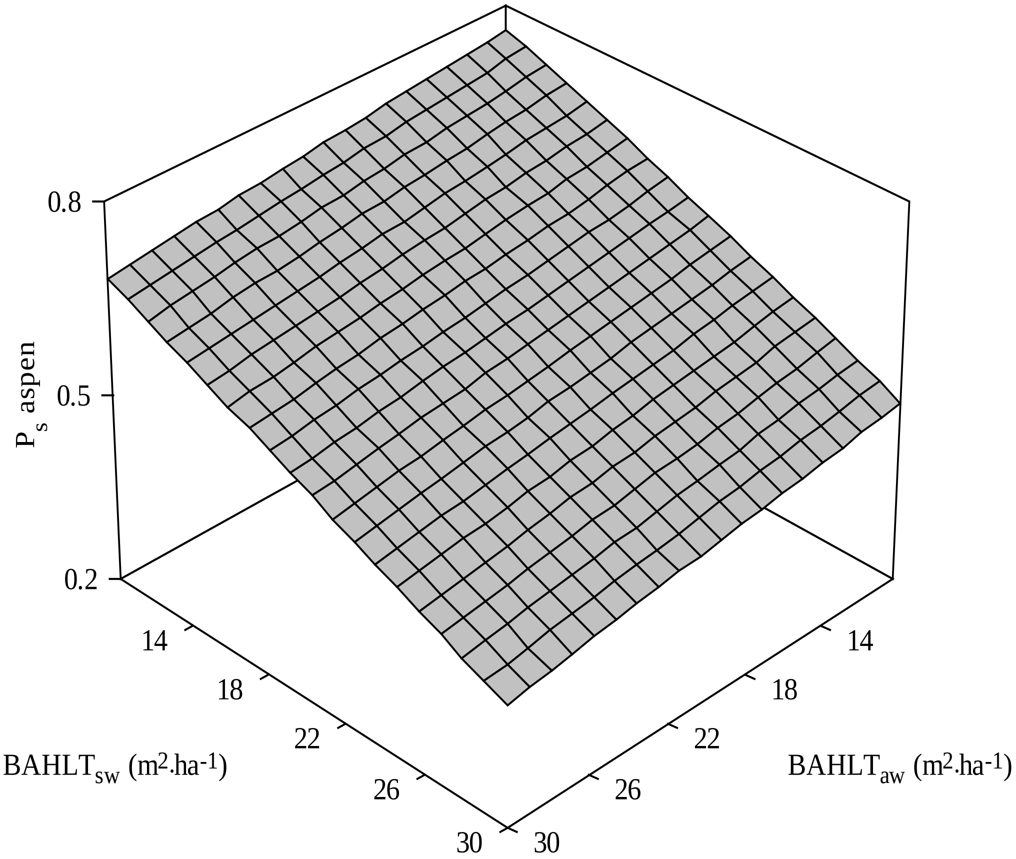


Figure 5.3 Probability of survival (P_s) for trembling aspen as related to changes in basal area of larger spruce trees ($BAHLT_{sw}$) and basal area of larger aspen trees ($BAHLT_{aw}$), diameter at breast height (DBH) held constant.

Model: $P_s=1/[1+\exp(-(0.91+(0.07*DBH)-(0.02* BAHLT_{aw})-(0.06* BAHLT_{sw}))))]$

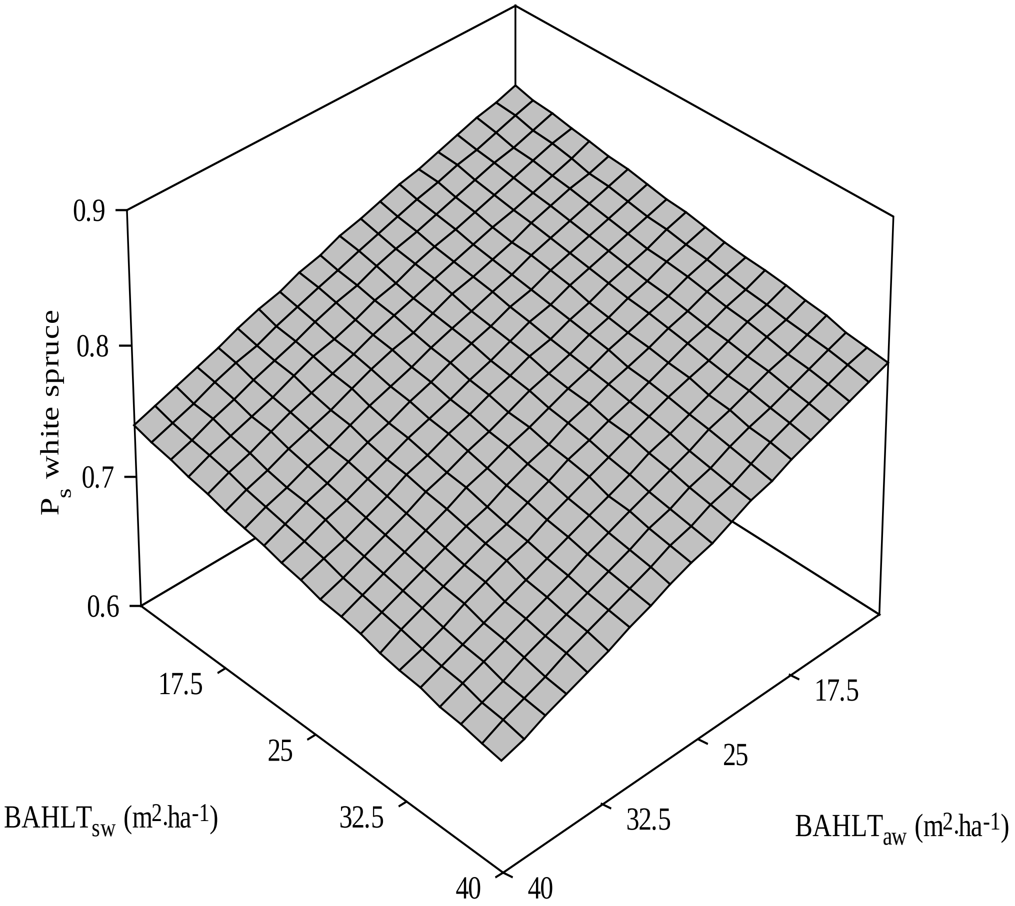


Figure 5.4 Probability of survival (P_s) for white spruce as related to changes in basal area of larger spruce trees ($BAHLT_{sw}$) and basal area of larger aspen trees ($BAHLT_{aw}$), diameter at breast height (DBH) held constant.

Model: P_s=1/[1+exp(-(1.34+(0.04*DBH)-(0.02* $BAHLT_{aw}$)-(0.01* $BAHLT_{sw}$)))].

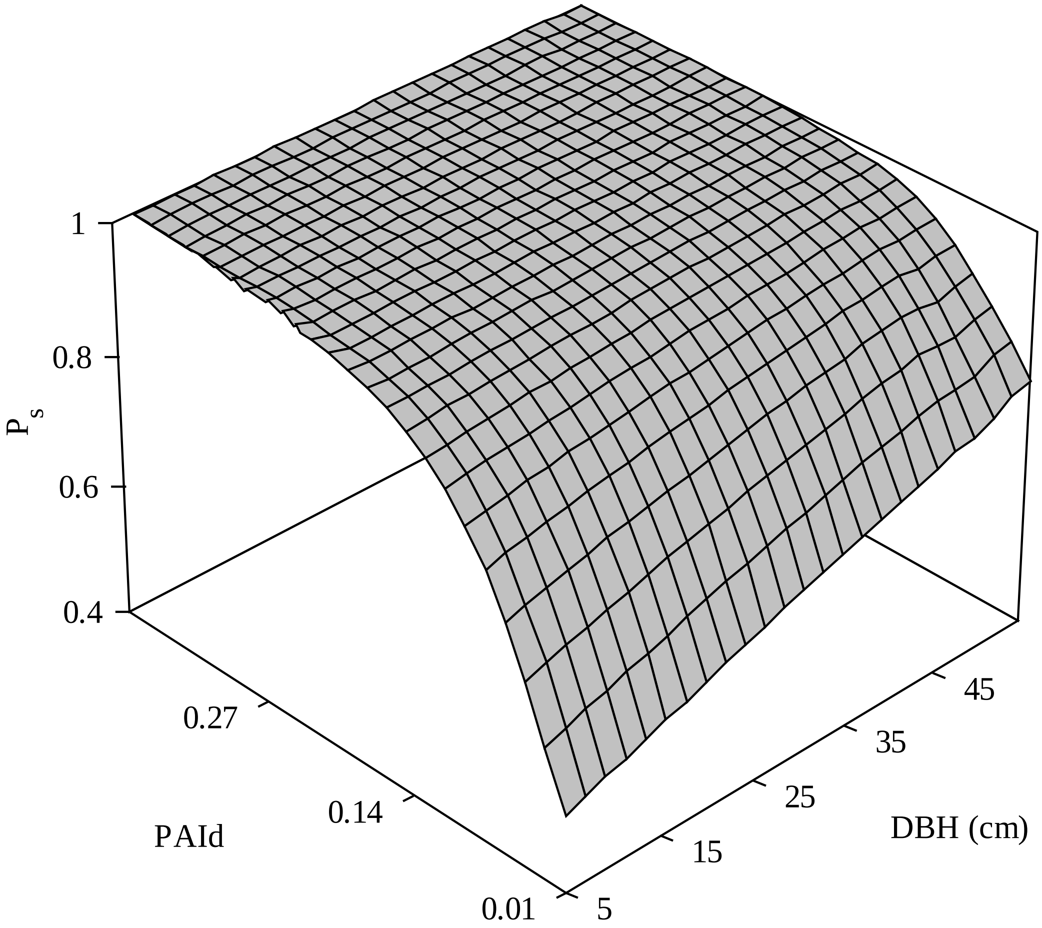


Figure 5.5 Probability of survival (P_s) for trembling aspen as related to changes in periodic annual increment in diameter (PAI_d) and diameter at breast height (DBH). Model: $\mathbf{P_s}$=1/[1+exp(-(-0.251+(0.022*DBH)+(21.39*PAI_d)))]

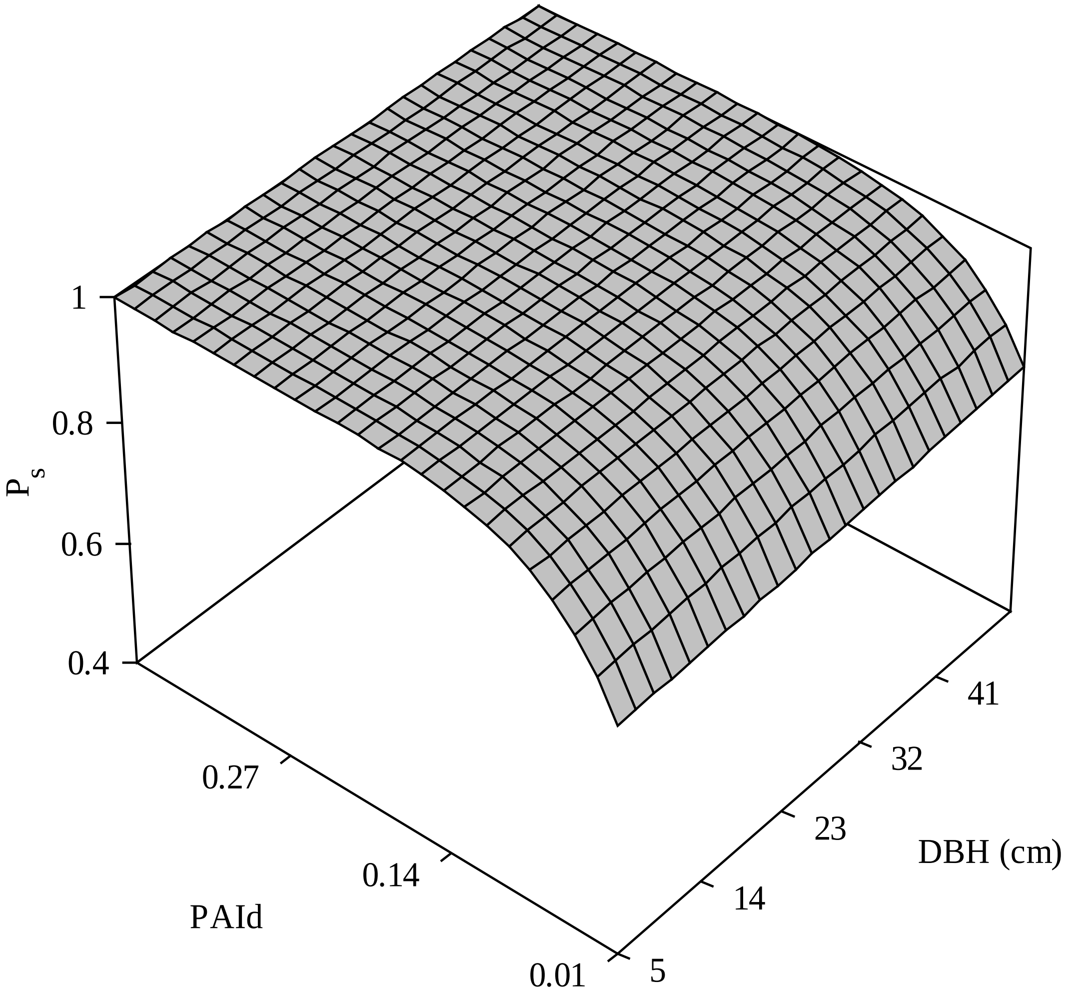


Figure 5.6 Probability of survival (P_s) for white spruce as related to changes in periodic annual increment in diameter (PAI_d) and diameter at breast height (DBH). Model: $\mathbf{P_s}$=1/[1+exp(-(0.965+(0.005*DBH)+(22.87*PAI_d)))]

Chapter 6 General conclusions

This Dissertation focuses on analyzing some key aspects of the dynamics of boreal mixedwood stands, comprised primarily by *Populus tremuloides* Michx. (Trembling aspen) and *Picea glauca* (Moench) Voss. (white spruce), in western Canada. In particular, the following specific research objectives were the focus of this study:

- To determine whether maximum size-density relationships (MSDR) can be developed for boreal mixedwoods stands;
- To evaluate the importance of stand composition and site characteristics on MSDRs for both pure and mixed stands of boreal mixedwoods;
- To determine the importance of relative density, competitor identity , and stand composition in explaining understory light in mid-rotation and mature boreal mixedwood stands;
- To document effects of stand composition and relative density have any influence on periodic annual increment in volume of conifers, deciduous, and of the whole stand, on both pure and mixed stands;
- To determine whether one-sided competition and/or two sided-competition are important in defining and explaining the probability of survival of trees in self-thinning boreal mixed and pure stands, and to evaluate whether relative density is useful as a measure of competition.

Analyses and results of chapter two show the importance of considering local stand variability in developing maximum size-density relationships (MSDR) for boreal mixedwoods. While the use of stochastic frontier functions showed that the slope and intercept of static MSDR vary depending upon stand composition, the use of mixed models for analyzing dynamic MSDR are helpful to clarify the manner in which individual stands develop and approach self-thinning.

A three-dimensional response surface is the most suitable approach to approximate the self-thinning process in boreal pure and mixed stands experiencing density-related mortality, which confirms similar findings for other types of forests (Puettmann *et* al., 1992). While many authors had anticipated invariance of slopes of MSDR (Reineke 1933; Kira *et* al. 1953; Yoda *et* al. 1963), several studies show that variation in slopes and intercepts of MSDRs can be due to many reasons (Weller 1987a; Zeide 1985, 1987; Bi 2001; Weiskittel *et* al. 2009; Morris 2002; Morris 2003; Comeau *et* al., 2010; Ogawa 2005; Zeide 2005; Westoby and Howell 1981). Results of this Chapter also suggest that stand characteristics such as composition and site quality (*i.e.* nutrient regime) are influencing both the slope and intercept of MSDRs for these stands, and that in general, maximum stockabilities are achieved as the proportion of trembling aspen increases in the stand.

Furthermore, changes in growth patterns and behavior (*i.e.* variation in allometric relationships) of these species might be expected as a consequence of changes on inter- and intraspecific competition (Garber and Maguire 2004; Amoroso and Turnblom 2006); the interchange in competitive and facilitative interactions also affect growth patterns and allometry of species growing together, as compared to when they grow in pure stands (Weiskittel *et* al., 2009).

Additional investigation of relationships between MSDRs and tree characteristics such as live crown ratio, height-diameter ratio, and others, could be useful to further clarify this subject.

Results in Chapter three agree with previous findings respecting the variability in the understory light environment in boreal mixedwoods, as high variability in diffuse non-interceptance (DIFN) and below total light was recorded for mid-rotation and mature boreal pure and mixed stands. Although previous research showed the usefulness of stand basal area and aspen basal area for explaining understory light in similar ecosystems (MacIsaac and Navratil 1996; Filipescu and Comeau 2007a), for the older stands that I analyzed in this chapter there appears to be a disconnection between simple stand measurements, such as basal area, with leaf area and consequently with light interception. Previous research had also suggested SDI to be a powerful stand characteristic to be used for explaining understory light (Vales and Bunnell, 1988); however, the use of SDI in my study did not represent any improvement for the models tested, suggesting also a weak linkage between size-density relationships and understory light for these stands.

Although the best model obtained for explaining total stand volume periodic annual increment (Iv_{tot}) for boreal stands in Chapter four is able to describe only 31 % of this variability, results of this chapter suggest a strong influence of site occupancy by component species on volume increment, which is indicated by the significance of dynamic SDI of both species. Results of this chapter and from chapter two, also point to variation in maximum stockability as one of the main factors influencing variation in stand volume increment. Furthermore, any decrease in stocking of trembling aspen or white spruce, result in a decrease in Iv_{tot}.

Chapter five shows that one-sided competition is the main driving force for competition related mortality for both trembling aspen and white spruce in boreal mixedwoods, and that basal area of larger deciduous and larger aspen trees is able to capture these effects. Even though individual size, represented by diameter at breast height, is an important variable for defining the probability of survival of trees and saplings in these forests, individual tree growth rate is the characteristic that most precisely and accurately helps to understand patterns of tree survival, regardless of species.

Results of Chapter 5 also help to confirm what was observed in chapter 2, as smaller trees are the most susceptible to die in stands experiencing density-dependent mortality (*i.e.* in the presence of competition). Results of this chapter also show that trembling aspen will experience an increase in their risk of mortality in later stages, although this mortality would be most likely due to loss of vigor and senescence rather than due to competitive effects from neighbors.

Data sets used in this study covered a wide range of species proportions, tree sizes, and sites. These characteristics made it possible to include a wide range of stand developmental stages in the analyses. Since changes in ecological interactions between these two species are expected to change with age and other factors (Filipescu and Comeau 2007b), the data provide a valuable and unique representation of various developmental stages in stands comprised by these two species. In addition, since no management or human intervention has been allowed on most of these sites, I would expect these results to represent stand dynamics under natural conditions. Additionally, the methodologies and statistical tools used in each of the data-chapters provide consistent and reliable outcomes.

One of the potential shortcomings may arise from the stands that were visited and sampled to collect additional data, as explained in chapter three (55 sites sampled in total in the boreal mixedwoods). Special and substantial effort was put on the approach used for ‘pre-selecting’ and sampling suitable sites (permanent sample plots); however, there were some unexpected factors that made it difficult to sample the best sites for the purposes of this study. Perhaps the ‘quality’ of the sites, in terms of presence/absence of disturbances, easy access, and other factors was not the greatest for some of the plots. This perhaps had some repercussions on the quality of the data that was collected.

Nonetheless, I think that results presented here are valuable. There is evidence supporting the use of SDI in evaluating and explaining some key aspects of the dynamics of boreal mixed and pure stands comprised by trembling aspen and white spruce. Although in some cases SDI did not perform any better than ‘simpler’ stand characteristics (such as stand density or basal area), I did not find a strong reason against the use and usefulness of SDI. Finally, I consider that there are valuable contributions from this Dissertation. One of the first main contributions has been already published, and many others are in preparation and are expected to come out in the near future.

6.1 References

Amoroso, M.M.; and Turnblom, E.C. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36:1484-1496.

Bi, H. 2001. The self-thinning surface. For. Sci. 47(3):361-370.

Comeau, P.G.; White, M.; Kerr, G.; and Hale, S.E. 2010. Maximum density-size relationships for Sitka spruce and coastal Douglas-fir in Britain and Canada. Forestry. 83(5):461-468. doi:10.1093/forestry/cpq028

Filipescu, C.; and Comeau, P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Garber, S.M.; and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. For. Sci. 50(1):92-105.

Kira, T.; Ogawa, H.; and Zakazaki, N. 1953. Intraspecific competition among higher plants. I Competition-yield-density interrelationship in regular dispersed populations. J. Inst. Polytech. Osaka City Univ. 4:1-16.

MacIsacc, D.A.; and Navratil, S. 1996. Competition dynamics in juvenile boreal hardwood-conifer mixtures. In: Silviculture of temperate and boreal broadleaf-conifer mixtures. P. G. Comeau, and K. D. Thomas (Eds.). B. C. Ministry of Forests. For. Land Manage. Handbook pp:23-34

Morris, E.C. 2003. How does fertility of the substrate affect intraspecific competition? Evidence and synthesis from self-thinning. Ecol. Res. 18:287-305.

Morris, E.C. 2002. Self-thinning lines differ with fertility level. Ecol. Res. 17:17-28.

Ogawa, K. 2005. Time-trajectory of mean phytomass and density during a course of self-thinning in a sugi (*Cryptomeria japonica* D. Don) plantation. For. Ecol. Manage. 214:104-110

Puettmann, K.J.; Hibbs, D.E.; and Hann, D.W. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: extension of size-density analysis to species mixture. J. Ecol. 80:449-458.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Vales, D. J. and Bunnell, F.L. 1988. Relationships between transmission of solar radiation and coniferous forest stand characteristics. Agric. For. Meteor. 43:210-233.

Weiskittel, A.; Gould, P.; and Hailemariam, T. 2009. Sources of variation in the self-thinning boundary line for three species with varying levels of shade tolerance. For. Sci. 55(1):84-93.

Weller, D.E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs. 57(1):23-43.

Westoby, M.; and Howell J. 1981. Self-thinning: the effect of shading on glasshouse populations of silver beet (*Beta vulgaris*). J. Ecol. 69:359-365.

Yoda, K.; Kira, T.; Ogawa, H.; and Homuzi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants). J. Biol. Osaka City Univ. 14:107-129.

Zeide, B. 2005. How to measure stand density. Trees. 19:1-14. doi: 10.1007/s00468-004-0343-x

Zeide, B. 1987. Analysis of the 3/2 power law of self – thinning. For Sci. 33 (2): 517-537.

Zeide, B. 1985. Tolerance and self-tolerance of trees. For. Ecol. Manage. 13:149-166.

Bibliography

Alberta Environmental Protection. 1998. The boreal forest natural region of Alberta. Natural Resources Services. Recreation and Protected Ares Division. Edmonton, AB.

Amoroso, M.M.; and Turnblom, E.C. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36:1484-1496.

Barbier, S.; Gosselin, F.; and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved- A critical review for temperate and boreal forests. For. Ecol. Manage. 254:1-15 doi:10.1016/j.foreco.2007.09.038

Barkman, J.J. 1992. Canopies and microclimate of tree species mixtures. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (eds). The ecology of mixed-species stands of trees. Blackwell Scientific Publications. Oxford, UK. pp:181-188

Bartemucci, P.; Messier, C.; and Canham, C.D. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Can. J. For. Res. 23:1969-1979.

Beckingham, J.D.; and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Special Report No 5. Natural Resources Canada. Canadian Forest Service-Northern forestry Centre. Edmonton, AB.

Bi, H. 2004. Stochastic frontier analysis of a classic self-thinning experiment. Aus. Ecol. 29:408-417.

Bi, H. 2001. The self-thinning surface. For. Sci. 47(3):361-370.

Bi, H.; Wan, G.; and Turvey, N.D. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. Ecol. 81(6):1477-1483.

Bi, H.; and Turvey, N.D. 1997. A method of selecting data points for fitting the maximum biomass-density line for stands undergoing self-thinning. Aus. J. Ecol. 22:356-359.

Binkley, D.; Stape, J.L.; Bauerle, W.L.; and Ryan, M.G. 2010. Explaining the growth of individual trees: light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. For. Ecol. Manage. 259:1704-1713.doi:10.1016/j.foreco.2009.05.037

Binkley, D. 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. For. Ecol. Manage. 190:265-271.

Binkley, D.; Stape, J.L.; and Ryan, M.G. 2004. Thinking about efficiency of resource use in forests. For. Ecol. Manage. 193:5-16.

Blenis, P. 2007. Impact of simulated aspen shoot blight on trembling aspen. Can. J. For. Res. 37:719-725

Bokalo, M.; Comeau, P.G.;and Titus, S.J. 2007. Early development of tended mixtures of aspen and spruce in western Canadian boreal forests. For. Ecol. Manage. 242(2-3):175-184.

Bouchard, M.; Kneeshaw, D.; and Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. Can. J. For. Res. 37:763-772. doi: 10.1139/X06-278

Brandt, J.P. 2009. The extent of the North American boreal zone. Environ. Rev.17:101-161.

Burkhart, H.E. 2013. Comparison of maximum size-density relationships based on alternate stand attributes for predicting tree numbers and stand growth. For. Ecol. Manage. 289: 404-408. *doi:10.1016/j.foreco.2012.10.041*

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

Callaway, R.M.; and Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology. 78:1958-1965.

Canham, C.D. 1998. An index for understory light levels in and around canopy gaps. Ecology 69 (5):1634-1638.

Canham, C.D.; Finzi, A.C.; Pacala, S.W.; and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For Res. 24:337-349

Canham, C.D.; Denslow, J.S.; Platt, W.J.; Runkle, J.R.; Spies, T.A.; and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20:620-631.

Caspersen, J.P.; and Kobe, R.K. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos. 92:160-168

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

Chen, H.Y.H.; Fu, S; Monserud, R.A.; and Gillies, I.C. 2008. Relative size and stand age determine *Pinus banksiana* mortality. For. Ecol. Manage. 255:3980-3984. doi:10.1016/j.foreco.2008.03.040

Claveau, Y.; Messier, C.; Comeau, P.G.; and Coates, K.D. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32:458-468. doi:10.1139/X01-220

Coates, K.D.; Canham, C.D.; Beaudet, M.; Sachs, D.L.; and Messier, C. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. 186: 297-310

Comeau, P.G.; White, M.; Kerr, G.; and Hale, S.E. 2010. Maximum density-size relationships for Sitka spruce and coastal Douglas-fir in Britain and Canada. Forestry. 83(5):461-468. doi:10.1093/forestry/cpq028

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

Comeau, P.G.; Kabzems, R.; McClarnon, J.; and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle. 81:559-574.

Comeau, P.; Filipescu, C.N.; Kabzems, R.; and DeLong, C. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern B.C. Can. J. For. Res. 34:2277-2283.

Comeau, P. G.; Wang, J.R.; and Letchford, T. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine-fir following spacing. Can. J. For. Res. 33:1962-1973. doi:10.1139/x03-117

Comeau, P. G.; Macdonald, R.; Bryce, R.; and Groves, B. 1998. Lite: a model for estimating light interception and transmission through forest canopies. User's manual and program documentation. Res. Br., Min. For., Victoria, B.C. Work. Paper 35/1998.

Comeau, P.G. 1996. Why mixedwoods? In: P.G. Comeau & K.D. Thomas (eds). Silviculture of temperate and boreal broadleaf-conifer mixtures. pp: 1-5 B. C. Min. For. Land Manage. Handbook 36. Victoria, B. C.

Constabel, A.J.; and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26:1008-1014.

Constabel, A.J. 1995. Light transmission through boreal mixedwood stands. M.Sc. Thesis. University of Alberta. Edmonton, AB.

Cumming, S.G. 2001. Type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecol. Appl. 11:97-110

Cooke, B.J.; MacQuarrie, C.J.K.; and Lorenzetti, F. 2011. The dynamics of forest tent caterpillar outbreaks across east-central Canada. Ecography. 35:422-435. doi: 10.1111/j.1600-0587.2011.07083.x

Cooke, B.J.; and Roland, J. 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. Can. J. For. Res. 37:1586-1598.

Coomes, D.A.; and Allen, R.B. 2007. Mortality and tree-size distributions in natural mixed-aged forests. Journal of Ecology. 95:27-40.

Courbaud, B.; De Coligny, F.; and Cordonnier, T. 2003. Simulating radiation distribution in a heterogeneous Norway spruce forest on a slope. Agric. For. Met. 116:1-18.

Curtis, R.O. 1970. Stand density measures: an interpretation. For. Sci. 16:403-414.

Danell, K.; HussDanell, K.; and Bergstrom, R. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66:1867-1878.

Davis, L.S.; Johnson, K.N.; Bettinger, P.; and Howard, T.E. 2001. Forest management: to sustain Ecological, Economic, and Social value. 4th Edition. Waveland Press, Inc. Illinois, USA. 804 pp.

Dean T.J.; and Baldwin Jr., V.C. 1996. The relationship between Reineke's stand-density index and physical stem mechanics. For. Ecol. Manage. 81:25-34.

DeBell, D.S.; Harms, W.R.; and Whitesel, C.D. 1989. Stockability: a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern United States. For. Sci. 35(3):708-719.

DeLong, D.L.; Simard, S.W.; Comeau, P.G.; Dykstra, P.R.; and Mitchell, S.J. 2005. Survival and growth response of seedlings in root disease infected partial cuts in the interior cedar hemlock zone of southeastern British Columbia. For. Ecol. Manage. 206: 365–379.

Del Rio, M.; Montero, G.; and Bravo, F. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142:79-87.

DesRochers, A.; and Lieffers, V.J. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. Can. J. For. Res. 31:1012-1018

Drew, T.J.; and Flewelling, W. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. 23(4):517-534.

Ducey, M.J.; and Knapp, R.A. 2010a. Rapid assessment of relative density in mixed-species stands of Northeastern United States. Int. J. For. Res. Vol. 2010. 8 p. doi: 10.1155/2010/212068.

Ducey, M.J.; and Knapp, R.A. 2010b. A stand density index for complex mixed species forests in the northeastern United States. For. Ecol. Manage. 260:1613-1622. doi:10.1016/j.foreco.2010.08.014.

Dwyer, J.M.; Fensham, R.J.; Fairfax, R.J.; and Buckley, Y.M. 2010. Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. J. Veg. Science. 21:573-585.

Feng, Z.; Stadt, K.J.; and Lieffers, V.J. 2006. Linking juvenile white spruce density, dispersion, stocking, and mortality to future yield. Can. J. For. Res. 36:3173-3182. doi:10.1139/X06-192

Filipescu, C.; and Comeau, P.G. 2007a. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 37:1701-1713.

Filipescu, C.; and Comeau, P.G. 2007b. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175-184.

Forest Management Branch. 2005. Permanent Sample plot (PSP) field procedures manual. Alberta Sustainable Resource Development. Public Lands and Forest Division. Edmonton, AB.

Fortin, M.; Bedard, S.; DeBlois, J.; and Meunier, S. 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in Southern Quebec, Canada. Ann. For. Sci. 65: 205(1-12).

Franco, M.; and Kelly, C.K. 1998. The interspecific mass-density relationship and plant geometry. Proc. Nat. Acad. Sci.-USA. 95(13):7830-7835.

Franklin, J.F.; and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. J. For. 102:22-28.

Garber, S.M.; and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. For. Sci. 50(1):92-105.

Gendron, F.; Messier, C.; and Comeau, P. G. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agric. For. Meteor. 92:55-70

Gersonde, R.; Battles, J.J.; and O'Hara, K.L. 2004. Characterizing the light environment in Sierra Nevada mixed conifer forests using a spatially explicit light model. Can. J. For. Res. 34:1332-1342.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecol. 63:469-481.

Groom, J. D.; Hann, D.W.; and Temesgen, H. 2012. Evaluation of mixed-effects models for predicting Douglas-fir mortality. For. Ecol. Manage. 276:139-145. doi:10.1016/j.foreco.2012.03.029

Groot, A. 1999. Effects of shelter and competition on the early growth of planted white spruce (*Picea glauca*). Can. J. For. Res. 29:1002-1014.

Groot, A.; and Carlson, D.W. 1996. Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. Can. J. For. Res. 26:1531-1538.

Guneralp, B.; and Gertner, G. 2007. Feedback loop dominance analysis of two tree mortality models: relationship between behavior. Tree Phys. 27:269-280.

Hale, S.E.; Edwards, C.; Mason, W.L.; Price, M.; and Peace, A. 2009. Relationships between canopy transmittance and stand parameters in Sitka spruce and Scots pine stands in Britain. Forestry 82: 503-513

Hale, S.E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. For. Ecol. Manage. 179:341-349.

Haeussler, S.; Bartemucci, P.; and Bedford, L. 2004. Succession and resilience in boreal mixewood plant communities 15-16 years after silvicultural site preparation. Fore. Ecol. Manage. 199:349-370.

Hamilton, Jr. D.A. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. For. Sci. 32:989-1000.

Hanley, J.A.; and McNeil, B.J. 1982. The meaning and use of the Area under a Receiver Operating Characteristic (ROC) Curve. Radiology. 143(1):29-36.

Hann, D.W.; Marshall, D.D.; and Hanus, M.L. 2003. Equations for predicting height-to-crown-base, 5-year-diameter-growth-rate, 5-year height-growth rate, 5-year mortality rate, and maximum size- density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest. Res. Contribution 40, Forest Research Laboratory, Oregon State University, Corvallis, OR. 83 pp.

Hardy, J.P.; Melloh, R.; Koenig, G.; Marks, D.; Winstral, A.; Pomeroy, J.W.; and Link, T. 2004. Solar radiation transmission through conifer canopies. Agric. For. Meteor. 126:257-270.

Harms, W.R.; Whitesell, C.D.; and DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126(1):13-24.

Harms, W.R.; DeBell, D.S.; and Whitesell, C.D. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Can. J. For. Res. 24:511-521.

Harper, J. L. 1977. Population biology of plants. School of Plant Biology. University College of North Wales. Academic Press. London. 892 pp.

Hart, S.A.; and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. Critical reviews in plant sciences. 25:381-397.

Hart, J.W. 1988. Light and plant growth. In: M. Black and J. Chapman (Eds.): Topics in plant physiology I. Unwin Hyman. 204 pp.

Helms, J.A. (ed). 1998. The dictionary of Forestry. Society of American Foresters. Bethesda, MD. USA. 210 pp.

Hodson, A.C. 1981. The response of aspen (*Populus tremuloides*) to artificial defoliation. Great Lakes Entomol. 14:167-169.

Holmgren, M.; Scheffer, M.; and Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. Ecology. 78:1966-1975.

Hosmer, D.W. Jr.; and Lemeshow, S. 2000. Applied logistic regression. 2nd Edition. New York. John Wiley & Sons. USA. 369 p.

Huang, J.G.; Stadt, K.J.; Dawson, A.; and Comeau, P.G. 2013. Modelling growth-competition relationships in trembling aspen and white spruce mixed boreal forests of western Canada. PLos ONE 8(10): e77607. doi:10.1371/journal.pone.0077607

Huang, S. 1994. Individual tree volume estimation procedures for Alberta: methods for formulation and statistical foundations. Forest Resources Information Branch. Land and For. Serv. Technical Report # 1. T/288. Edmonton, AB. 80 pp.

Huang, S.; Titus, S.J.; Lakusta, T.W.; and Held, R.J. 1994. Ecologically based individual tree height-diameter models for major Alberta tree species. Alberta Env. Protection. Land and Forest Services. Forest Management Division. 27 p.

Hutchings, M.J.; and Budd, C.S.J. 1981. Plant competition and its course through time. Bioscience 31(9):640-645.

Hutchinson, M. 1983. Ecology's law in search of a theory. New Scientist. 98:765-767

Innes, J.C.; Ducey, M.J.; Gove, H.J.; Leak, W.B.; and Barrett, J.P. 2005. Size-density metrics, leaf area, and productivity in eastern white pine. Can. J. For. Res. 35: 2469-2478.

Jack, S.B.; and Long, J.N. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. For. Ecol Manage. 86:205-220.

Jennings, S.B.; Brown, N.D.; and Shell, D. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover, and other measures. Forestry 72:59-73.

Jerabkova, L.; Prescott, C.E.; and Kishchuk, B.E. 2006. Nitrogen availability in soil and forest floor of contrasting types of boreal mixedwood forests. Can. J. For. Res. 36: 112 -122.

Jonckheere, I.; Nackaerts, K.; Muys, B.; Coppin, P. 2005. Assessment of automatic gap fraction estimation of forests from digital hemispherical photography. Agric. For. Meteor. 132: 96-114.

Jose, S.; Williams, R.; and Zamora, D. 2006. Belowground ecological interactions in mixed-species forest plantations. For. Ecol. Manage. 233: 231-239.

Kashian, D.M.; Turner, M.G.; and Romme, W.H. 2005. Variability in leaf area and stemwood increment along a 300-year lodgepole sapling pine chronosequence. Ecosystems. 8:48-61.

Kelty, M.J. 2006. The role of species mixtures in plantations forestry. For. Ecol. Manage. 233: 195-204

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed species stands. In: M. J. Kelty, B. C. Larson and C. D Oliver (eds). The ecology and silviculture of mixed species forests. pp 125-141. Kluwer Academic Publishers. Dordrecht. 287 p.

Kenkel. N.C.; Hendrie, M.L.; and Bella, I.E. 1997. A long-term study of *Pinus banksiana* population dynamics. J. Veg. Sci. 8:241-254.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017-1024.

Kimmins, J.P. 2004. Forest Ecology: a foundation for sustainable forest management and environmental ethics in Forestry. 3rd edition. Prentice Hall. 611 p.

Kira, T.; Ogawa, H.; and Zakazaki, N. 1953. Intraspecific competition among higher plants. I Competition-yield-density interrelationship in regular dispersed populations. J. Inst. Polytech. Osaka City Univ. 4:1 -16.

Kitajima, K.; Mulkey, S.S. and Wright, S.J. 2005. Variation in crown light utilization characteristics among tropical canopy trees. Annals of Bot. 95:535-547.

Kneeshaw, D.D.; and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology. 79:783-794.

Kobe, R.K.; and Coates, K.D. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of Northwestern British Columbia. Can. J. For. Res. 27: 227-236.

Kozlowski, T.T.; Kramer, P.J.; and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press. New York. 657 pp.

Kunstler, G.; Coomes, D.A.; and Canham, C.D. 2009. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. J. Ecol. 97:685-695.

Kutner, M.H.; Nachtsheim, C.J.; Neter, J.; and Li, W. 2005. Applied linear statistical models. Fifth edition. McGraw Hill. International edition. New York, USA. 1396 pp.

Lambert, M.C.; Ung, C.H.; and Raulier, F. 2005. Canadian national tree aboveground biomass equations. Can J. For. Res. 35:1996-2018. doi:10.1139/X05-112

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog (About thinning in even-aged stands of spruce, fir and pine), Meddel. f.d. Norske Skogforsoksvesen. 8: 131-216.

Legare, S.; Pare, D.; and Bergeron, Y. 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. Can. J. For. Res. 34:405-416. doi: 10.1139/X03-251

Lhotka, J.M.; and Loewenstein, E.F. 2008. An examination of species-specific growing space utilization. Can. J. For. Res. 38: 470 – 479.

Lieffers, V.J.; Pinno, B.D.; and Stadt, K.J. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. For. Chron. 78(1):137-145.

Lieffers, V.J.; Messier, C.; Stadt, K.J.; Gendron, F.; and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29:796-811.

Lieffers, V.J.; Macmillan, R.B.; MacPherson, D.; Branter, K.; and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72(3):286-292.

Lieffers, V.J.; Stadt, K.J.; and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26:1002-1007

Lieffers, V.J.; and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Lieffers, V.J.; and Campbell, J.S. 1984. Biomass and growth of *Populus tremuloides* in northeastern Alberta: estimates using hierarchy in tree size. Can. J. For. Res. 14:610-616.

Littell, R.C.; Milliken G.A.; Stroup, W.W.; Wolfinger, R.D.; and Schabenberger, O. 2006. SAS® for mixed models, Second Edition. SAS Institute Inc. Cary, N.C. 814 pp.

Lochhead, K.D.; and Comeau, P.G. 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. For. Ecol. Manage. 284: 12-22. doi:10.1016/j.foreco.2012.07.029

Long, J.N.; and Shaw, J.D. 2010. The influence of compositional and structural diversity on forest productivity. Forestry. 83(2): 121-128. doi:10.1093/forestry/cpp033

Long, J.N.; and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. For. Ecol. Manage. 53: 53-64.

Long, J.N. and Daniel, T.W. 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For. 5:93-96.

Long, J.N.; and Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var *latifolia* forests: the influence of site quality and stand structure. J. Appl. Ecol. 27:847-856.

Long, J.N.; and Dean, T.J. 1986. Sapwood area of *Pinus contorta* stands as a function of mean size and density. Oecologia. 68:410-412.

Long, J.N. 1985. A practical approach to density management. For. Chron. 61:23-27.

Lonsdale, W.M.; and Watkinson, A.R. 1983. Plant geometry and self-thinning. J. of Ecol. 71(1):285-297.

Lonsdale, W.M.; and Watkinson, A.R. 1982. Light and self-thinning. New Phytologist. 90 (3):431- 445

Luo, Y.; and Chen, H.Y.H. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. J. of Ecol. 99:1470-1480.

MacDonald, G.B. 1996. The emergence of boreal mixedwood management in Ontario: background and prospects. In: Advancing boreal mixedwood management in Ontario. Ed: C.R. Smith and G.W. Crook. Natural Resources Canada. CFS. Sault Ste. Marie, Ontario. 11 pp.

MacIsacc, D.A.; and Navratil, S. 1996. Competition dynamics in juvenile boreal hardwood-conifer mixtures. In: Silviculture of temperate and boreal broadleaf-conifer mixtures. P. G. Comeau, and K. D. Thomas (Eds.). B. C. Ministry of Forests. For. Land Manage. Handbook pp:23-34

MacPherson, D.M.; Lieffers, V.J.; and Blenis, P.V. 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For. Chron. 77:451-356

Maguire, D.A.; Halpern, C.B.; and Phillips, D.L. 2007. Changes in forest structure following variable-retention harvests: target and non-target effects. For. Ecol. Manage. 242, 708–726.

Man R.; and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75:505-513.

Mencuccini, M.; Martinez-Vilalta, J.; Vanderklein, D.; Hamid, H.A.; Korakaki, E.; Lee, S.; and Michiels, B. 2005. Size-mediated ageing reduces vigor in trees. Ecol. Letters. 8:1183-1190.

Messier, C.; Parent, S.; and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9:511-520.

Messier, C.; and Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Can. J. For. Res. 25:343-354.

Monserud, R.A. 1976. Simulation of forest tree mortality. For. Sci. 22: 438-444.

Monserud, R.A.; and Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113:109-123.

Morris, E.C. 2003. How does fertility of the substrate affect intraspecific competition? Evidence and synthesis from self-thinning. Ecol. Res. 18:287-305.

Morris, E.C. 2002. Self-thinning lines differ with fertility level. Ecol. Res. 17:17-28.

Newton, P.F. 2006. Asymptotic size-density relationships within self-thinning black spruce and jack pine stand-types: parameter estimation and model reformulation. For. Ecol. Manage. 226: 49-59.

Niinemets, U.; and Valladares, F. 2006. Tolerance to shade, drought, and water logging of temperate Northern Hemisphere of trees and shrubs. Ecol. Monographs. 76: 521-547.

Norberg, R.A. 1988. Theory of growth geometry of plants and self-thinning of plant populations: geometric similarity, elastic similarity, and different growth models of plant parts. Amer. Nat. 131:220-256.

Nyland, R.D. 2002. Silviculture: concepts and applications. Waveland Press, Inc. Illinois, USA. 682 pp.

O'Hara, K.L.; and Gersonde, R.F. 2004. Stocking control concepts in uneven-aged silviculture. Forestry. 77:131-143.

O'Hara, K.L.; and Valappil, N.I. 1995. Sapwood-leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Can. J. For. Res. 25: 1553-1557.

Oliver, C.D.; and Larson, B.C. 1996. Forest stand dynamics. Wiley, New York. 520 pp.

Ogawa, K. 2005. Time-trajectory of mean phytomass and density during a course of self-thinning in a sugi (*Cryptomeria japonica* D. Don) plantation. For. Ecol. Manage. 214:104-110

Osawa, A.; and Allen, R. 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology 74(4):1020-1032.

Partel, M.; Laanisto, L.; and Zobel, M. 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. Ecology. 88: 1091-1097.

Peet, R.K.; and Christensen, N.L. 1980. Succession: a population process. Vegetatio 43(1/2):131-140.

Perry, D.A.; Oren, R.; and Hart, C.S. 2008. Forest Ecosystems. Second Edition. The John Hopkins University Press. Baltimore, MD, USA. 606 pp.

Peterson, E.B.; and Peterson, N.M. 1995. Aspen manager's handbook for British Columbia, Canada. British Columbia Partnership Agreement. FRDA II. FRDA Report #230. Victoria, B.C. 121 pp.

Peterson, E.B.; and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces. Can. For. Serv. North. Cent. Spec. Rep. 1. 252 pp.

Pinno, B.D.; Lieffers, V.J.; and Stadt, K.J., 2001. Measuring and modeling the crown and light transmission characteristics of juvenile aspen. Can. J. For. Res. 31: 1930– 1939.

Poage, N.J.; Marshall, D.D.; and McClellan, M.H. 2007. Maximum stand density index of 40 western Hemlock-Sitka spruce stands on southeast Alaska. West. J. Appl. For. 22(2):99-104.

Pretzsch, H. 2009. Forest dynamics, growth and yield: from measurement to model. Springer-Verlag. Berlin Heidelberg. 664 p.

Pretzsch, H. 2006. Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands. Oecologia. 146:572-583. DOI 10.1007/s00442-005-0126-0

Pretzsch, H.; Block, J.; Dieler, J.; Dong, P.H.; Kohnle, U.; Nagel, J.; Spellmann, H.; and Zingg, A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67(712). doi: 10.1051/forest/2010037

Pretzsch, H.; and Biber, P. 2005. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51 (4): 304-320.

Pritchard, J.M.; and Comeau, P.G. 2004. Effects of opening size and stand characteristics on light transmittance and temperature under young trembling aspen stands. For. Ecol. Manage. 220:119-128.

Pritchard, J.M. 2003. The effect of opening size on light, temperature and the growth of white spruce under a trembling aspen canopy. Master of Science Thesis. University of Alberta. Edmonton, AB. 145 p.

Puettmann, K.J.; Hibbs, D.E.; and Hann, D.W. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: extension of size-density analysis to species mixture. J. Ecol. 80:449-458.

Ratkowsky, D.A. 1990. Handbook of nonlinear regression. Marcel Dekker, Inc. New York. 241 p.

Rea, R.V.; and Booth, A.L. 2011.Use of trembling aspen bark by moose in a browse-abundant habitat during winter. Wildlife Afield. 8(1):104-107.

Reifsnyder, W.E.; Furnival, G.M.; and Horowitz, J.L. 1971. Spatial and temporal distribution of solar radiation beneath forest canopies. Agric. Meteorol. 9:21-37.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Reyes-Hernandez, V.; Comeau, P. G.; and Bokalo, M. 2013. Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. For. Ecol. Manage. 289:300-311.

Reynolds, J.H.; and Ford, D. 2005. Improving competition representation in theoretical models of self-thinning: a critical review. J. Ecol. 93: 362- 372.

Ridler, W.; and Calvard, S. 1978. Picture thresholding using an iterative selection method. IEEE. Trans. Syst. Man, Cyber. 8 (8): 630-632.

Rowe, J.S.; and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. 3:444-464.

Rowe, J.S. 1972. Forest regions of Canada. Publication No 1300. Dep. Environ. Can. For. Serv. Ottawa, ON.

SAS. 2010. Statistical Analysis System for windows, V 9.2. SAS-Institute, Inc. Cary, N.C. USA.

Saunders, M.K.; and Puettmann, K.J. 2000. A preliminary white spruce density management diagram for the Lake states. Staff paper series No 145. College of Natural Resources. University of Minnesota. St. Paul, Minnesota. USA. 13 pp

Sharpe, F.; Shaw, D.C.; Rose, C.L.; Sillet, S.C.; and Carey, A.B. 1996. The biologically significant attributes of forest canopies to small birds. Northwest Sci. 70:86-93.

Shaw, J.D. 2000. Application of stand density index to irregularly structured stands. West. J. Appl. For. 15: 40-42.

Shinozaki, K.; Yoda, K.; Hozumi, K.; and Kira, T. 1964. A quantitative analysis of plant form- the pipe model theory I. Basic analysis. Japan. J. Ecol. 14: 97–105.

Shinozaki, K.; and Kira, T. 1956. Intraspecific competition among higher plants. Logistic theory of the C-D effect. J. Inst. Pol. Osaka City Univ. 7:35-72.

Schutz, J.P.; and Zingg, A. 2010. Improving estimations of maximal stand density by combining Reineke's size-density rule and the yield level, using the example of spruce (*Picea abies* (L.) Karst.) and European Beech (*Fagus sylvatica* L.). Ann. For. Sci. 67:507 12 pp.

Smith, F.W.; and Long, J.N. 2001. Age-related decline in forest growth: an emergent property. For. Ecol. Manage. 144:175-181

Smith, D.J.; and Woods, M.E. 1997. Red pine and white pine density management diagrams for Ontario. Tech. Report # 48. Ontario Ministry of Nat. Res. Sault Ste. Marie, ON. 31 p.

Smith, D.M.; Larson, B.C.; Kelty, M.J.; and Ashton, P.M.S. 1997. The practice of Silviculture: applied forest ecology. 9th edition. John Wiley and Sons. New York, USA. 537 p.

Stoll, P.; Weiner, J.; Muller-Landau, H.; Muller, E.; and Hara, T. 2002. Size symmetry of competition alters biomass-density relationships. Proc. R. Soc. Lond. B. 269:2191-2195. doi: 10.1098/rspb.2002.2137

Stadt, K.J.; Huston, C.; Coates, K.D; Feng, Z.; Dale, M.R.T.; and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth n mature boreal mixed forests. Ann. For. Sci. 64:477-490

Stadt, K.J.; and Lieffers, V.J. 2005. Comparing PAR transmission models for forest understorey vegetation. App. Veg. Sci. 8: 65-76.

Tobin, B.; Black, K.; Osborne, B.; Reidy, B.; Bolger, T.; and Nieuwenhuis, M. 2006. Assessment of allometric algorithms for estimating leaf biomass, leaf area index and litter fall in different-aged Sitka spruce forests. Forestry. 79:453-465

Torres-Rojo, J.M.; and Velázquez-Martínez, A. 2000. Índice de densidad relativa para rodales coetáneos mezclados. Agrociencia. 34: 497-507.

Turner, M.G.; Romme, W.H.; Gardner, R.H.; and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. 67:411-433.

Vales, D. J. and Bunnell, F.L. 1988. Relationships between transmission of solar radiation and coniferous forest stand characteristics. Agric. For. Meteor. 43:210-233.

Valladares, F.; and Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. Ann. Rev. Ecol. Evol. Syst. 39:237-257.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge University Press. Cambridge, MA. 237 pp.

VanderSchaaf, C.L. 2010. Estimating individual stand size-density trajectories and a maximum size-density relationship species boundary line slope. For. Sci. 56(4): 327-335.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007a. Using segmented regression to estimate stages and phases of stand development. For. Sci. 54(2): 167-175.

VanderSchaaf, C.L.; and Burkhart, H.E. 2007b. Comparison of methods to estimate Reineke’s maximum size-density relationship species boundary line slope. For. Sci. 53(3):435-442.

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

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience. 37(8):569-574.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecol. and Evol. 5: 360-364.

Weiskittel, A.; Gould, P.; and Hailemariam, T. 2009. Sources of variation in the self-thinning boundary line for three species with varying levels of shade tolerance. For. Sci. 55(1):84-93.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? - a reply to Osawa and Sugita. Ecology. 71(3): 1204-1207.

Weller, D.E. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the -3/2 power rule of self-thinning. American Naturalist 133(1):20-41.

Weller, D.E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs. 57(1):23-43.

Weller, D.E. 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. Ecology 68(4):813-821.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167-225.

Westoby, M.; and Howell J. 1981. Self-thinning: the effect of shading on glasshouse populations of silver beet (*Beta vulgaris*). J. Ecol. 69:359-365.

White, J. 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89:475-500.

White, J. 1980. Demographic factors in populations of plants. In: Demographic and evolution in plant populations. O. T. Solbrig (ed.). Blackwell Sci. Publications, Oxford. pp: 21-48.

Woodall, C.W.; Miles, P.D.; and Vissage, J.S. 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. For. Ecol. Manage. 216: 367-377.

Woodall, C.W.; Fiedler, C.E.; and Milner, K.S. 2003. Stand density index in uneven-aged ponderosa pine stands. Can. J. For. Res. 33: 96-100.

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

Yachi, S.; and Loreau, M. 2007. Does complementarity resource use enhance ecosystem functioning? A model of light competition in plan communities. Ecology Letters. 10:54-62.

Yang, Y.; and Huang, S. 2013. A generalized mixed logistic model for predicting individual tree survival probability with unequal measurement intervals. For. Sci. 59(2): 177-187.

Yang, Y.; Titus, S.J.; Huang, S. 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Model. 163:209-222.

Yang, R.C. 1989. Growth response of white spruce to release form trebling aspen. Northern Forestry Centre. Forestry Canada. Information report NOR-X-302. Edmonton, AB. Canada. 24 p.

Yao, X.; Titus, S.J.; and MacDonald, S.E. 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. Can. J. For. Res. 31(2):283-291.

Yoda, K.; Kira, T.; Ogawa, H.; and Homuzi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants). J. Biol. Osaka City Univ. 14:107-129.

Zeide, B. 2005. How to measure stand density. Trees. 19:1-14. doi: 10.1007/s00468-004-0343-x

Zeide, B. 1987. Analysis of the 3/2 power law of self – thinning. For Sci. 33 (2): 517-537.

Zeide, B. 1985. Tolerance and self-tolerance of trees. For. Ecol. Manage. 13:149-166.

Zhang, L.; Bi, H.; Gove, J.H.; and Heath, L.S. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. Can. J. For. Res. 35: 1507-1514. doi: 10.1139/X05-070

Appendix A

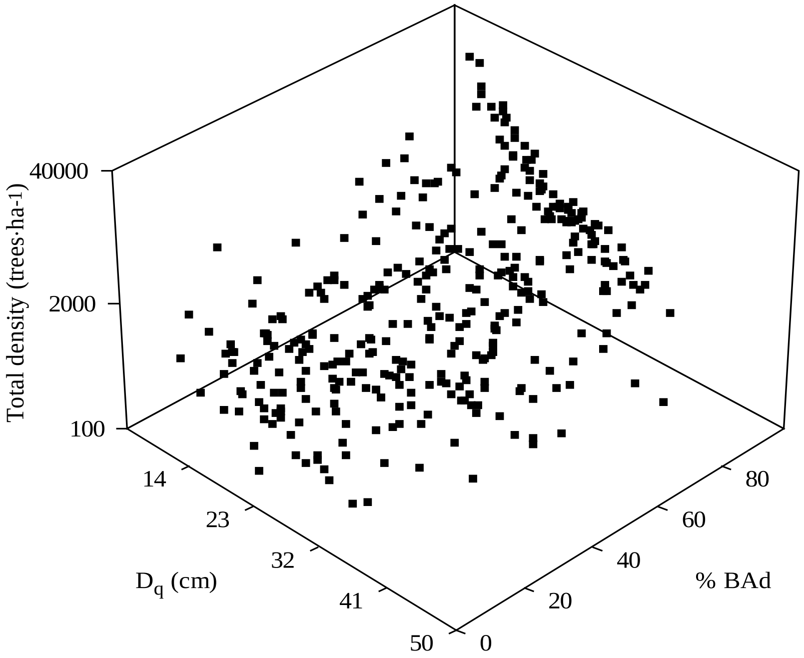


Figure 1. Scatter plot of raw data used to fit the static self-thinning line for the total density-quadratic mean diameter relationship, using stochastic frontier function regression in Chapter 2.

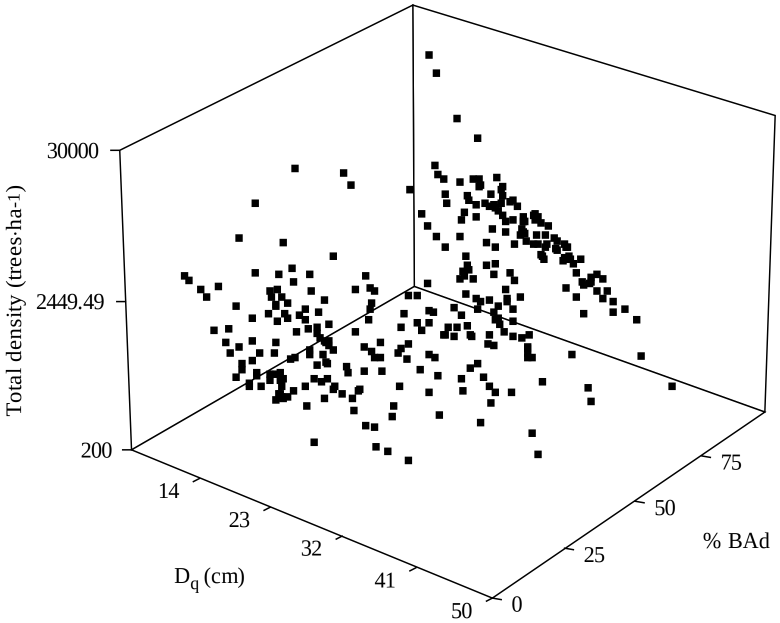


Figure 2. Scatter plot of raw data used to fit the dynamic self-thinning line for the total density-quadratic mean diameter relationship, using mixed models in Chapter 2.

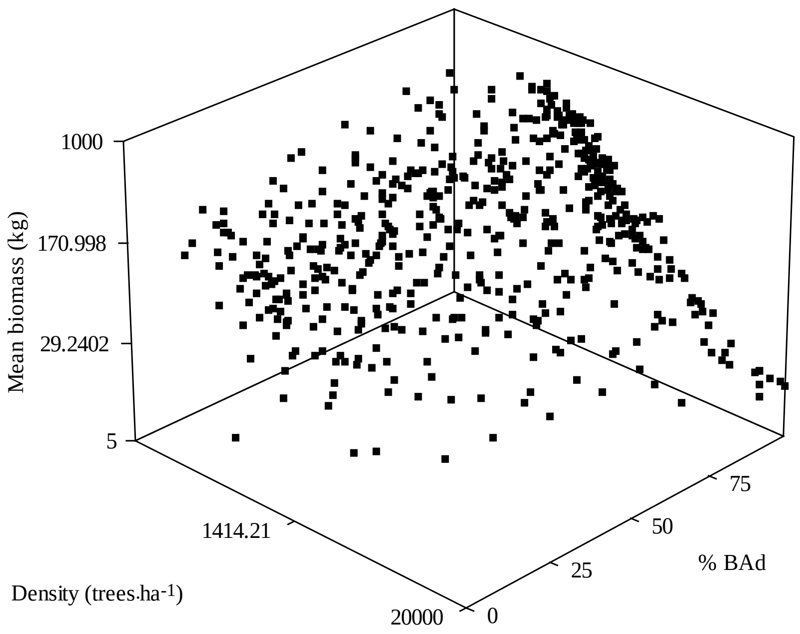


Figure 3. Scatter plot of raw data used to fit the static self-thinning line for the mean biomass-total density relationship, using stochastic frontier function regression in Chapter 2.

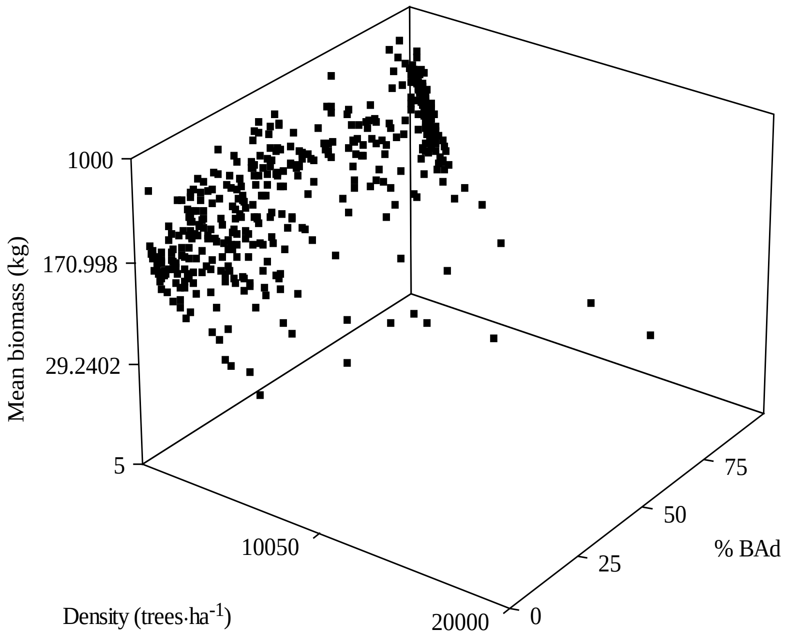


Figure 4. Scatter plot of raw data used to fit the dynamic self-thinning line for the mean biomass-total density relationship, using mixed models in Chapter 2.

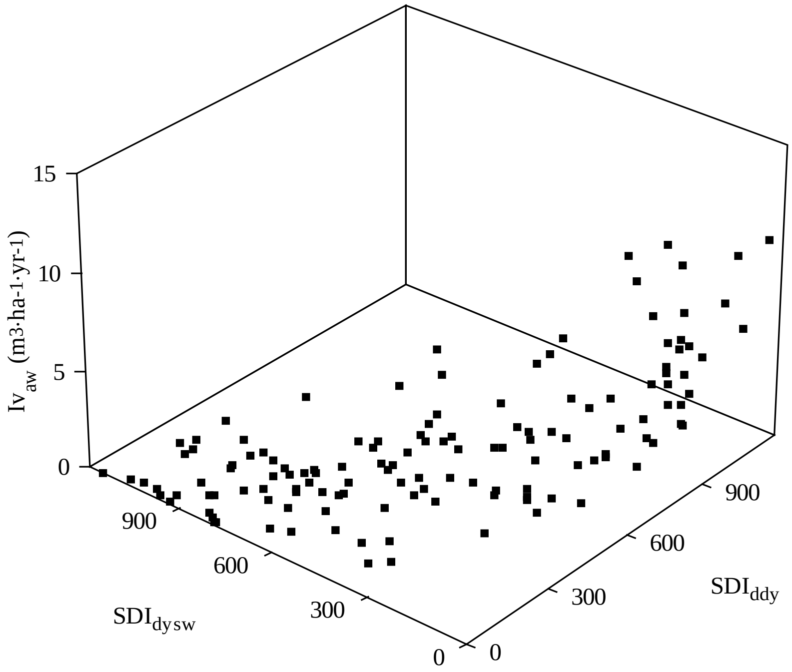


Figure 5. Scatter plot of trembling aspen volume increment data (Iv_{aw}) as related to deciduous dynamic SDI (SDI_{ddy}) and spruce dynamic SDI (SDI_{dysw}), used in Chapter 4.

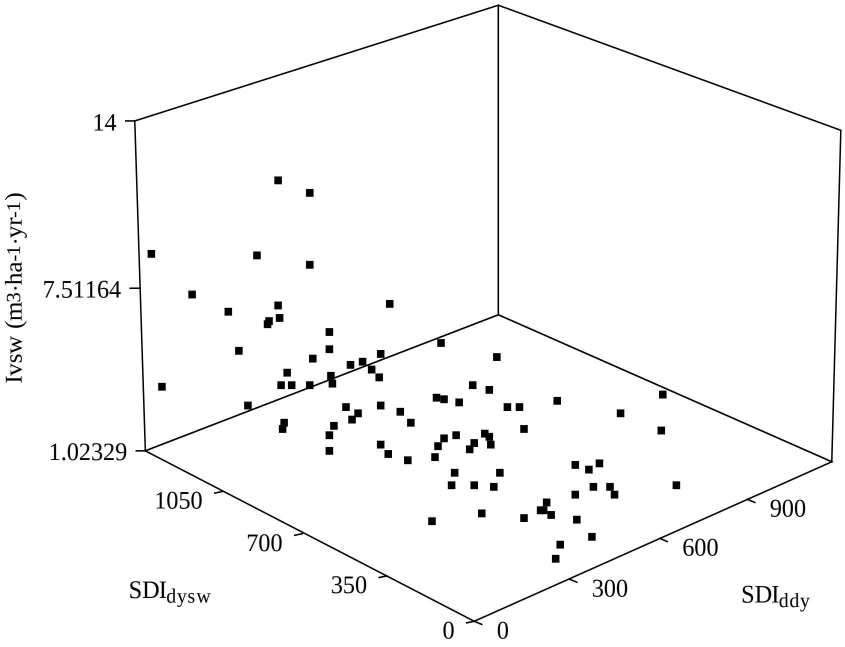


Figure 6. Scatter plot of white spruce volume increment data (Iv_{sw}) as related to deciduous dynamic SDI (SDI_{ddy}) and spruce dynamic SDI (SDI_{dysw}), used in Chapter 4.

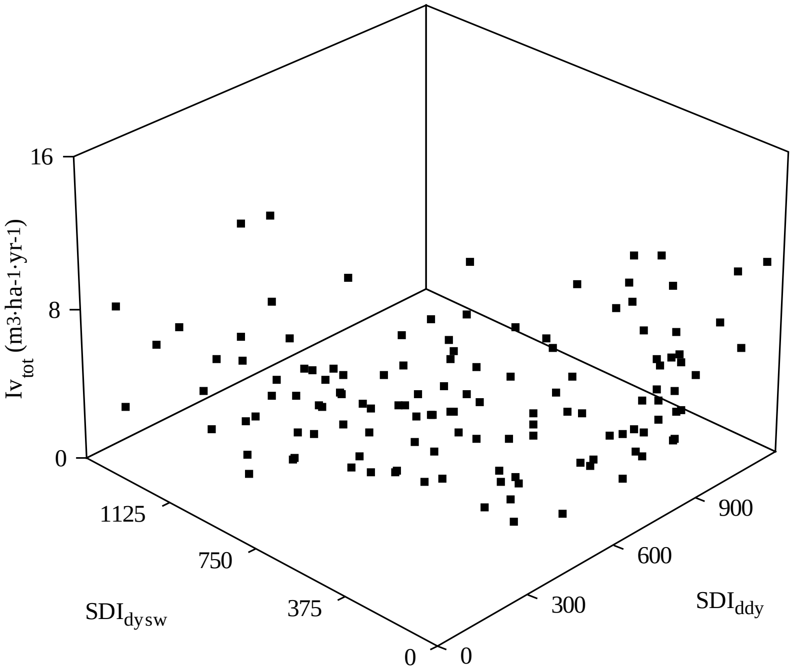


Figure 7. Scatter plot of total stand volume increment data (Iv_{tot}) as related to deciduous dynamic SDI (SDI_{ddy}) and spruce dynamic SDI (SDI_{dysw}), used in Chapter 4.