

INVESTIGATION INTO THE PRODUCTIVITY OF
FIRE-ORIGIN LODGEPOLE PINE
AND LODGEPOLE PINE-BLACK SPRUCE STANDS

by

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ABSTRACT

The purpose of this study was to develop a better understanding of the growth differences between unmanaged, fire-origin, even-aged lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud) and lodgepole pine-black spruce (*Picea mariana* (Mill.) B.S.P.) stands. Both species commonly grow together on "d" (Labrador tea-mesic) ecosites of the Upper Foothills subregion of Alberta. During the summer of 2000, 27 study stands were selected to assess growth, structure and productivity of pine and pine and pine-spruce stands. These stands were stratified into (i) two stand types: pine and pine-spruce; and (ii) four age classes: (1) 50 - 60, (2) 60 - 80, (3) 90 - 100, and (4) 100 - 120 years at breast height.

Vegetation, soil, and stand data were collected and analyzed to determine: (a) site quality, (b) site index, (c) stand structure (diameter, height, and crown height frequency distributions), (d) height and basal area growth, and (e) stand volume. The vegetation and soil analyses confirmed the initial field assessment of fresh, nitrogen-poor sites. The variation in pine site index across age classes varied between 12.3 m and 13.9 m and was not significantly different. Similarly, there was no difference in the mean pine site indices between pine stands (13.5 m) and pine-spruce stands (12.6 m). It was concluded that the sampled plots were ecologically equivalent and were suitable for the productivity comparison of pine vs. pine-spruce stands.

Growth of pine in height and diameter was not impeded when it grew with spruce. There was no significant difference between the mean dimensions of pine trees (dbh, height, and height to live crown) in pine vs. pine-spruce stands. The relatively small differences in stand characteristics in both species between age class 2 and 3 stands were attributed to density-dependent mortality and the progressive ingress of spruce into the canopy. Pine-spruce stands were consistently two-storied across age classes with pine in the upper canopy stratum.

The basal area growth of dominant pine trees was weakly influenced by the presence of spruce. Compared to spruce, the growth of pine was faster and more variable, likely reflecting the history of stand density. Compared to pine, the basal area growth of spruce was slower but less variable and more consistent across age classes. Height growth of dominant pine trees was variable between age classes, but not between stand types. Given that there were only minor differences in height and basal area growth of pine between pine and pine-spruce stand types, competition did not appear to impede the development of dominant pine trees, despite expectations of increased competition for resources between pine and spruce on these nitrogen-poor sites.

Comparisons of stand volume showed significant differences between age classes and stand types. Relative density was an important determinant of stand productivity. For the younger stands, the mean gross volume was higher by $25 \text{ m}^3 \text{ ha}^{-1}$ in pine stands compared to pine-spruce stands and the merchantable stand volume was higher by $18 \text{ m}^3 \text{ ha}^{-1}$. However, in the older stands, pine-spruce stands had a higher volume than pine stands. This increase is attributed to the large ingress of spruce into the upper canopy. When the management objective is timber production and harvesting is planned for the period between 100 and 120 years (@ bh), then pine-spruce stands provided approximately $87 \text{ m}^3 \text{ ha}^{-1}$ or 28% more net stand volume and approximately $44 \text{ m}^3 \text{ ha}^{-1}$ or 16% more merchantable stand volume than pine stands.

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1 INTRODUCTION

1.1 Sustainable Forest Management And Its Implications

Since 1992, official commitments have been made by the Alberta government to shift from sustained yield to sustainable forest management (Canada Forest Accord 1992). Whereas sustained yield management considers only the supply of fiber, sustainable forest management also considers the preservation of environmental and social values. Consequently, the forest industry is pressured to practice "ecological management" (sensu Bourgeron and Jensen 1993) and maintain biodiversity (sensu Lähde *et al.* 1999) (AFCS 1997). Forest companies are to implement cautious and monitored harvest plans. They also must set landscape level age-class goals that retain a full array of indigenous species and age classes. For forest managers, complying with these requirements often means maintaining a constant flow of timber from a smaller land base and/or from economically less attractive species. To sustain both biodiversity and productivity, it is therefore important to understand the processes under which existing forest conditions have evolved, which would help forecasting and planning the future under different management practices (AFMSC 1997).

Weldwood of Canada Ltd. manages the oldest Alberta Forest Management Agreement (FMA). Weldwood has made biodiversity and age-class structure conservation a part of its forest management plan for 2000, aiming to further improve ecological management. To date, this type of management has proven beneficial to the company (Bonar 2001), but it has chiefly been applied to single-species, even-aged stands. Lack of knowledge regarding complex stand development has slowed the application of appropriate ecological management practices in mixed-species stands. A better understanding of complex stand development is thus required to further improve management of such stands.

1.2 Lodgepole pine and black spruce mixed-species stands

Mixed-species stands of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud) and black spruce (*Picea mariana* (Mill.) B.S.P.) are frequently found on upland intermediate sites (ecosite

"d" or Labrador tea-mesic) in the Upper Foothills of west central Alberta (Beckingham *et al.* 1996). These sites represent approximately 26% of the area in the Weldwood FMA (Hinton Division) (Downing 1999). The commercial importance of these two species (Huang and Titus 1992) further motivated the study of such a mixture. Available over relatively short rotations, lodgepole pine combines many desirable properties: strong yet light, small knots, pale colour, and high quality fibre (Koch 1996). Black spruce wood has long fibres that are desirable for high quality pulp; however, slower growth and small diameter limit its use as sawtimber (Viereck and Johnston 1990).

The concept of a potential increase for productivity in mixed-species stands has long been discussed, particularly in Europe (Assman 1970). However, it seldom was incorporated into forestry practice (Kelty 1992). Mixed-species stands can lead to greater structural diversity and volume yields than single-species stands (Eckhart *et al.* 1961; Moser 1964; Bachmann 1967; Zakopal and Mares 1968; Zohrer 1969; Assman 1970; Buzun 1970; Kramer and Kozlowski 1979; Binkley 1984; Smith 1986). Differences in yields between single- and mixed-species stands are attributed to the autecology of the species present in a stand: their shade tolerance (Oliver and Larson 1996), developmental stage (Pallardy 1985; De Bell *et al.* 1997), age and structure of the stand (Stubblefield and Oliver 1978; Wierman and Oliver 1979), and the spatial pattern of tree distribution (Mielikainen 1980, 1985; Simard 1990). In short, mixed-species stands can be expected to have a higher productivity than single-species stands if there is differential resource use among the species (Assman 1970; Vandermeer 1989). Equal or lower productivity will likely result if there is a division of the total resources among species in a mixture (Kelty 1992). Increasing productivity by selecting the most productive species or mixture of tree species for a given site might result in the full capture of the productivity potential of the site under management.

Comparing productivity and development of mixed-species vs. single species stands implies that the amount of resources available to trees should be equivalent among the stands compared. Differences in site quality can make it very difficult to compare the single vs. mixed species stands as difference in productivity may be the product of difference in site quality rather than difference in species composition. Therefore, it becomes crucial that the sites on which selected stands are located are ecologically equivalent. It is assumed that site quality controls what vegetation grows

and develops in an area (Avery and Burkhart 1994). It should be possible to measure site quality directly by determining soil nutrient, soil moisture, soil aeration, and temperature regimes. However site quality is also altered by the plants and other organisms the area supports and the aforementioned site characteristics can be confounding (Carmean 1970,1976; Tesh 1981; Packee 1988; Powers *et al.* 1990). Assuming that the soil-site factors that control the presence and relative abundance of the associated understory also control the height growth of trees (Ellenberg 1988; Klinka *et al.* 1989; Wilson *et al.* 2001), it is believed that vegetation can be a reliable indicator of site quality.

1.3 Objectives

The purpose of this investigation was to examine growth and structure differences between stands of lodgepole pine and mixed-species stands of lodgepole pine and black spruce along a selected segment of a development gradient (between 50 and 120 years approximately) on Labrador tea-mesic sites. The specific objectives were to determine whether:

- (1) the selected stands had similar site quality,
- (2) pine-spruce stands develop a stratified canopy structure,
- (3) pine-spruce stands have greater volume than pine stands for a given age class; and
- (4) the site quality, the canopy structure and the volumes of pine and spruce, and lodgepole pine site index remain constant over time.

These objectives were accomplished by comparing differences among species, stand types, and age classes in:

- (1) vegetation and soil characteristics, site index and positions of the stands on the stand density management diagram,
- (3) height, diameter, and crown height frequency distributions,
- (4) patterns of height and basal area growth and
- (5) net and merchantable volume.

2 SILVICS OF LODGEPOLE PINE AND BLACK SPRUCE

2.1 Regeneration and Establishment

In the Upper Foothills, stands containing black spruce and lodgepole pine are typically fire-origin and even-aged (Horton and Lees 1961; Duffy 1964). In general, black spruce, like lodgepole pine, becomes established following wildfire (Viereck and Johnston 1990). This process, however, takes place over a variable and considerably broader time span than for pine. Horton (1956) and Horton and Lees (1961) suggested that spruce would continue to seed in until the pine canopy closes. If canopy closure in pine stands occurs early, then age range of spruce may be only 10-15 years, the time required for canopy closure of pine.

The ability of lodgepole pine to regenerate depends on many factors but post-fire conditions, favourable seedbed and abundant seed source in particular, are likely the main cause of the initial high densities in 'repressed' lodgepole pine stands (Horton 1953; Dumanski *et al.* 1973). Serotinous cones of lodgepole pine accumulate on the trees and ground over time (Lotan and Critchfield 1990). The higher this accumulation is, the greater the establishment density. Past densities are thus an important determinant of stand initial density in pine stands (Horton 1956; Lotan and Critchfield 1990). This could explain the extreme variation in the density observed amongst stands of similar site quality and age (Smithers 1961; Duffy 1964).

Once established, lodgepole pine and black spruce are well adapted to upland sites conditions (Lotan and Critchfield 1990; Viereck and Johnston 1990). Mortality appears to depend upon initial density and, although heavy mortality can occur even at advanced ages, initially dense stands tend to remain relatively dense (Horton and Lees 1961; Smithers 1961).

2.2 Early Growth

On upland sites, black spruce is at a competitive disadvantage with its relatively steady but slower growth rate than lodgepole pine (Horton and Lees 1961; Viereck and Johnston 1990). Over an 80-year rotation, black spruce clearly remains in the understory of lodgepole pine (Horton 1956; Horton and Lees 1961; Morris *et al.* 1988; Viereck and Johnston 1990). Horton and Lees (1961)

suggested that black spruce trees might exhibit height growth rates similar to lodgepole pine provided adequate spacing. However, increased height growth rate would likely diminish survival (Walters *et al.*, 1993; Kobe and Coates 1997; Wright *et al.*, 1998). Moreover, the slower growth habit of black spruce is thought to persist regardless of light availability and photosynthetic potential (Leverenz and Hinkley 1990). Nonetheless, diameter growth of black spruce may be maintained over a long time under the canopy before height growth release (Morin and Gagnon 1991; Paquin and Doucet 1992; Boily and Doucet 1993; Doucet 2000) due to its branching habit and shoot structure (Carter and Smith 1985).

In contrast, shade-intolerant lodgepole pine appears to display less morphological plasticity, with fast height growth and strong apical dominance being the rule under all types of light regimes (Chen *et al.* 1996). Unlike black spruce, lodgepole pine survival in the understory is rare (Minore 1979). Lodgepole pine grows rapidly at an early age to occupy the site (Spurr and Barnes 1980; Heinselman 1981), but exhibits a sharp growth decline relatively early compared to black spruce (Clyde and Titus 1987). This was believed by many authors to be related to the progressive reduction in leaf area and leaf area efficiency following canopy closure rather than related to increased maintenance costs associated with older and larger trees (Long and Smith 1992; Sampson and Smith 1993; Ryan and Waring 2001). Canopy closure, a function of site quality and density, is expected to play an important role in early height growth development.

2.3 Late Growth

Lodgepole pine height growth tends to level off early, although dominant pines maintain height growth rates for a longer period (Clyde and Titus 1987). In contrast, substantial diameter growth has been observed in lodgepole pines as old as 200 years (Brisco 2001). In vigorous dominant black spruces, both diameter and height growth curves tend to level off at advanced ages. In suppressed black spruce, the uniform height growth lasts even longer (Horton and Lees 1961). After a suppression period of up to 100 years under the pine canopy, black spruce begins to match lodgepole pine height (Hortons and Lees 1961). There are two possible causes for black spruce release. According to Horton and Lees (1961), lodgepole pine mortality was causing the release.

They remarked that only a few black spruces approached the canopy level in fully stocked mature mixed stands, whereas most remained suppressed. Pine mortality would cause the release of the remaining black spruces later. Another possible cause of black spruce release is its plasticity; study of black spruce response to light found this species demonstrates a strong increase in height growth with only slight increase in low light levels (Wright *et al.* 1998). As height growth brings black spruce closer to the canopy, an increase in light could trigger an increased height growth response. Regardless of the cause, black spruce release results in an increased proportion of black spruce (measured by volume and number of stems) in a stand (Horton 1956; Morris *et al.* 1988).

If the growth rate of black spruce decreases with age more slowly than that of pine, there may come a point when black spruce reaches lodgepole pine in the canopy. When this might happen would depend upon the initial proportion of black spruce and density (*cf.* Horton 1956). A study of stand dynamics in the lodgepole pine-black spruce stands in the Upper Foothills could help determine the effects of initial species proportion and density through time. This would facilitate accurate predictions of how long the growth trends measured at a given point in time would last. There may come a point at which lodgepole pine volume has not yet declined (only levelled), whereas black spruce has reached much larger dimensions after its release. When would that situation happen and how long would it last before lodgepole pine mortality causes the stand volume to drop? What kind of net stand volume can be expected compared to pure lodgepole pine stands? What is the proportion of large vs. small black spruce stems at this stage? These are some of the questions that need to be addressed if mixed-species stands of lodgepole pine and black spruce are to be properly managed for timber and/or age-class conservation.

2.4 Density Effects

Although at extremely high densities, stand productivity levels off (Curtis *et al.* 1997) or decreases (*e.g.* stagnant stands), it is clear that stand total volume increment reaches a maximum at higher densities (Curtis *et al.* 1997; Zeide 2001). Zeide (2001) concluded that trees do not 'harm' each other directly in any significant way, as parasitism and allelopathy are of minor importance in most stands, including lodgepole pine-black spruce stands. In addition, lodgepole pine and black

spruce are more sensitive to intraspecific rather than interspecific competition (Horton 1956; Smithers 1956, 1961; Newton and Joliffe 1998). Therefore, I will not consider direct competition between species and focus on the effect of resource reduction and partitioning in high-density stands.

The most obvious impact of high density on lodgepole pine is a decrease in diameter and height growth. Growth of lodgepole pine is sensitive to density levels as low as 500 trees per hectare on poor sites (Smithers 1961). However, the effect of density is not constant throughout the development of the stands. Although density effects may be negligible in very young stands before crown closure, they increase as crowding intensifies until the growth-density relationship stabilizes in mature stands. Causes for growth reduction are not well understood and many different explanations have been proposed. Excessive respiration and a shortage of moisture (Mitchell and Goudie 1980) and decreased sapwood conductivity (Keane and Weetman 1987) are possible explanations.

Another effect of density is to modify the biomass allocation pattern of the tree. King (1993) built a model of the influence of root and foliage biomass allocation on forest productivity. Stand wood production was maximized by quite low allocation to roots for a specified availability of nitrogen, whereas the wood production of individuals was maximized by higher allocation to roots. The reason for this was that high biomass allocation to roots resulted in high survival of a great number of small trees. This 'co-operative optimum' is not an unknown concept in the literature (e.g., see King (1990) for tree height growth or Roughgarden (1979) for coevolution of competing species). However, density effects on tree biomass allocation are species-specific. Lodgepole pine clearly allocates more biomass to the roots in high-density situations (Worrall *et al.* 1985). However, lodgepole pine patterns of biomass allocation are not readily modified by more favourable environmental conditions. For instance, Worrall *et al.* (1985) showed that the growth following a reciprocal grafting experiment using scions and rootstock from both vigorous and stagnant (repressed) stands, was governed entirely by the type of root stock.

Like lodgepole pine, black spruce biomass allocation is affected by density. However, black spruce is more plastic and responds readily to changes in light availability by increasing

aboveground biomass allocation (Wright *et al.* 1998). This species is also less likely to develop the 'cooperative optimum' mentioned above, as suggested by the variability in spruce seedling biomass allocation (Benjamin and Hardwick 1986; Lieffers and Titus 1989). The fact that crowns can grow into each other and still be photosynthetically efficient (Leverenz 1996; Newton and Joliffe 1998) further supports that black spruce would have more resources to self-thin in high-densities compared to lodgepole pine (Lieffers and Titus 1989) and thus shift allocation to aboveground biomass.

High densities could also affect succession patterns. Horton (1956) observed that pine has a higher longevity when black spruce is less abundant in the stand. High initial densities or other conditions adverse to spruce development would slow the release of black spruce associated with lodgepole pine decline (Horton 1956). Density can also slow successional processes via the root systems. There is evidence lodgepole pine roots of intermingling extensively (Parsons *et al.* 1994a) despite infrequent intraspecific root grafts (Pemberton 1920; Horton 1956, 1958). Parsons *et al.* (1994b) observed that active fine-root and mycorrhizae densities in the absence of canopy gaps were not significantly different than within small canopy gaps (1 to 5 dead trees). Taken together, these observations might mean that root overlap and mycorrhizal interconnections could maintain the overall integrity and continuity of the root mat despite the creation of canopy gaps that occurs later in stand development. This could also slow succession from pine to spruce in dense stands.

2.5 Below Ground Considerations

Tree root-soil interactions are at the core of tree moisture and nutrient acquisition, which are major determinants of carbohydrate synthesis. On infertile and drier soils, light is no longer the only limiting resource and belowground resource availability impacts tree growth. Nutrient-poor sites without a water deficit, can lead to a dense array of 'miniaturized' plants, whereas nutrient-poor sites with water deficits lead to widely spaced dominants and a lack of interstitial plants (Coomes and Grubb 2000). Coomes and Grubb (2000) explained this phenomenon as follows: when water is not limiting growth, the depletion of the already-limited below ground resources stops trees from gaining enough nutrients to outgrow others without killing them. Self-thinning of the stand is thus slowed. The 'miniaturized trees' observations lead to new questions: is it possible to induce mortality and

thus favor self-thinning by increasing water stress? If nutrient availability to lodgepole pine remains unchanged, would black spruce increase self-thinning of stands by intercepting some of the water resource available to lodgepole pine?

Belowground mechanisms could also be involved in the stand dynamics and succession processes through higher nutrient uptake rates of one species over the other, increased quantities of fine roots, and varied rooting depth for more effective and less competitive resource extraction (Strong and La Roi 1983). Tree roots may play an important role in determining the direction and rate of plant succession in boreal forests, possibly through nutrient and water deprivation or niche partitioning (Strong and La Roi 1983). Both processes might be involved in pine-spruce systems with varying intensity throughout stand development.

One of the many effects of fire on upland boreal forests is reduction or loss of the surface organic horizons (Austin and Baisinger 1955; Foster and Morrison 1976). Nutrient exchange in post-fire seral forests must, therefore, occur mainly in mineral soil horizons until new organic horizons develop. Hence, it is to be expected that the absorption roots of seral lodgepole pine would be concentrated in mineral soil while those of climax black spruce are found mainly in the forest floor, a rich but later developed source of nutrients. In the early stages of development, roots of lodgepole pine are indeed found in the mineral soil floor (Horton 1958; Smithers 1961; Strong and La Roi 1983), whereas black spruce roots are mainly located in the forest floor (Armson 1975; Strong and La Roi 1983; Viereck and Johnston 1990). The rooting zone is thus partitioned vertically between the two tree species and this niche partitioning might explain why the species coexist so frequently in the upland soils of the Upper Foothills. However, in the older stages of development, the black spruce root network becomes extensive and located above the lodgepole pine roots, has a better opportunity to absorb water and recycled nutrients (Strong and La Roi 1983). The coexistence of both species could then be the result of incomplete competition processes.

2.6 Stand Dynamics And Succession Patterns

Stand density and site quality can be viewed as key factors in the growth of lodgepole pine-black spruce stands. In high-density stands, on poor sites with an adequate supply of moisture, a large number of small stems can survive with slow growth (Coomes and Grubb 2000). At the early stages of stand development, lodgepole pine in the upper canopy intercepts a large amount of light, whereas black spruce experience low light availability. Lodgepole pine draws nutrients from the mineral soil whereas black spruce draw nutrients from the poorly developed forest floor. The early fast growth of lodgepole pine and slow growth for black spruce could match their resource uptake strategies and it is possible that both species can coexist without interfering with each other's growth in the early stages of development. High densities have a stronger effect on pine development (height and diameter growth, canopy closure and leaf area index) than spruce (Duffy 1964; Clyde and Titus; 1987; Lieffers and Titus 1989; Lotan and Critchfield 1990; Viereck and Johnston 1990), probably because high density opposes fast height growth and canopy photosynthetic efficiency, whereas the inherent slow growth and shade tolerance of spruce are tailored to the conditions created by high density. Black spruce is more likely to self-thin and to respond to changes in light availability because of the species' plasticity (Roughgarden 1979; King 1990; see also Lieffers and Titus 1989). I have also described the progressive ingress of black spruce in the canopy and its release coupled with the reduction of pine growth in mature and senescing development stages of lodgepole pine-black spruce stands. The canopy structure of the mixed species stands, as an integrator of the many processes taking place in such stands (e.g. light capture strategy, density and crown engagement/disengagement, self-thinning, specific growth patterns), could be an indicator of the onset and length of the period during which spruce attains larger dimensions and pine trees have not yet undergone severe dieback.

Provided fire does not occur, upland lodgepole pine-black spruce stands in the Upper Foothills will develop into a black spruce climax community (Horton 1956; Horton and Lees 1961; Beckingham *et al.* 1996). Following disturbances in these areas, lodgepole pine will characteristically dominate the forest for 200-250 years (Horton 1956; Strong and La Roi 1983).

The factors responsible for the replacement of one boreal species by another have not been well documented. However, differential life span, shade tolerance, and nutrient uptake ability of species, as well as biologically induced changes in site conditions are often considered (Daubenmire 1968; Barbour *et al.* 1987). From what is known about lodgepole pine and black spruce, these species have comparable life spans of about 250 years in the Foothills (Horton 1956; Horton and Lees 1961). Smith (1984) found that black spruce continues to grow in height at a fairly constant rate throughout the life of black spruce and Jack pine-black spruce stands and that the stands deteriorate and collapse before an asymptotic height is reached. Horton (1956) observed that at the climax stage, there are old spruce in the canopy with scattered intermediate and suppressed spruce and regeneration in the openings left by the death of pine. Layering was found to be the main source of reproduction of black spruce at later ages resulting in uneven-aged clumps of black spruce around parent trees (Horton 1956). The true climax stage is uneven-aged and entirely constituted from vegetative reproduction by layering and rooting (Horton and Lees 1961; Armson 1975).

2 MATERIALS AND METHODS

2.1 Study Area

The study was conducted in the Upper Foothills natural subregion within the Forest Management Agreement area of Weldwood of Canada Ltd. (Hinton division) in Alberta. The study area is affected by a continental montane boreal climate and is within the boreal forest region of Canada. Study plots were established in the southern, eastern, and northern portions of the study area, specifically in the Berland, Embarras, and McLeod working circles (Figure 1).

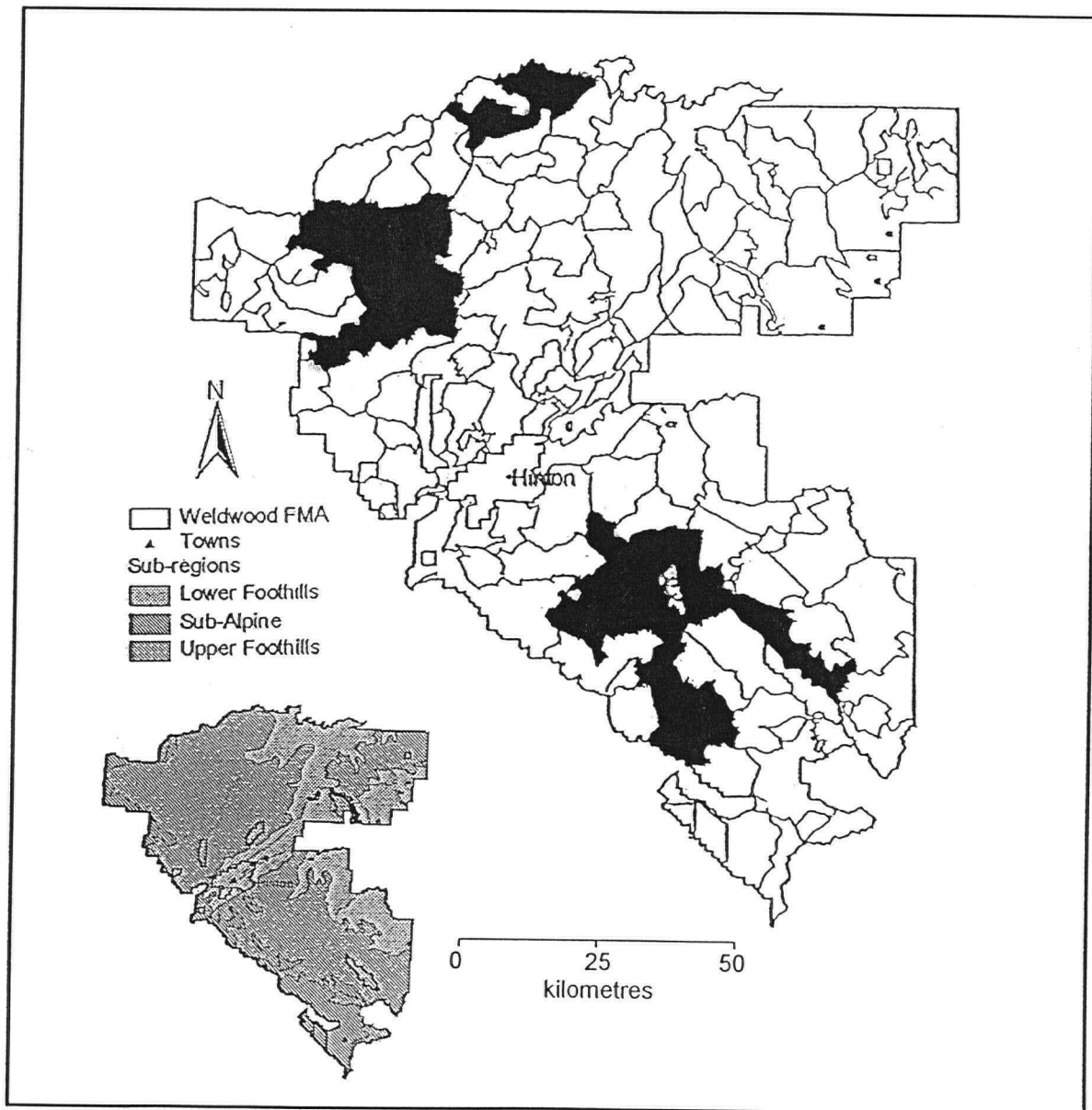


Figure 1. Location of the three sampling areas in Weldwood FMA

3.2 Study Stands

Ideally, studying stand development would be accomplished by growing and studying permanent sample plots on similar sites. A more feasible option was to locate stands at different developmental stages. Finding such stands and demonstrating that they have developed under the same condition are inherent weaknesses of this method. Pojar *et al.* (1987) proposed that selecting stands using the principles of ecological equivalence would best approximate permanent sample plots. The selection of stands was thus based on these principles.

Stand selection was based on the principle of ecological equivalence, i.e., the stands were located on sites with similar growing conditions (productivity) and potential vegetation (Pojar *et al.* 1987). All selected stands had naturally regenerated after wildfires, had no apparent evidence of disease, damage, or disturbance, were fully stocked (the mean number of trees ranged from 2,066 to 8,533 stems per hectare), and were located on "d" (Labrador tea-mesic) ecosites (Beckingham *et al.* 1996). Following this approach helps to limit some of the uncertainty associated with chronosequence studies based on stands sampled at a point in time. The range of edaphic site conditions encompassed by the Labrador tea-mesic ecosite is relatively broad (slightly dry to fresh and very poor to poor). Vegetation and soil characteristics were used for identification of the ecosite in the field following Green and Klinka (1994). Single-species spruce stands were excluded from the study, as these stands are most often located on very moist and wet sites. Selected stands were limited to fresh and poor sites. Four pine stands and four pine-spruce stands were initially selected in each of the following four age classes: (1) 50 - 60, (2) 60 - 80, (3) 90 - 100, and (4) 100 - 120 yrs @ bh (Figure 2). Stand age was approximated by the breast-height age of dominant pine. A frequency distribution of stand ages (Figure 2) shows that the stands could be stratified into four age classes, which can be interpreted as stand development stages to facilitate the interpretation of analyses. Development stages may display specific characteristics, which would not be as apparent if an age gradient alone was used for the analyses.

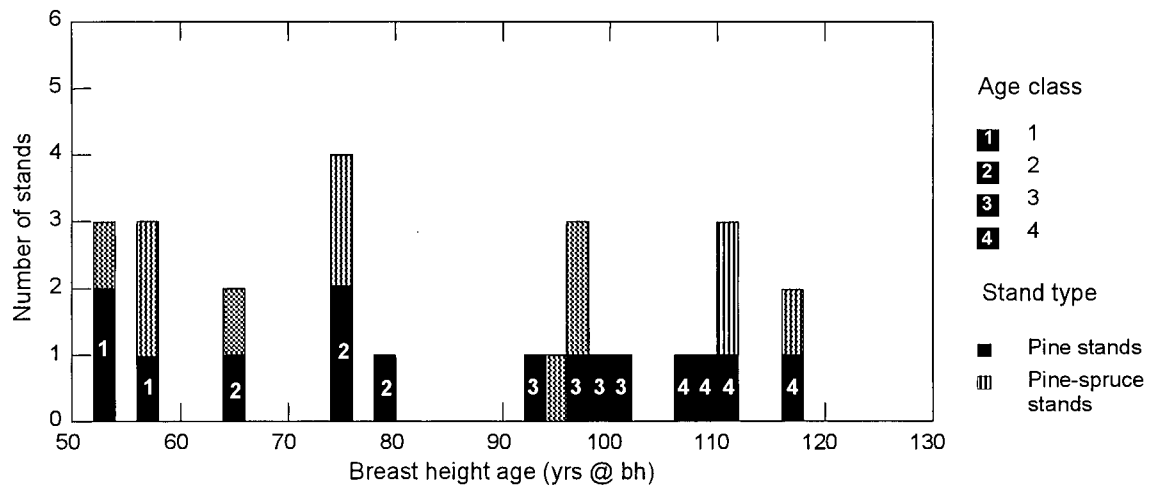


Figure 2. Frequency distribution of study stands according to breast-height age

Study stands were stratified into eight categories based on the combination of two stand types and four age classes (Table 1). Given the fire origin of the stands, stand density was generally high and variable. Assignment of each stand into a stand type was based on species composition, the percent contribution of each study species to stand basal area (Equation [1]).

$$[1] \quad SC_{sp} = \frac{\sum BA_{sp}}{\sum BA}$$

where SCsp is the species composition of the target species, BA_{sp} is the basal area of a tree the target species (m² ha⁻¹) from and BA is the basal area of any tree present in the stand.

Table 1. Number of study stands according to two stand types and four age classes.

Age class (yrs @ bh)	Stand type		Total
	Pine	Pine-spruce	
1 – 50 to 60	3	3	6
2 – 60 to 80	4	3	7
3 – 90 to 100	4	4	7
4 – 100 to 120	3	4	8
Total	14	14	28

Huang and Titus (1994) noted that this was the best approximation to the "true ratio" defined by Assman (1970) and that the use of basal area ratio would be a more comprehensive index of composition than tree number per hectare as it takes into account both size and number of trees.

Stands with >95% basal area of pine were assigned to the pine stand type (referred to as PI stands); stands were assigned to the pine-spruce stand type when spruce contributed between 15 and 40% to the total stand basal area (referred to as PISB stands) (Figure 3). Other tree species never exceeded 1% of the total basal area. Of the 40 selected stands, 28 were considered suitable for the analyses (Table 1, Figures 4 to 11).

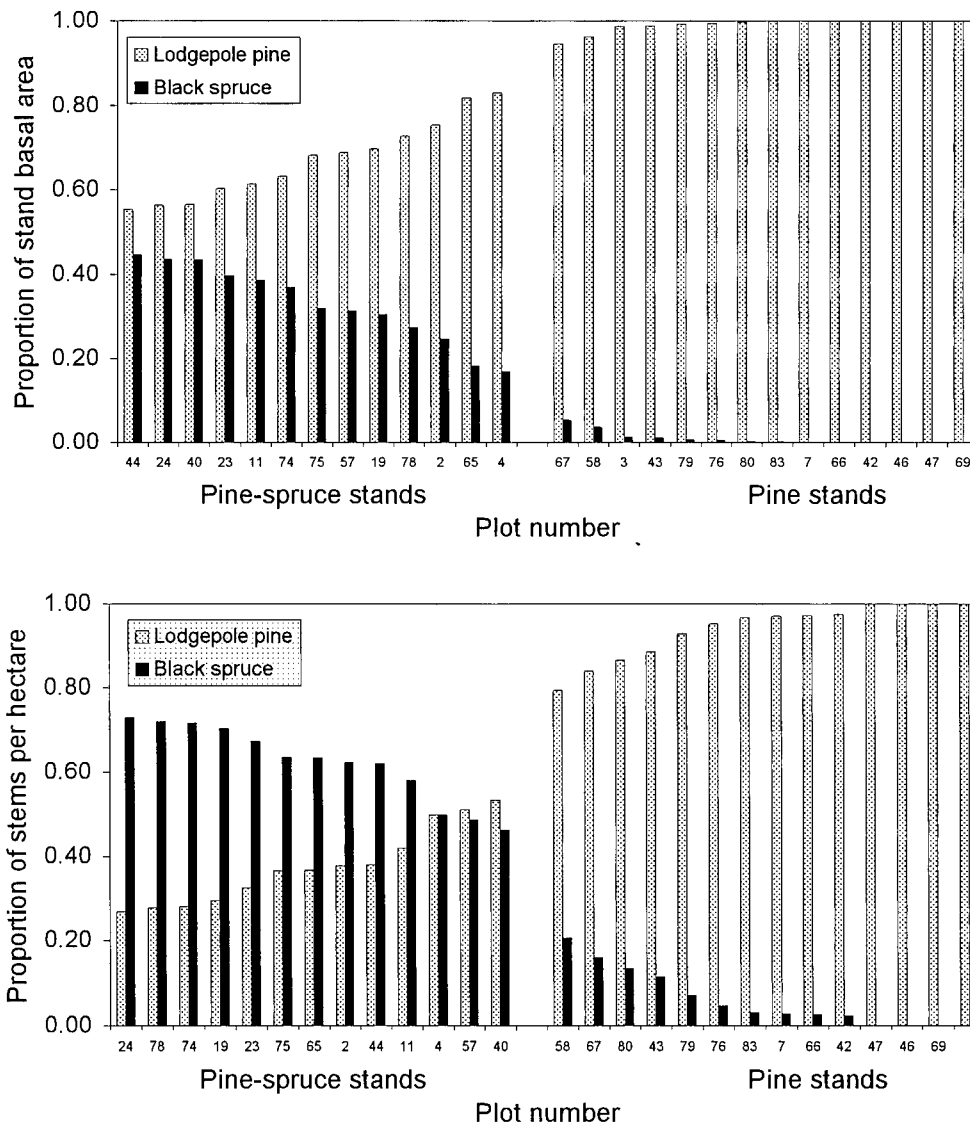


Figure 3. Proportion (%) of the basal area and stems per hectare contributed by pine and spruce in study stands.



Figure 4. A fully stocked, age class 1 pine stand with scattered spruce in the understory.

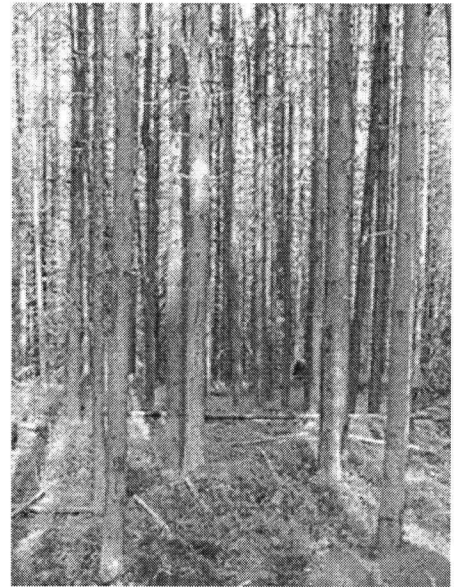


Figure 6. A uniform, fully stocked, age class 2 pine stand with a well-developed understory of shrubs (*Ledum groenlandicum* and *Vaccinium vitis-idaea*) and mosses (*Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*).



Figure 5. A fully stocked, age class 3 pine stand with well-developed understory of shrubs (*Ledum groenlandicum*) and mosses (*Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*).



Figure 7. A uniform, fully stocked, age class 4 pine stand. Note the strong canopy differentiation.



Figure 8. A fully stocked, age class 1 pine-spruce stand. The majority of spruce trees occupy the upper (B1) and lower (B2) shrub layers.



Figure 10. A fully stocked, age class 2 pine-spruce stand. The majority of spruce trees occupy the upper (B1) shrub and the lowest canopy (tree) layers.



Figure 9. A fully stocked, age class 3 pine-spruce stand with a well-developed understory of shrubs and mosses. At this stage, the majority of spruce trees occupy the lowest canopy (tree) layer. Note their clumped distribution.



Figure 11. The edge of an age class 4 pine-spruce stand. Note the presence of spruce trees in the canopy (tree) layer, with some trees attaining a dominant position.

3.3 Data Collection

Within each study stand a square sample plot was established with the following dimensions: 10 x 10 m (0.01 ha) for stands in age class 1 and 2 stands, and 12 x 12 m (0.0144 ha) for age class 3 and 4 stands. Smaller plots were used to facilitate sampling in the denser and more homogenous younger stands; the larger plots were used to capture the higher structural variability of older stands. The size difference is not likely to influence the subsequent analyses and their conclusions as the increase of size was relatively small (0.0044 ha) compared to the variability of stands. Furthermore, the slight difference in plot size is unlikely to introduce significant bias above or beyond that inherent in the selection of the 10 x 10 m plots.

In each plot, the age of two dominant pine trees was determined via increment coring; the age of the largest spruce trees in pine-spruce stands was determined using the same technique. It was noted that these spruces were consistently 5 to 10 years younger at breast height than pines in the same stand. Although black spruce established after a fire event at the same time as pine, it reached breast height later because of slower initial height growth than pine (Horton and Lees 1961). Stands were categorized into the four age classes as explained before. There were no certainties about the shape of the statistical relationships in which age would be a predictor variable, thus I used the indicator variable (age class) approach for 'age' in most analyses in order to obtain information about the shape of the response function without making assumptions about its functional form (Neter *et al.* 1996).

The tree characteristics measured were diameter at breast height (dbh), height of all live trees above 1.3 m, and height from ground to live crown (live crown height). All trees over 1.3 m in height were assigned into dominant, codominant, intermediate, or suppressed canopy classes. Number of stems, basal area, height, site index and volume were calculated for each plot (Tables 2 and 14). In addition, for one randomly selected sample plot within each stand category, the three largest diameter dominant trees without visible evidence of abnormal growth or damage were felled for stem analysis. Discs were cut at 0.3, 0.8 and 1.3 m above the ground surface and then at one-meter intervals from 1.3 m to the top of each tree. The number of rings was recorded and the ring

width was measured along 2 radii per disc using the WinDendroTM measuring system (Windendro Version 6.5C 2000).

Table 2. Means and standard deviations (in parentheses) of selected stand characteristics for pine in pine (PI) stands and pine and spruce in pine-spruce (PISb) stands by age class.

Stand type/ Age class	Mean number of stems per hectare	Mean dominant tree height* (pine ¹ spruce ²) (m)	Mean dominant tree age (pine) (yrs @ 1.3m)	Mean site index* (pine ¹ spruce ²) (m @ 50 yr bh)
PI (n=3) Age class 1	6467 (3134)	15.4 (1.0)	54 (3)	14.6 (1.4)
PISb (n=3) Age class 1	8533 (750)	15.4 ¹ (0.6) 8.7 ² (1.4)	54 (3)	14.5 (0.6)
PI (n=4) Age class 2	3650 (1698)	16.4 (4.2)	73 (6)	13.0 (2.9)
PISb (n=3) Age class 2	7400 (1833)	16.4 ¹ (5.1) 10.0 ² (1.1)	71 (6)	13.2 (3.9)
PI (n=3) Age class 3	3379 (1403)	19.5 (1.9)	95 (3)	13.5 (1.7)
PISb (n=3) Age class 3	3889 (1102)	16.9 ¹ (1.3) 14.3 ² (1.3)	96 (1)	11.2 ¹ (0.8) 8.8 ² (1.0)
PI (n=4) Age class 4	2066 (229)	20.7 (1.0)	113 (7)	13.7 (0.7)
PISb (n=4) Age class 4	5017 (822)	19.7 ¹ (1.5) 16.3 ² (0.9)	107 (6)	12.8 ¹ (0.9) 9.5 ²

*Mean ages, dominant tree heights, and mean site index of pine were calculated from the five pines with biggest dbh in every stand. Mean dominant tree heights were also calculated for the five spruce with biggest dbh in pine-spruce stands. Mean site index was calculated for spruce when it was present in the canopy layer (age classes 3 and 4).

Understory vegetation and environmental properties were recorded for each plot. Vegetation description included species composition and percent cover in the tree, shrub, herb, and moss layers. The environmental description included records of elevation, slope gradient, aspect, slope position, microtopography, surface substrate, potential rooting depth, soil parent materials, soil texture and structure, coarse fragment content, thickness and sequence of soil horizons, humus type, and soil type. Samples of forest floors and 0-30 cm mineral soil were collected, composited, air-dried, ground or sieved, and analyzed for pH, total carbon, total nitrogen, mineralizable-N, and extractable phosphorus, calcium, magnesium, and potassium using standard methods of soil chemical analysis (Lavkulich 1981).

3.4 Data Analysis

3.4.1 Vegetation Analysis

Vegetation data were collected to determine floristic differences between stand types and age classes. Tabular, similarity, and indicator plant analyses were performed with VTAB Ecosystem Reporter, Revision 19907a (Emanuel 1999).

Differentiated tables produced by the tabular comparison showed floristic similarities and differences between stand categories using differential and dominant-differential species (Pojar *et al.* 1987). It was hypothesized that strong floristic similarities reflect strong similarities in site quality among study stands. To quantify floristic affinities between stands, a similarity analysis was conducted using the Sørensen index based on the presence/absence of species (SI_a) (Magurran 1988) (Equation [2]) and the species cover (SI_b) (Qian *et al.* 1997) (Equation [3]).

$$[2] \quad SI_a = \frac{2c}{(a + b)} \quad \text{where} \quad \begin{array}{l} a = \text{the number of species in the first unit,} \\ b = \text{the number of species in the second unit, and} \\ c = \text{the number of species common to both units.} \end{array}$$

$$[3] \quad SI_b = \frac{2C}{(A + B)} \quad \text{where} \quad \begin{array}{l} A = \text{the cover sum of all species in the first unit,} \\ B = \text{the cover sum of all species in the second unit, and} \\ C = \text{the sum of the lower of the two cover values for the} \\ \quad \text{species common to both units.} \end{array}$$

A spectral analysis (Klinka *et al.* 1989) was employed to compare vegetation, climatic and edaphic conditions of the study stands. In spectral analysis, plant species are grouped according to selected criteria, e.g., life form, climatic, soil moisture, and soil nitrogen indicator values.

3.4.2 Soil Analysis

The forest floor and mineral soil samples were analysed for selected nutrient properties to demonstrate similarity in soil nutrient conditions among study sites. An analysis of variance based on Equation [4] was performed to establish whether soil characteristics varied among stand types and age classes. This analysis was done for each soil characteristic measured. Since I was interested in several individual comparisons without concern about the effects of multiple inferences, I used

multiple means t-tests to further explore differences in soil nutrient properties between stand type and among age classes.

$$[4] \quad \text{Nutrient}_{ij} = \beta_0 + \beta_1 \text{Age}_{1ij} + \beta_2 \text{Type}_{2ij} + \beta_3 \text{Age}_{1ij} \text{Type}_{2ij} + \varepsilon_{ij}$$

where, Nutrient_{ij} is the stand measure of nutrient or pH characteristic, Age_{ij} is age class (50 - 60, 60 - 80, 90 - 100, 100 - 120 yrs), and Type_{ij} is stand type.

3.4.3 Site Index and Stand Density Management Diagram

Site index was estimated using polymorphic height growth curves for lodgepole pine at breast height age 50 (Huang *et al.* 1997). Spruce site index could not be estimated because of suppression; thus, the height for three trees with the largest dbh was reported. Only in age class 3 and 4 pine-spruce stands (Table 2) was black spruce present in the dominant position of the canopy. For these stands, black spruce site index was calculated using the model developed by Huang *et al.* (1997). The stands were plotted in a Stand Density Management Diagram (SDMD) developed and calibrated for lodgepole pine in the interior British Columbia and west-central Alberta by Craig Farnden (1996).

3.4.4 Stand Structure Analysis

The variance of mean dbh, height, and height to live crown (referred to as crown height) were compared among plots using the Brown and Forsythe test ($\alpha=0.05$) (Conover 1999). Analysis of variance (ANOVA) is appropriate for analyses where the variables are random and where there may be several error terms (Neter *et al.* 1996). Furthermore, ANOVA is more appropriate than regression analysis when the purpose of the analysis is to measure the relative contribution of different sources of variation (factors or combinations of factors) to total variation in the dependent variable and test hypotheses about group means for dependent variables (Neter *et al.* 1996). An ANOVA was thus performed to compare the mean values of dbh, height, and height to live crown among stand categories. A two-way ANOVA included age class, stand type, and their interaction as factors. To further explore the relationships between stand structure and other stand attributes, a

one-way ANOVA was used to compare age class, stand types within age classes, and the two species in pine-spruce stands.

In view of the large variance within and between stands, dbh, total height and height to live-crown were standardized to z scores, with means adjusted to 0 and a standard deviation of 1. Frequency distributions of dbh, tree height, and height to live-crown were calculated for each study species in each stand. A Kernel density curve was fitted to examine the frequency distribution of these stand attributes. The Kernel density curve was constructed with a bandwidth (degree of smoothing in the estimate of the density function) based on the approximated mean integrated square error (AMISE). Silverman (1986) observed that the Kernel distribution renders an objective approximation of data closely and the presence of large modes in the frequency distributions was considered as evidence for canopy stratification (Varga *et al.* 2001).

In addition, vertical stand structure diagrams were constructed to illustrate the development of pine and spruce, as well as spruce ingress into the canopy during the later stages of development. The canopy was defined by the space between pine top height and pine crown height. Pine top height and crown height were calculated as the average of the top height and height to live crown of stands from one age class x stand type category. The average total height was also included in the diagram. The same calculations were used with spruce on the pine-spruce stands to examine the spruce ingress.

3.4.5 Height Growth Analysis

Raw data from the stem analysis were corrected according to the procedure of Carmean (1972), adjusted by Newberry (1991) to determine tree height for each living year. A height over age curve was developed for each tree by fitting the Chapman-Richards function (Equation [5]) (Richards 1959).

$$[5] \quad Y = a[1 - e^{-bx}]^c$$

where Y is tree height (m), x is total age, a is asymptote or maximum height, b is rate at which this maximum is reached and c is a form coefficient.

The average height growth curve for each species in each age x stand type category was calculated as the average height growth of the sampled trees of this category. The fitted curves were examined for differences in height growth trends of pine and spruce in each stand type. I calculated mean basal area growth and fitted cubic polynomial equations for each species according to stand type and age class. The average height growth curves for dominant pine trees and the largest - diameter spruce trees based on all stands were constructed and examined, as an increased sample size would provide a more reliable estimate of growth patterns. Comparisons between stand types were done using average height growth curves for (i) age class 1 stands and all stands with a cut-off point of 60 years (@ bh) and (ii) age class 2 stands and all stands with a cut-off point of 75 years (@ bh).

3.4.6 Basal Area Growth Analysis

Annual radial increments were measured along two radii on discs taken at breast height (from pith to the 1998 ring). Ring widths were averaged for the two radii measured on each disc. A quadratic method was used to average the radius from the pith to each successive ring (Equation [6]) (Siostrzonek 1958). The basal area for each year (cm^2) was calculated based on the ring developed during that year as follows (Equation [7]):

$$[6] \quad R_{Av} (mm) = \sqrt{(\sum (R_1 + R_2)^2) / 2}$$

$$[7] \quad A (\text{cm}^2) = \pi \times R_{Av}^2 / 100$$

where R_{Av} is the average radius of a given disc in mm, R_1 and R_2 are the two radius measures in mm, and A is the area of a given disc in cm^2 .

For each sampled tree, basal area was plotted against age. For each plot and species, the mean curve of basal area against age was calculated from the mean ring series. The mean ring series were calculated as the average of individual radial series measured from the three trees of each species. Year-to-year ring width variation was accounted for in the averaging process. Such variation is usually associated with weather, particularly with temperature variations (McNally and Doyle 1985).

Empirical radial growth trends were approximated by fitting cubic polynomial curves for each species and plot (Graybill 1982). The difference between the average basal area over age curves between pine and pine-spruce stands should indicate if radial growth of pine is influenced by the presence of spruce. The greater the difference between the curves, the stronger the influence of spruce on pine growth. I calculated mean basal area growth and fitted cubic polynomial equations for each species according to stand type (i) for a given age class only and (ii) for all age classes combined. Thus, the first series of average curves is based only on the data from stands of age class 1 and the second series is based on the data from all stands, with a cut-off point at 60 years. This process increased statistical power, thus gaining insight into basal area growth patterns for pine and spruce.

3.4.7 Stand Volume Analysis

Gross tree volume was calculated using dbh and height according to the equations obtained from the BC Ministry of Forests (Anonymous 1976) for black spruce (Equation [8]) and from Brockley (1989) for small-size lodgepole pine (Equation [9]). Although these equations were not developed specifically for the Upper Foothills, Alberta, they were developed for climatically similar areas. These equations were chosen in view of the overall size and age of the trees, as well as the fire-origin and high establishment density characteristics upon which they were calibrated.

$$[8] \quad \text{Log}_{10} V_{\text{spruce}} = -4.379777 + 1.783940 \log_{10} (\text{dbh}) + 1.146280 \log_{10} (\text{ht})$$

$$[9] \quad V_{\text{pine}} = 3235.77 + (32.7 * \text{dbh}^2 * \text{ht}) / 1000000$$

where V is tree volume (m^3), dbh is measured in centimetres, and ht represents tree height (m)

Volumes calculated using these equations were not statistically different from those derived from the volume tables in use by Weldwood (Figure 12.). Furthermore, the use of dbh and height as determinant of tree volume was perceived as a gain in precision. Stand volume was calculated as the sum of individual tree volume ($\text{m}^3 \text{ ha}^{-1}$) and was compared among stands.

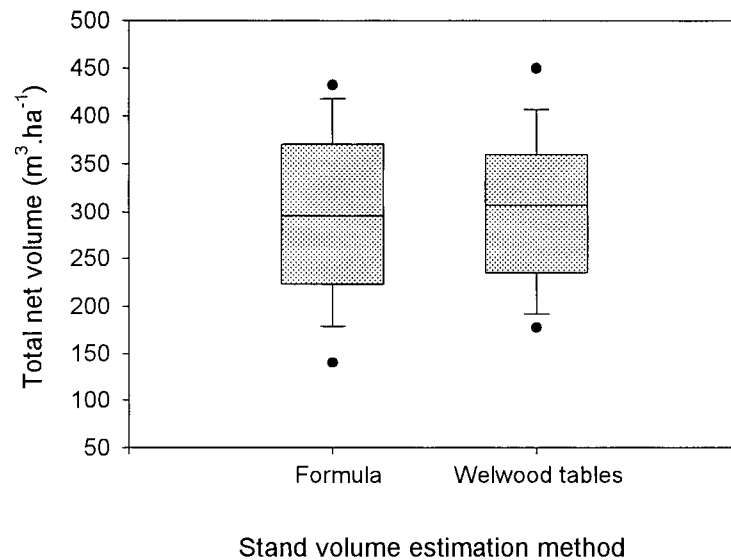


Figure 12. Boxplot of estimated total net stand volume. 'Formula' represents the stand volumes calculated from the formula presented in the text. 'Welwood tables' represents the stand volumes calculated from the tables calibrated by Welwood Ltd. for the different tree species. The horizontal lines show the 10th, 25th, 75th and 90th and the circles show the 5th and 95th percentiles. A two-sample paired t-test compared the different means based on 31 degrees of freedom and provided a t-value of 1.79 with a significance of 0.081.

Net stand volumes and merchantable volumes were compared amongst stands using multiple linear regression, analysis of covariance and ANOVA. The regression function describes the nature of the statistical relation between the mean response and the levels of the predictor variables (Neter et al. 1996). Furthermore, regression analysis uses quantitative data, which maximizes the number of degrees of freedom associated with the Mean Squared Error (MSE). Analysis of covariance differs from the regression principally in using indicator rather than quantitative variables. In ANOVA models, no assumption is made regarding the nature of the statistical relation between factor variables and response variable (Neter *et al.* 1996).

Stand age, proportion of spruce basal area, interaction factor, and stand density index factor were used as predictor variables in the regression model. The variables included in the covariance analysis were stand type and age class, a stand type x age class interaction factor and a stand density index factor as covariate. Three-way interaction and two-way interactions between the density term and other variables were tested in both analyses, but being non-significant ($\alpha = 0.01$), they were excluded from the final models (Equations [10], [11] and [12]).

Regression model:

$$[10] \quad Volume_i = \beta_0 + \beta_1 Age_i + \beta_2 PPspruce_i + \beta_3 Density Index_i + \beta_4 Age_i \times Type_i + \varepsilon_i$$

where *Volume* is stand volume in $m^3 ha^{-1}$, *Age* is the stand age, *PPspruce* is the contribution of spruce basal area to the stand total basal area, and *Density Index* is SDI or RD

Analysis of covariance model:

$$[11] \quad Volume_{ij} = \beta_0 + \beta_1 Age_{ij} + \beta_2 Type_{ij} + \beta_3 Density Index_{ij} + \beta_4 Age_{ij} \times Type_{ij} + \varepsilon_{ij}$$

where *Volume* is stand volume in $m^3 ha^{-1}$, *Age* is the stand age class, *Type* is pine or pine-spruce stand, and *Density Index* is SDI or RD.

Analysis of covariance model:

$$[12] \quad Volume_{ij} = \beta_0 + \beta_1 Age_{ij} + \beta_2 Type_{ij} + \beta_3 Age_{ij} \times Type_{ij} + \varepsilon_{ij}$$

where *Volume* is net stand volume or merchantable volume in $m^3 ha^{-1}$, *Age* is the stand age class, *Type* is pine or pine-spruce stand, and *Density Index* is SDI or RD.

Two different stand density indices were used: Curtis's Relative Density (RD; Equation [13]) and Reineke Stand Density Index (SDI; Equation [14]) (Reineke 1933; Curtis 1982). These two indices were chosen for their frequent occurrence in the literature.

$$[13] \quad RD = \frac{BA}{QMD^{0.5}}$$

$$[14] \quad SDI = \frac{TPA}{(QMD / 10)^b}$$

where BA is stand basal area ($m^2 ha^{-1}$) and QMD is quadratic mean diameter (calculated from BA and density of stocking). In the calculation of SDI, a value for b of 1.74 was used because of many indications found in the literature that b is greater than 1.6 (Dahms 1964; Wykoff 1990).

Net stand volume and merchantable volume were tested for normality using normal probability plots, and for homogeneity using Bartlett's test (Bartlett 1937). The equal slope assumption of the analysis of covariance was checked by the lack of interaction between factors and covariates. The residual plots were analyzed to detect potential outliers. Tukey's multiple comparison test (Neter *et al.* 1996) was used to detect differences in volume between stand

categories (stand types and age classes). The probability of committing type I error was held at 5% in all analyses.

Statistical analyses were performed using SAS Version 8.0 (SAS Institute 2000) and SYSTAT (version 10) statistical package (SPSS Inc. 2000a). Sigmaplot 2000^{TN} was used for curve fitting and plotting (SPSS Inc. 2000b). was used in data analysis. Sigmaplot 2000 was used for curve fitting and plotting (SPSS Inc. 2000b).

4 RESULTS AND DISCUSSION

4.1 Ecological Equivalence Of Study Sites

In this section, I will examine the selected stands for equivalence through assessment of environmental and understory vegetation characteristics on one hand and site index and the stand density management diagram on the other hand. It is necessary that all study stands are of similar site quality for comparisons among them to be valid.

4.1.1 Site Characteristics

Fifty percent of all study stands were situated on flat terraces or benches and had no predominant slope aspect. The aspects of the remaining stands alternated between west to north-west slopes and north-east to east slopes. There was no indication of more frequent occurrence of any stand type for a particular aspect. The average slope gradient was 9%, and the average elevation was 1,406 m. Again, no significant trends were detected between age classes and stand types with respect to aspect and slope (Table 3). There was no apparent relationship between site index and aspects of the stands. It is possible that the extent to which topography and slope influence growth may be confounded by other influences. Duffy (1964) found similar results in his study of lodgepole pine. Specific site conditions are useful, but presenting more variability than site indices, they are insufficient to adequately explain growth (see also Kayahara 1989; Kayahara *et al.* 1998).

The climatic and edaphic characteristics of the stands fell within a very narrow range (Table 3). The spectral analysis produced the same climatic spectra for each stand type and age class (not shown), implying similarity of local climatic conditions. Soil moisture regime (SMR) and soil nutrient regime (SNR) of most stand sites were estimated in the field as fresh and poor, respectively. These estimates were corroborated by the spectral analysis. The soil moisture spectra were dominated by the moderately dry-fresh and fresh-very moist groups, indicating that both stand types had fresh SMR (Figure 13). The soil moisture spectra for stand types indicated somewhat wetter conditions for

pine stands than for pine-spruce stands. Although there is always a possibility that this observation is simply an artefact from vegetation sampling, it is reasonable to think that the decreased moisture level is due to the greater density of pine-spruce stands (Table 3). The presence of spruce roots in the forest floor (Horton and Lees 1961) is likely to result in greater water uptake at the surface (Strong and la Roi 1983; Coomes and Grubb 2000). The soil moisture spectra for age classes 2 and 3 were similar, while that for the age class 1 indicated slightly drier conditions and that for the age class 4 slightly wetter conditions. Stand development has been shown to affect the site quality and to result in variation in resources availability (Coomes and Grubb 2000). In the youngest age class, the trees are growing fast, particularly pine (Smithers 1961), and the water uptake is likely to be the greatest during this highly productive stage.

Table 3. Means and ranges (in parentheses) of selected site characteristics of study stands stratified by stand type.

Stand type Number of stands	Pine 14	Pine-spruce 14
Climate (subzone)	Upper Foothills (BWBSwk [†])	Upper Foothills (BWBSwk [†])
Elevation (m)	1,390 (1,170 - 1,905)	1,422 (1,040 - 1,905)
Slope gradient (%)	8 (0 - 20)	2 (0 - 10)
Aspect	flat (easterly slope)	flat (westerly slope)
Slope position	variable (mostly mid-slope)	variable (mostly mid-slope)
actual soil moisture regime	slightly dry - fresh	slightly dry - fresh
Soil nutrient regime	Poor	Poor
Forest floor (cm)	9.5 (2.5 - 16.0)	11.0 (8.0 - 14.0)
Humus thickness (cm)	6.8 (1.5 - 14.0)	7.5 (5.0 - 10.0)
Humus form	Hemimor (Mormoder)	Hemimor (Mormoder)
Soil Great Group	BR.GL/E.DYB	O.GL/E.DYB
Texture Class	silty-clay	silty-clay/silty-clay loam
Potential rooting depth (cm)	54 (29 - 90)	53 (35 - 83)
Tree layer cover (%)	36 (20 - 65)	48 (20 - 70)
Shrub layer cover (%)	90 (41 - 100)	43 (1 - 100)
Herb layer cover (%)	3 (0 - 30)	<1
Moss layer cover (%)	86 (71 - 98)	92 (85 - 97)
Decaying wood cover (%)	11 (2 - 20)	10 (0 - 20)
Organic matter cover (%)	86 (30 - 98)	85 (0 - 99)
Bedrock & coarse fragment cover (%)	<1	<1
Mineral soil cover (%)	<1	<1
Site index (m @ bha 50)		
Lodgepole pine	13.5 (1.2)	12.7 (1.6)

[†] According to biogeoclimatic ecosystem classification, the study area has the strongest climatic and floristic affinities to the neighbouring Wet Cool Boreal White and Black Spruce (BWBSwc) subzone of British Columbia

The soil nitrogen spectra showed a very consistent and high proportion (approximately 95%) of nitrogen-poor indicators across stand types and age classes (Figure 13). Neither the denser pine-spruce stands nor the younger age class showed any sign of reduced nutrient availability, which is not consistent with other findings (see Tilman 1988; Schultze *et al.* 1995; Coomes and Grubb 2000). The 'cooperative optimum' from the model developed by King (1993) or the 'miniaturized plants' described by Coomes and Grubb (2000) are two possible explanations for the low variability observed among the nutrient regimes of different age classes and stand types. The poor sites support many trees, which survive because of the assured water supply. While individual tree growth is low, it prevents any tree from reaching greater dimensions and thus to 'deplete' (*sensu* Newton and Joliffe 1998) the soil nutrient resources.

Regardless of stand type or age class, the predominant humus form (approximately 7 cm thick) was Hemimor, with sporadic Mormoder and Moder humus forms (comparable to the description of Labrador tea-mesic sites). The cover of ground surface materials was similar across sites, with randomly scattered accumulations of woody debris occupying about 10% of the ground surface (Table 3). Most stands were associated with either silty clay or silty clay loam Gray Luvisols (GL) or Eluviated Dystric Brunisols (E.DYB). The rooting depth ranged from 30 to over 90 cm, with a mean depth of 53 cm. These results agree with other studies conducted in the study area (Duffy 1964; Dumanski *et al.* 1972; Strong and La Roi 1983; Beckingham *et al.* 1996).

The absence of correlation between site index and soil characteristics (humus form and thickness, soil group, soil depth) in this study further confirmed the similar quality of the study stands.

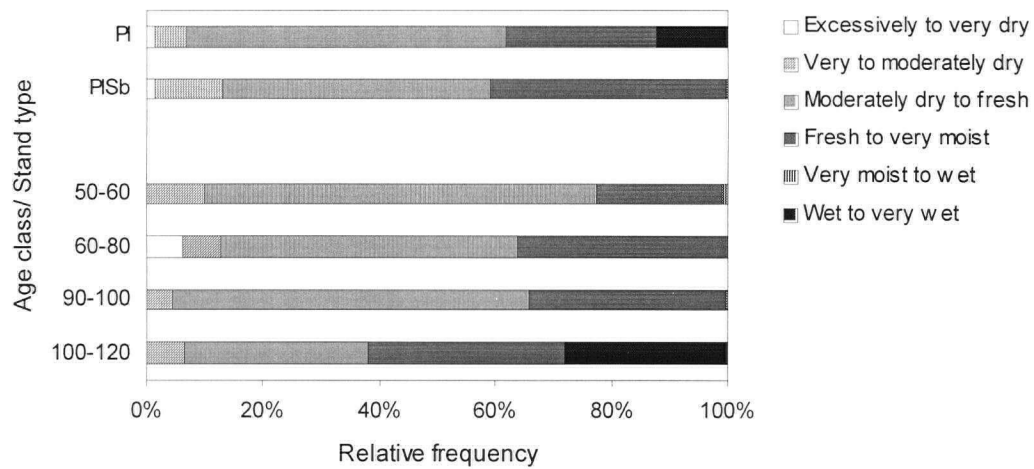


Figure 13. Soil moisture spectra of study stands according to stand type and age class (PI - pine stands, PISb - pine-spruce stands).

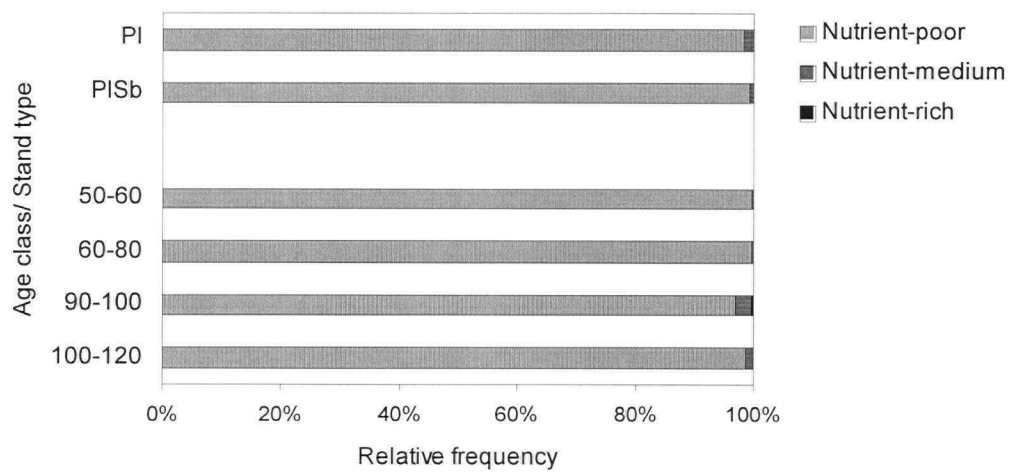


Figure 14. Soil nitrogen spectra of study stands according to stand type and age class (PI - pine stands, PISb - pine-spruce stands).

4.1.2 Vegetation Characteristics

Similarity analysis, tabular comparison, and life form spectra indicated very high floristic affinities between stand types (Tables 4 and 5, Figure 15). Labrador tea (*Ledum groenlandicum*) was the constant dominant understory species. Other species with a high presence were: *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Vaccinium vitis-idaea*, and *Cornus canadensis* (Table 5). Plant species and their abundance were consistent with previous vegetation sampling of the study area by Horton (1956) and Horton and Lees (1961). No differential species were detected for any stand type, except for a trend of higher presence and cover of *Arnica cordifolia* and *Leymus innovatus* in pine stands. Life form spectra indicated only minor differences among proportions of life forms in the understory vegetation of each stand type. Compared to the pine-spruce stands, pine stands had a higher frequency of shrubs, dwarf woody plants, and herbs, but a lower frequency of mosses and coniferous trees (predominantly advanced regeneration of spruce) (Figure 15). Both similarity indices were high (>70%), indicating that pine stands and pine-spruce stands are floristically very similar in species composition and species relative abundance (Table 4). Based on the marginal differences in the floristic composition of understory vegetation among stand types, I concluded that the study stands are associated with sites of similar quality.

Table 4. Matrix of floristic similarities for pine and pine-spruce stands showing the Sørensen index based on the species presence/absence (S_{la}) and the species cover (S_{ib})

Sørensen index – S _{la}	Pine stands	Pine-spruce stands
Pine stands	1.000	0.713
Pine-spruce stands	0.713	1.000

Sørensen index – S _{ib}	Pine stands	Pine-spruce stands
Pine stands	1.000	0.727
Pine-spruce stands	0.727	1.000

All species common to all stand types were also found in all age classes, e.g., *Ledum groenlandicum*, *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Vaccinium vitis-idaea*, and *Cornus canadensis* (Table 6). The results of the similarity analysis supported the tabular comparison (Table 7). There were minor floristic differences among age classes in both species composition and relative abundance and the most pronounced differences occurred between the youngest and oldest age classes with a correlation index of 60% and 75%, respectively

(Table 7). The relative frequency of graminoids was the only difference in the life form spectra between the understory vegetation of the different age classes (Figure 15) and it was the highest in the youngest age class. Taking into account this and previous comparisons, I would attribute the floristic differences between age classes to microclimatic and micro-edaphic changes associated with stand development along a time gradient, rather than differences in site quality. It appears that pine stands have a relatively warmer microclimate compared to the pine-spruce stands.

Table 5. Differentiated summary table showing floristic affinities in the understory vegetation between stand types. Species with presence class <III are not listed.

Stand type	Pine-spruce	Pine
Number of stands	14	13
Plant species	Presence class and mean species significance	
Species common to pine and pine-spruce stands		
<i>Cornus canadensis</i>	V 5	V 5
<i>Hylocomium splendens</i>	V 7	V 6
<i>Ledum groenlandicum</i>	V 6	V 7
<i>Linnaea borealis</i>	IV 3	V 5
<i>Lycopodium annotinum</i>	IV 2	III 3
<i>Peltigera aphthosa</i>	V 2	V 2
<i>Picea mariana</i>	V 6	V 4
<i>Pleurozium schreberi</i>	V 7	V 7
<i>Ptilium crista-castrensis</i>	V 7	V 7
<i>Vaccinium myrtilloides</i>	III h	III 4
<i>Vaccinium vitis-idaea</i>	V 5	V 7

Species common pine stands		
<i>Arnica cordifolia</i>	I t	IV 2
<i>Leymus innovatus</i>	I h	III 4

Species common pine-spruce stands		
<i>Picea mariana</i>	V 6	IV 3

Presence class: I - percent presence = 0 – 20, II - percent presence = 21 – 40, III - percent presence = 41 – 60, IV - percent presence = 61 – 80, V - percent presence = 81-100. Presence is in boldface whenever percent presence ≥ 41 .

Mean cover is the average cover value for ecosystem unit. The scale used for cover values is the Domin-Krajina scale where percent cover ranges for symbols printed: t - (0.001 - 0.009), h - (0.010 - 0.099), + - (0.100 - 0.299), 1 - (0.300 - 0.499), 2 - (0.500 - 0.999), 3 - (1.000 - 1.999), 4 - (2.000 - 4.999), 5 - (5.000 - 9.999), 6 - (10.000 - 19.999), 7 - (20.000 - 49.999), 8 - (50.000 - 69.999), 9 - (70.000 - 100.000).

Table 6. Differentiated summary table showing floristic affinities in the understory vegetation among age classes. Species with presence class <III are not listed.

Age class (yrs @ bh)	1 (50-60)	2 (60-80)	3 (90-100)	4 (100-120)
Number of stands	6	7	6	8
Plant species	Presence class and mean species significance			
Species common to all stands				
<i>Comus canadensis</i>	V 5	V 5	V 6	V 5
<i>Dicranum flagellare</i>	III 3	II h	I h	II h
<i>Hylocomium splendens</i>	V 6	IV 5	V 7	V 7
<i>Ledum groenlandicum</i>	V 7	V 7	V 7	V 7
<i>Linnaea borealis</i>	IV 3	V 5	V 4	V 5
<i>Lycopodium annotinum</i>	IV h	IV 2	V 4	II +
<i>Peltigera aphthosa</i>	V +	V 2	V 2	V 3
<i>Picea mariana</i>	V 5	V 6	V 5	V 4
<i>Pleurozium schreberi</i>	V 7	V 7	V 7	V 7
<i>Ptilium crista-castrensis</i>	V 7	V 7	V 7	V 7
<i>Vaccinium vitis-idaea</i>	V 6	V 5	V 7	V 6
Species common to age class 1, 2, and 3 stands				
<i>Lycopodium annotinum</i>	IV h	IV 2	V 4	II +
<i>Vaccinium caespitosum</i>	V 2	III 4	IV 5	I 4
Species common to age class 1 stands				
<i>Leymus innovatus</i>	V 5	I 2	II +	I h
<i>Polytrichum juniperinum</i>	III 4	I h	II h	
Species common to age classes 2 and 3 stands				
<i>Vaccinium membranaceum</i>	I h	III 3	IV 5	II h
Species common to age class 2 stands				
<i>Dicranum fuscescens</i>		III h		
Species common to age class 4 stands				
<i>Vaccinium myrtilloides</i>	II 2	II h	II h	IV 3
<i>Arnica cordifolia</i>	II h	II h	I 1	IV 2

Presence class: I - percent presence = 0 – 20, II - percent presence = 21 – 40, III - percent presence = 41 – 60, IV - percent presence = 61 – 80, V - percent presence = 81-100. Presence is in bold font whenever percent presence >= 41.

Mean cover is the average cover value for ecosystem unit. The scale used for cover values is the Domin-Krajina scale where percent cover ranges for symbols printed: t - (0.001 - 0.009), h - (0.010 - 0.099), + - (0.100 - 0.299), 1 - (0.300 - 0.499), 2 - (0.500 - 0.999), 3 - (1.000 - 1.999), 4 - (2.000 - 4.999), 5 - (5.000 - 9.999), 6 - (10.000 - 19.999), 7 - (20.000 - 49.999), 8 - (50.000 - 69.999), 9 - (70.000 - 100.000).

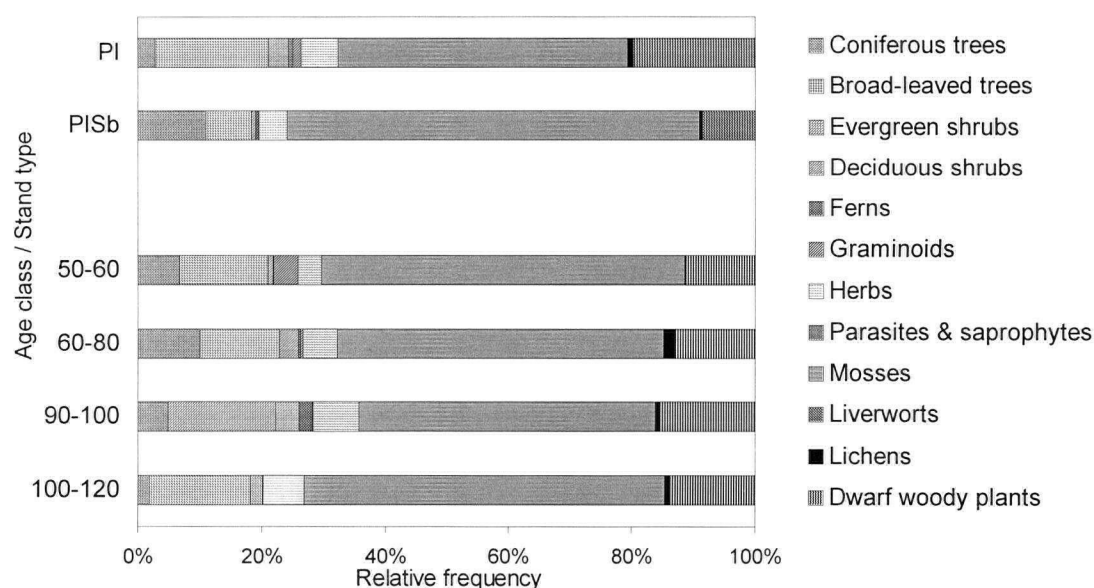


Figure 15. Life form spectra of the understory vegetation of study stands by stand type and age class (yrs @bh). PI - pine stands, PISb - pine-spruce stands.

Table 7. Matrix of floristic similarities showing the Sørensen index based on the species presence/absence of species (SI_a) and on the species cover (SI_b) for pine and pine-spruce stands by age class.

Sørensen index (SI _a)	Age class 1	Age class 2	Age class 3	Age class 4
Age class 1	1.000			
Age class 2	0.632	1.000		
Age class 3	0.703	0.732	1.000	
Age class 4	0.606	0.676	0.694	1.000

Sorenson index (SI _b)	Age class 1	Age class 2	Age class 3	Age class 4
Age class 1	1.000			
Age class 2	0.759	1.000		
Age class 3	0.783	0.719	1.000	
Age class 4	0.746	0.720	0.794	1.000

4.1.3 Soil Chemical Characteristics

The purpose of soil chemical analysis was (i) to obtain quantitative data on soil nutrient conditions of study sites and (ii) to verify estimates of soil nutrient regime derived field estimates and indicator plants. I compared selected soil nutrient properties among stand types and age classes (Tables 8 and 9). Comparisons between stand types showed significant differences only in total nitrogen, mineralizable nitrogen, and extractable potassium of the forest floor, with higher

concentrations in pine stands (Table 8). Compared to pine stands, lower nitrogen concentrations and higher C:N ratios indicating slower decomposition of the forest floor material in pine-spruce stands (see Zinke 1962; Challinor 1968; Swift *et al.* 1979). The litter quality may be affected by the presence of black spruce litter fall and climatic conditions in mixed-species stands, which would affect subsequent decomposition processes (Stump and Binkley 1993).

Table 8. Means and standard deviations (in parentheses) of selected soil nutrient properties in the forest floor and upper mineral soil layers according to stand type. Values in the same row with asterisks are significantly different (Least square means different at P (0.05).

Stand type	Pine stands (n =14)	Pine-spruce stands (n =13)
Forest floor layer		
pH	3.92 (0.21)	3.92 (0.36)
Total C (cg g ⁻¹)	44.24 (3.04)	44.04 (3.54)
Total N (cg g ⁻¹)	1.11* (0.12)	0.97* (0.13)
Mineralizable-N (mg kg ⁻¹)	446* (300)	285* (239)
Extractable P (mg kg ⁻¹)	120 (56)	96 (40)
Extractable Ca (mg kg ⁻¹)	1419 (329)	1720 (723)
Extractable Mg (mg kg ⁻¹)	360 (54)	448 (292)
Extractable K (mg kg ⁻¹)	1025* (277)	756* (197)
C:N ratio	40.4 (6.2)	46.2 (7.3)
0 - 30 cm mineral soil layer		
pH	5.02 (0.14)	5.07 (0.15)
Total C (cg g ⁻¹)	0.906 (0.262)	0.997 (0.453)
Total N (cg g ⁻¹)	0.055 (0.015)	0.057 (0.012)
Mineralizable-N (mg kg ⁻¹)	5.4 (2.8)	6.2 (3.5)
Extractable P (mg kg ⁻¹)	11 (6)	13 (9)
Extractable Ca (mg kg ⁻¹)	555 (287)	685 (382)
Extractable Mg (mg kg ⁻¹)	131 (47)	164 (101)
Extractable K (mg kg ⁻¹)	51.6 (11.6)	57.9 (11.2)
C:N ratio	16.8 (2.9)	17.7 (8.9)

There were no significant differences in nutrient concentration of the forest floor and the upper mineral soil layer across stand types and age classes. Considering the forest floor depth and

minor differences in nutrient concentrations in the forest floor, it is reasonable to conclude that the observed differences are associated with micro-edaphic changes occurring as a result of stand development rather than in site quality. Further, the different values encountered for each soil characteristic fell well within range of accepted characteristics of nutrient poor soils (Duffy 1964; Brisco 2001).

Table 9. Means and standard deviations (in parentheses) of selected soil nutrient properties in the forest floor and upper mineral soil layers according to age class. Values in the same row with asterisks are significantly different (Least square means different at P (0.05).

Age class (yrs @ bh)	1 (50-60) (n=6)	2 (60-80) (n=7)	3 (90-100) (n=6)	4 (100-120) (n=8)
Forest floor layer				
pH	4.0 (0.26)	3.84 (0.26)	4.0 (0.36)	3.9 (0.28)
Total C (cg g ⁻¹)	43.5 (3.5)	43.8 (2.0)	45.2 (2.8)	43.9 (4.4)
Total N (cg g ⁻¹)	1.03 (0.09)	1.14 (0.20)	1.02 (0.18)	0.98 (0.12)
Mineralizable N (mg kg ⁻¹)	305 (250)	576 (380)	277 (170)	328 (172)
Extractable P (mg kg ⁻¹)	102 (21)	89 (38)	112 (61)	120 (63)
Extractable Ca (mg kg ⁻¹)	1691 (386)	1305 (367)	1978 (927)	1563 (447)
Extractable Mg (mg kg ⁻¹)	396 (19)	364 (54)	605 (468)	346 (48)
Extractable K (mg kg ⁻¹)	893 (195)	797 (237)	858 (379)	863 (211)
C:N ratio	42.3 (5.5)	39.9 (10.4)	45.0 (6.2)	45.7 (7.3)
0 - 30 cm mineral soil layer				
pH	5.08 (0.12)	4.96 (0.14)	5.17 (0.08)	5.00 (0.18)
Total C (cg g ⁻¹)	1.20 (0.68)	0.85 (0.18)	0.79 (0.28)	1.02 (0.19)
Total N (cg g ⁻¹)	0.05 (0.01)	0.06 (0.01)	0.05 (0.01)	0.06 (0.01)
Mineralizable N (mg kg ⁻¹)	5.9 (2.7)	6.2 (2.3)	5.6 (4.3)	7.7 (2.8)
Extractable P (mg kg ⁻¹)	10.5 (5.9)	11.1 (3.8)	13.1 (5.9)	14.3 (9.8)
Extractable Ca (mg kg ⁻¹)	533 (402)	771 (362)	467 (151)	525 (175)
Extractable Mg (mg kg ⁻¹)	120 (56)	184 (69)	103 (32)	128 (24)
Extractable K (mg kg ⁻¹)	52.5 (9.3)	54.3 (8.8)	48.2 (14.5)	61 (9.9)
C:N ratio	23.4 (13.8)	15.0 (3.1)	17.2 (3.2)	16.2 (1.6)

4.1.4 Site Index

The mean site index (m @ 50 yrs bh or SI50) of pine ranged from 12.9 m in pine-spruce stands to 13.5 m in pine stands (Table 2, Figure 16). This difference was not significant and further confirmed that study stands were located on ecologically-equivalent sites. Despite the lack of statistical significance, pine had a lower site index in PISb stands than in PI stands. In view of the potential negative effect of trees competing against each other for resources, it is possible that spruce affected the height growth of pine either through interspecific competition mechanisms or simply by contributing to higher stand densities (see volume growth section), thereby decreasing the general amount of resources available for pine growth. Mean site indices of pine were not significantly different across age classes and there was no noticeable trend for site index in relation to age classes. The site indices estimated in this study are consistent with site index given by Beckingham *et al.* (1996) for lodgepole pine on Labrador tea-mesic ecosites (SI50= 12.9 \pm 0.2 m).

Black spruce was found amongst the dominant trees only in age classes 3 and 4, and correspondingly, black spruce SI50 was only calculated for these age classes (Table 2). The resulting site indices (8.8 and 9.5 m) are also consistent with those given by Beckingham *et al.* (1996) (SI50= 9.7 \pm 0.3 m). In even-aged mixed-species stands site index is meaningless for a species that does not occur in the canopy as a dominant tree (Wykoff 1990). Black spruce site index does not reflect site quality.

Site index, based on the relationship between age and the average height of dominant largest-diameter trees, is one of the most reliable indicators of forest productivity. Indeed, mean site indices demonstrated little variation in the present study, which supports its use as an estimator of site quality.

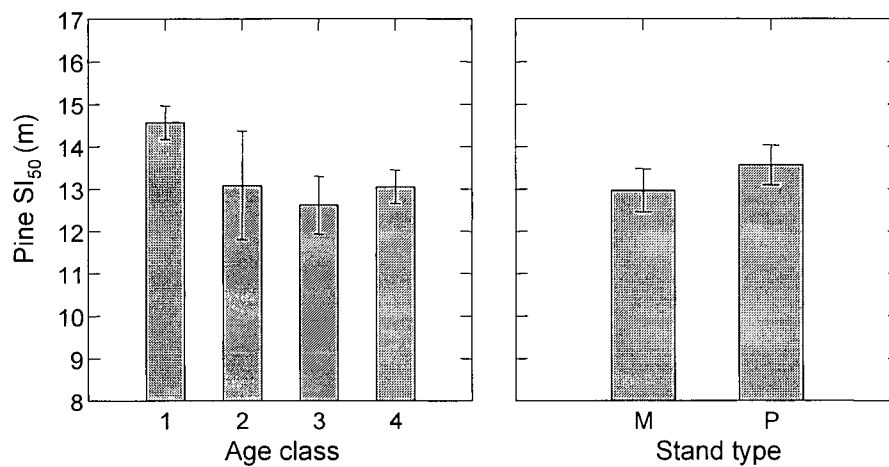


Figure 16. Change in pine site index (m at 50 years BHA) by stand type and age classes.

However, individual stand site indices for pine were quite variable, with SI₅₀ ranging from 10 to 16 m regardless of stand type or age class (Table 2, Figure 16). Note that there are several plausible explanations for the variation among individual stand indices. For most coniferous species in pure stands, site index is independent of density over a wide range of stand densities (Cieszewski and Bella 1993), whereas site index of lodgepole pine is strongly influenced by stand density regardless of the site (Smithers 1956, Holmes and Tackle 1962). This introduces a bias in the relationship between age, dominant height and site (Alexander *et al.* 1967). Smithers (1956) and Alexander *et al.* (1967) therefore pointed out that the strong effect of density on dominant height in lodgepole pine stands precludes the meaningfulness of site index in customary use (i.e., as a site quality estimator), as it often underestimate the true potential of the site (see also Smithers 1961). However, Duffy (1964) showed that site index was nevertheless better for predicting growth than measures such as basal area or stand volume.

The stand density management diagram (SDMD) is a common tool used by foresters to assess the effect of different site qualities and silvicultural treatments on stand development. SDMD's take into account the effect of density upon stand characteristics (volume, quadratic mean diameter and site index). The study stands were plotted on a SDMD, using the height curve and density. Most of the stands were located above the imminent competition induced mortality line and often beyond the density range that is believed to maximize cumulative annual increment (CAI) (Figure 17). Stands of similar initial densities should follow the same path on the SDMD, with the

sole difference being the rate at which the progression occurs, which depends on site quality. Most of the age class 3 and 4 stands are found at the higher end and age class 1 and 2 stands at the lower end of the diagram with similar initial densities above 10 000 stems per hectare (Figure 17). This supports other results showing the similarity of site quality of the study stands.

There are however some young stands present in the higher portion of the diagram and some older stands still in the lower portion. If difference in site quality is discarded as the source of these discrepancies, then the assumed relationship between density and stand volume might be a cause. In addition, although this SDMD was built and calibrated with stands of the same general area as the present study, the quadratic mean diameter was often overestimated when stands were plotted in the diagram using density and dominant height. Correspondingly, when stands were plotted in the diagram from quadratic mean diameter and density, dominant height was underestimated. Cameron (1988) also reported discrepancies between real and estimated measures from the appropriate SDMD. From the previous discussion with site index, it follows that the stand density management diagram's four-dimensional relationships (density, average tree volume, average height and diameter) are not linear and plotting them gives questionable relationships (see also Willcocks and Bell 1995). The relationship between mean tree volume and stand density has been shown to be solid and effective for determining change in tree size versus stand density over time for a number of species. However, lodgepole pine is more sensitive to density. It may be more desirable to use results from SDMD's conceptually rather than literally in high-density stands of lodgepole pine.

Johnstone's productivity index (1976), Duffy's basal area (1964), Alexander's crown competition factor (1967) or SDMD's are all attempts to incorporate density into the relationship between site quality and forest productivity. Most have demonstrated limited accuracy. This might be caused by the fact that density affects so many aspects of tree growth non-linearly (such as leaf area, photosynthetic efficiency, nutrient and water uptake, photosynthate transport, respiration and carbon allocation). Cieszewski and Bella (1993) did attempt to integrate those effects through modelling growth, which could be potentially produce more accurate site indices. However, their model lacks the applicability that site index and SDMD offer to the forester.

LODGEPOLE PINE STAND DENSITY MANAGEMENT DIAGRAM (NATURAL STANDS)

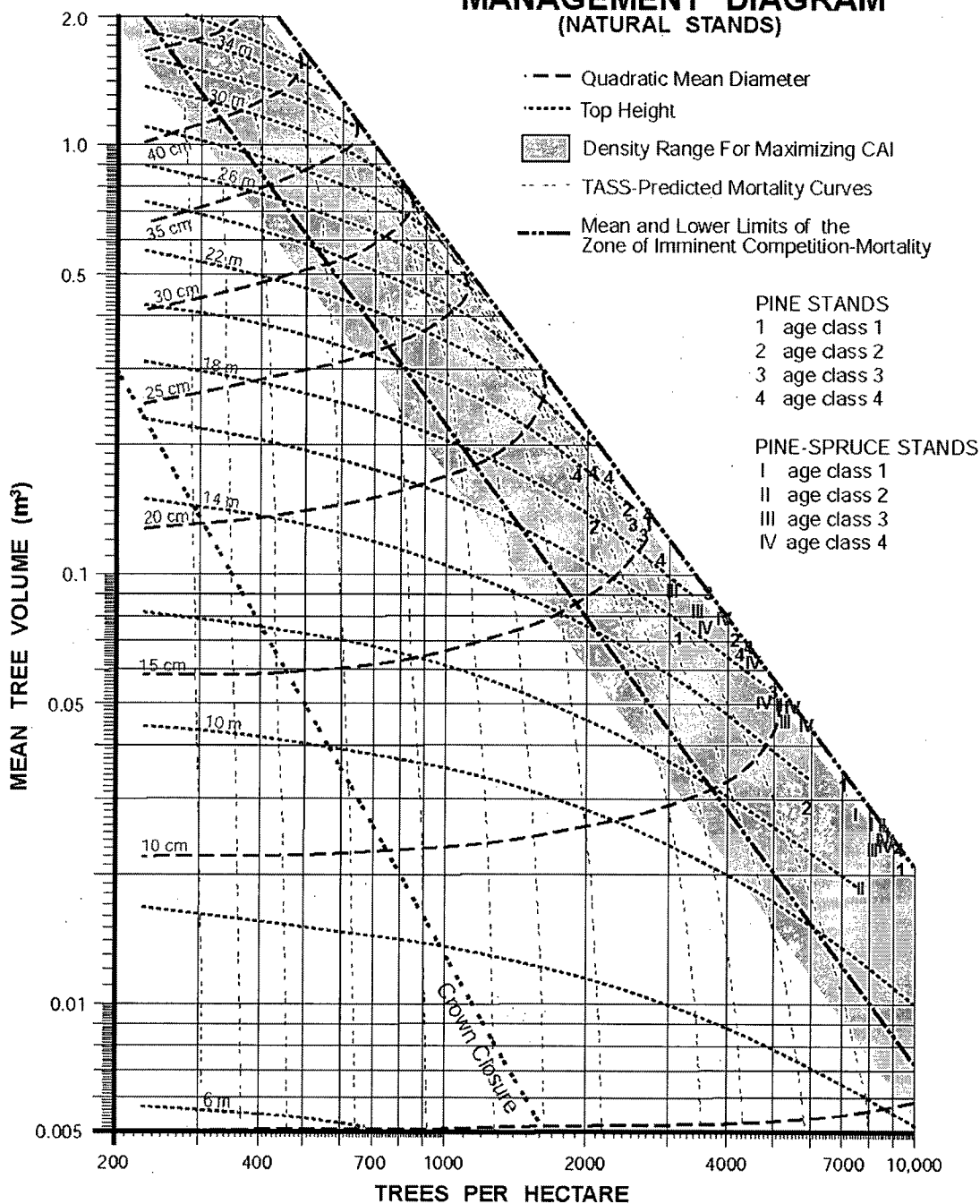


Figure 17. Position of study stands on the stand density management diagram developed by Craig Farnden (Canadian Forest Service, Pacific and Yukon Region). Data Source: TASS generated managed stand yield tables contained in the computer program WINTIPSY (B.C. Ministry of Forest, Productivity and Decision Support section).

Vegetation has held as a reliable indicator of site quality (as expressed by site index) in some studies (e.g. lodgepole pine, Strong *et al.* 1991) although not in others (e.g. black spruce, Payandeh 1986). It may be inaccurate to determine the growth environment through vegetation alone because trees respond to and also modify their environments in various ways which might impact understory vegetation. Vegetation in my study appeared to be an appropriate indicator of soil nutrient regime when compared to soil results. However, vegetation alone, may not fully explain the observed pine site index (Kayahara 1989; Kayahara *et al.* 1998). Density is also likely to affect tree growth, which could cloud the effect of site quality as examined through pine site index and SDMD's.

4.2 Stand Structure

The importance of stand structure and canopy development on tree growth has been stressed earlier. Studying stand structure to check whether stand structure remained constant over time in pine and pine-spruce stands could provide further insight in the dynamics of lodgepole pine-black spruce stands. The analyses of variances comparing pine dimensions between stand types were never significant and the results are therefore not presented.

The variances of dbh, height, and live crown height of pine were reasonably similar among stand types for a given age class, but varied with age class (Tables 10, 11, 12, and 13, Figure 18). The maximum variance was observed for age class 2 stands (Table 11). Pine was consistently larger than spruce across all age classes (Figures 18 to 22).

In age class 1, the differences in dbh, height, and crown height of pine between the two stand types were not significant (Table 10, Figure 18). Spruce trees were notably smaller than pine trees and nearly all were confined to the shrub layer (Table 10, Figure 18).

Table 10. Descriptive statistics for age class 1 (50 - 60 years) study stands (N is number of trees).

Stand property	Stand type	N	Mean	Standard deviation	Minimum	Maximum
Dbh (cm)	Pine in pine stands	172	8.8	3.3	2.4	16.9
	Pine in pine-spruce stands	104	10.2	3.6	2.8	20.1
	Spruce in pine-spruce stands	151	4.5	2.5	0.4	11.7
Height (m)	Pine in pine stands	172	10.4	2.9	3.0	19.0
	Pine in pine-spruce stands	104	11.1	2.5	4.1	16.2
	Spruce in pine-spruce stands	151	5.0	2.0	1.3	13.0
Crown height (m)	Pine in pine stands	172	6.2	2.2	1.2	14.6
	Pine in pine-spruce stands	104	7.7	1.7	1.3	11.7
	Spruce in pine-spruce stands	151	1.8	0.7	0.1	4.0

In age class 2 stands, dbh, height, and crown height of pine were similar between stand types (Table 11, Figure 18). Compared to age class 1 pine-spruce stands, differences between pine and spruce were larger, indicating faster growth of pine than that of spruce (Table 11, Figures 18 and 22). The larger standard deviations for dbh, height, and crown height of pine suggested imminent density-dependent mortality (Benjamin and Hardwick 1986; Lieffers and Titus 1989). This conjecture is further corroborated by the bimodal distribution of pine height to live crown and the pseudo-bimodal distribution of pine height in age class 2 stands. This denotes the presence of suppressed trees (short trees with small crowns), not present in the older age classes. However, the distribution of dbh was not bimodal. This is possibly the result of allocation to height growth being a priority in dense stands with a small biomass increment per unit of height growth (Lieffers and Titus 1989; Chen *et al.* 1996; Williams *et al.* 1999). This strategy would result in the development of small stems for trees in any canopy position.

Table 11. Descriptive statistics for age class 2 (60 - 80 years) study stands (N is number of trees).

Stand property	Stand type	N	Mean	Standard deviation	Minimum	Maximum
Dbh (cm)	Pine in pine stands	132	11.9	5.0	2.8	24.7
	Pine in pine-spruce stands	90	11.1	4.7	2.4	25.0
	Spruce in pine spruce stands	133	5.0	2.9	0.4	16.0
Height (m)	Pine in pine stands	132	12.1	4.9	2.5	20.1
	Pine in pine-spruce stands	90	11.7	4.7	3.0	20.8
	Spruce in pine spruce stands	133	4.8	2.1	1.5	11.6
Crown height (m)	Pine in pine stands	132	7.9	3.6	1.7	15.4
	Pine in pine-spruce stands	90	7.6	3.2	1.8	13.8
	Sb in pine-spruce stands	133	1.6	0.9	0.1	4.5

In age class 3 stands, the mean dimensions of pine trees were not significantly different between stand types; however, dbh of pines was slightly higher in pine-spruce stands (Table 12, Figure 18). Although spruce trees were generally smaller than pine trees, the height of spruce was closer to mean pine height and some spruce were found in the canopy layer (Figure 22). This increase in the overall height of spruce is possibly explained by a high responsiveness to increase in light (Wright *et al.* 1998). Spruce dimensions exhibited large standard deviations and more or less

bimodal height frequency distribution, suggestive of self-thinning in this age class. An alternative explanation for the bimodal distribution of height and diameter in spruce is the development of a new spruce cohort in small gaps following pine mortality (Horton 1956; Horton and Lees 1961). The bimodal height to live crown distribution for spruce was not expected as an indicator of self-thinning or presence of a new cohort, since black spruce retains foliage to the bottom of the stem (Carter and Smith 1985). This age class appears to manifest the onset of spruce release with a general increase in height growth and self-differentiation. The possibility that spruce presence in the stand might favour self-thinning of pine was not supported by these findings as pine dimensions and their distributions were similar, regardless of stand type, in age class 3 stands, the age class following the self-thinning event. In addition, no indications of self-thinning were observed earlier for pine in pine-spruce stands.

Table 12. Descriptive statistics for age class 3 (90 -100 years) study stands (N is number of trees).

Stand property	Stand type	N	Mean	Standard deviation	Minimum	Maximum
Dbh (cm)	PI in pine stands	140	12.1	4.6	2.8	22.9
	PI in pine-spruce stands	63	14.7	4.1	7.8	27.0
	Sb in pine-spruce stands	105	7.5	5.7	0.1	20.5
Height (m)	PI in single-species stands	140	13.7	3.5	1.3	22.8
	PI in pine-spruce stands	63	13.6	2.2	9.0	18.6
	Sb in pine-spruce stands	105	7.3	4.5	1.3	18.6
Crown height (m)	PI in pine stands	140	8.9	2.4	2.3	13.9
	PI in pine-spruce stands	63	8.6	1.9	3.0	11.6
	Sb in pine-spruce stands	105	2.3	1.6	0.2	9.2

In age class 4 stands, the mean dbh, height, and crown height of pine trees were again not significantly different between stand types (Table 13, Figure 18). Compared to age class 3 pine-spruce stands, a larger proportion of spruce trees had grown into the main canopy (Figure 22), but the mean dbh, height, and crown height for spruce were still significantly lower than for pine (Table 13, Figure 22). The presence of a bimodal height distribution gives evidence that PISb stands remained stratified. The occurrence of spruce self-thinning might have corresponded to the onset of spruce release; however, pine still displayed large height gain in age class 4 with spruce remaining lower (Figures 18, 20 and 22). Two explanations are possible: (i) the appearance of a younger

cohort of small spruce in age class 3 stands might have limited the average spruce height (Horton and Lees 1961; Larson 1992) or (ii) spruce is largely unresponsive to increase in light in high light conditions, although highly responsive to small increase in light in low light conditions (Wright *et al.* 1998).

Table 13. Descriptive statistics for age class 4 (100-120 years) study stands (N is number of trees).

Stand property	Stand type	N	Mean	Standard deviation	Minimum	Maximum
Dbh (cm)	PI in pine stands	115	15.2	4.7	5.2	26.8
	PI in pine-spruce stands	98	15.8	4.1	6.3	24.0
	Sb in pine-spruce stands	190	8.9	3.8	1.9	21.8
Height (m)	PI in pine stands	115	16.9	3.2	4.6	24.3
	PI in pine-spruce stands	98	16.8	2.4	10.0	24.4
	Sb in pine-spruce stands	190	9.9	3.4	1.3	17.9
Crown height (m)	PI in pine stands	115	10.6	2.7	1.8	16.1
	PI in pine-spruce stands	98	11.9	2.1	7.1	18.9
	Sb in pine-spruce stands	190	4.5	1.8	0.1	10.0

The dbh frequency distributions were bimodal only in age class 3 pine-spruce stands (Figure 19). Taken with the basal area results, it is a further clue that pine and spruce experience similar diameter growth. The height frequency distributions were bimodal in the pine-spruce stands for all age classes (Figure 20). The modes in the height frequency distributions were most distinct in age class 3 stands and least distinct in age class 4 stands. The crown height frequency distributions also showed modes in the pine-spruce stands of all age classes, as well as in age class 2 pine stands (Figure 21). The observed differences in the frequency distributions between pine and spruce in the pine-spruce stands are a result of stand development and differentiation that was most strongly manifested between age classes 2 and 3 stands. However, the differences between the species decreased in the age class 4 pine-spruce stands because of decreasing pine growth and continuing ingress of spruce into the canopy (Figure 22).

Most of the mixed-species stands that have been studied show a stratified height structure (Larson 1992). Predictions of the future stand structure demand knowledge of whether the height dominance pattern will shift or remain the same. Most often, the dominance patterns can be anticipated from knowledge of the species autecology and interaction response (Larson 1992; Oliver

1992). However, these are rarely accurately predicted (Oliver 1992) and the length of the period over which these shift occur is unknown. The bimodal stand height frequency distribution provides the best indication of canopy stratification (Varga *et al.* 2001). However, the time span considered in this study (50 to 120 years) proved insufficient in dating the hypothesized shift from pine to spruce dominance although the available data are consistent with the later spruce dominance. Between 90 and 120 years, spruce began to ingress into the main canopy. Horton (1956) documented the onset of pine and spruce coexistence in the canopy between 70 and up to 160 years (average 125 years) and the complete disappearance of pine between 225 and 375 years in average (290 years in average). The large window during which spruce surpasses pine thus remains largely undefined and should be considered within the species life span characteristics.

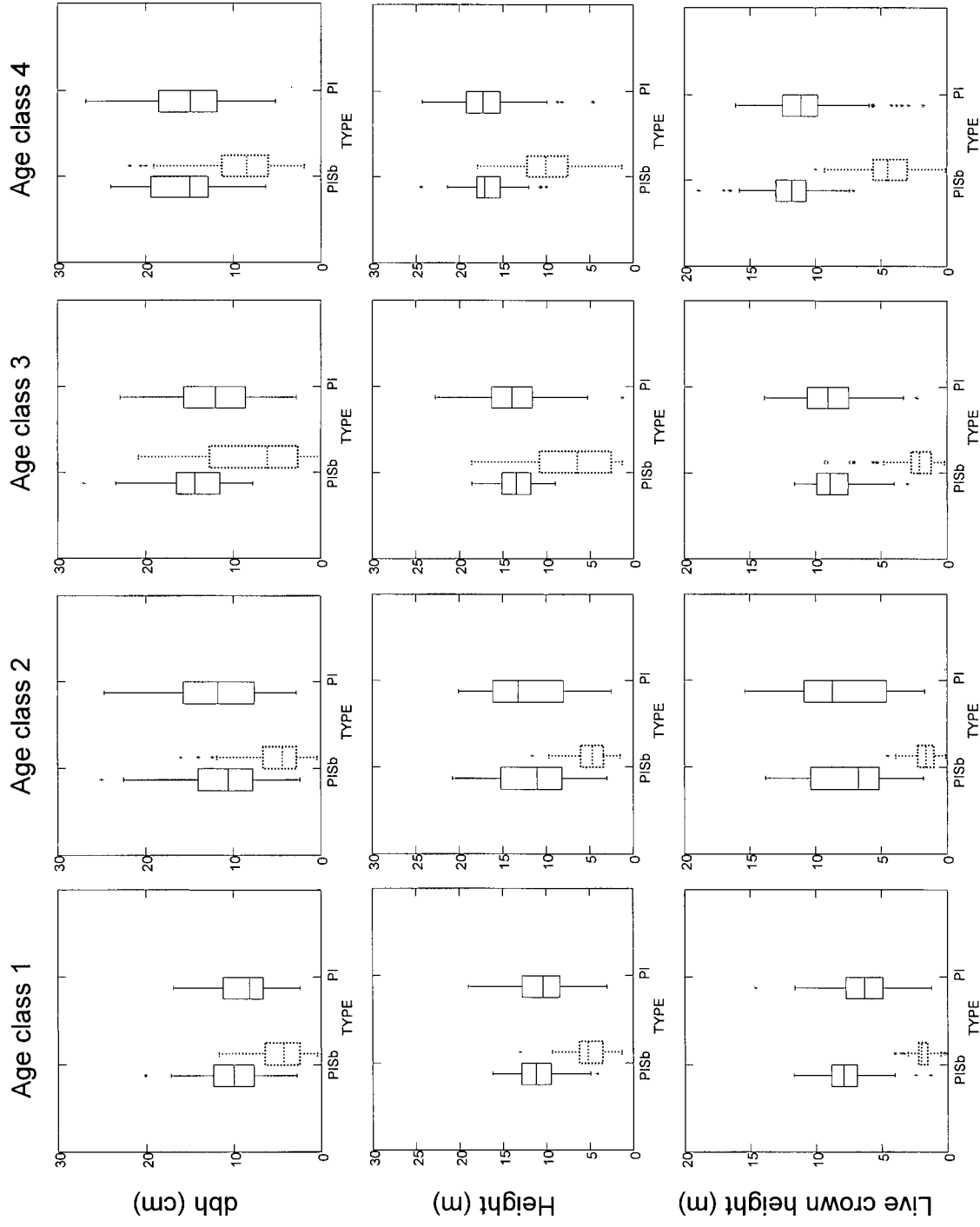


Figure 18. Box plots of diameter, height, and height to live crown for pine and spruce according to stand type and age class. Plain lines are used to represent pine and dotted line spruce. The box indicates the 25th and 75th data percentiles; inside the box the solid line indicates the median; asterisks denote outside values.

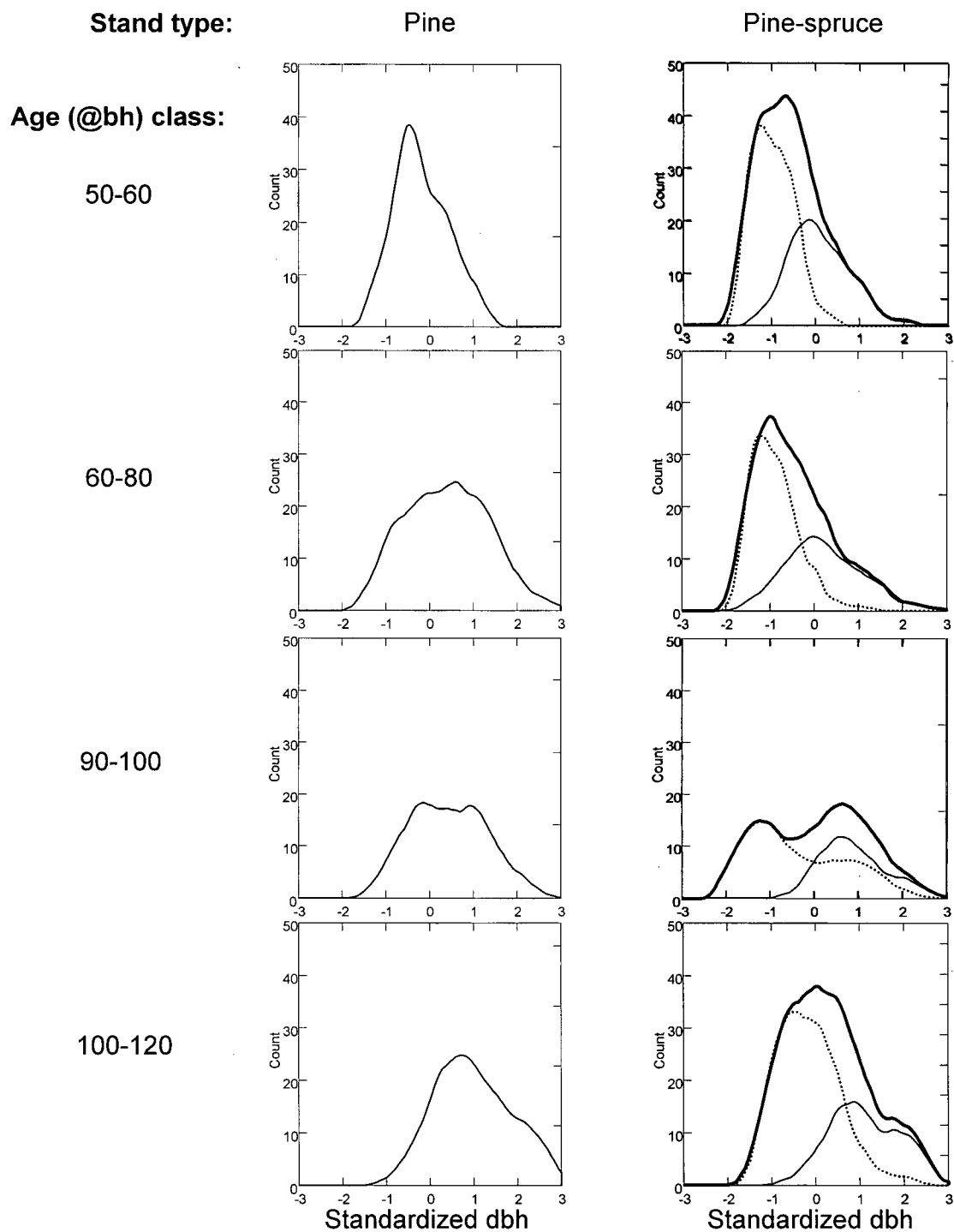


Figure 19. Diameter frequency distributions based on standardized dbh (cm). Thin lines – pine, dotted lines – spruce, thick lines - both species.

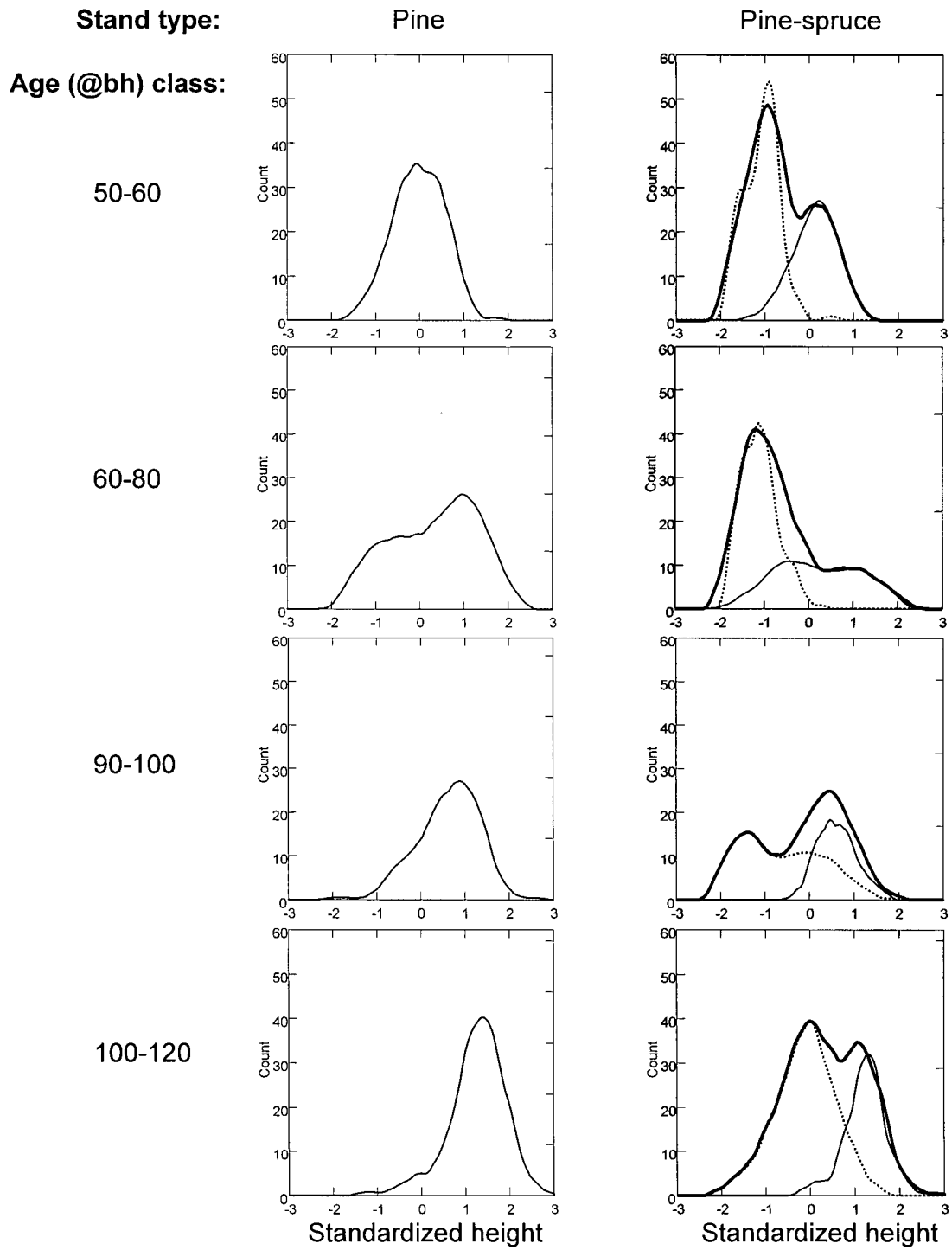


Figure 20. Height frequency distributions based on standardized dbh (cm). Thin lines – pine, dotted lines – spruce, thick lines - both species.

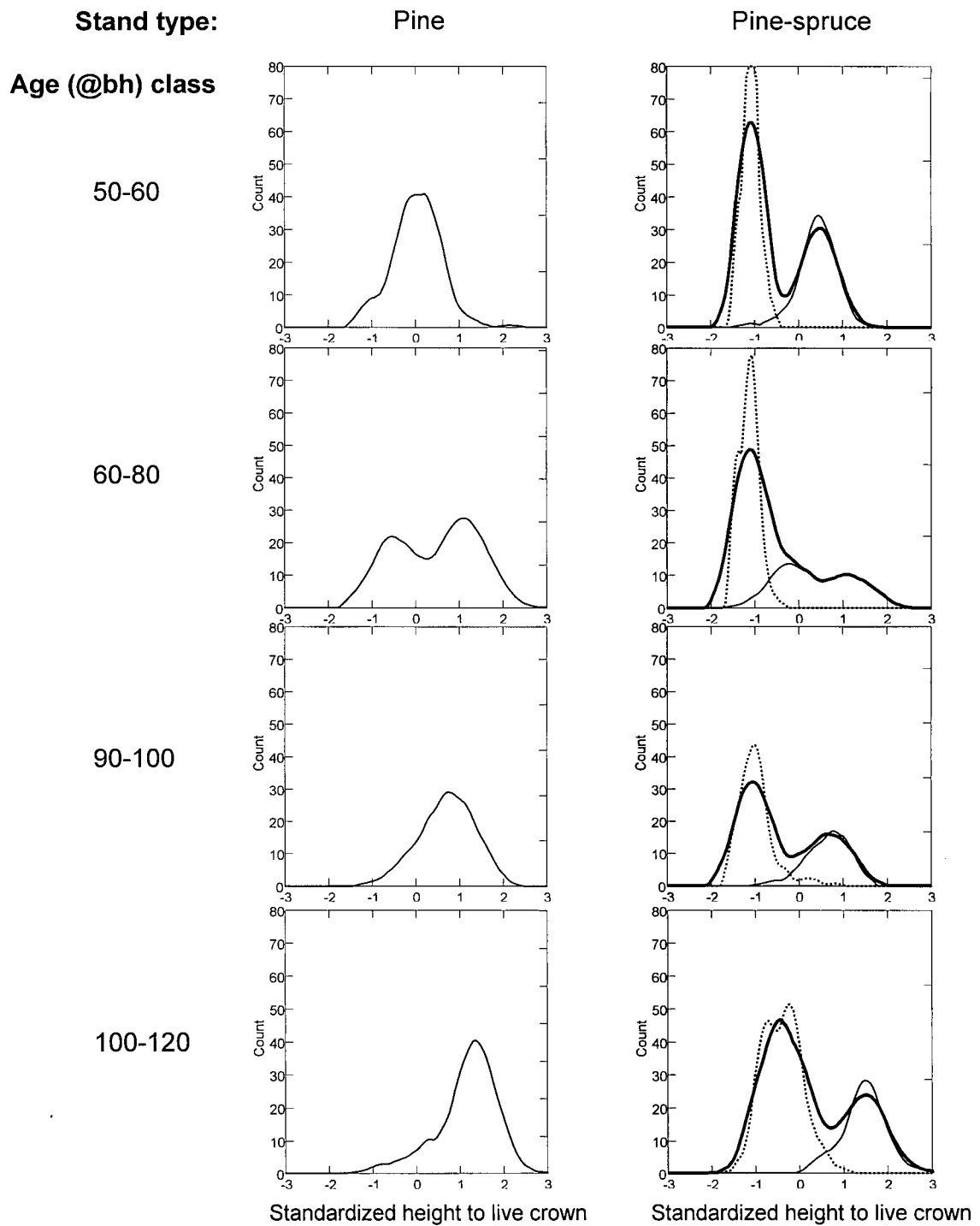


Figure 21. Height to live crown frequency distributions based on standardized dbh (cm). Thin lines – pine, dotted lines – spruce, thick lines - both species.

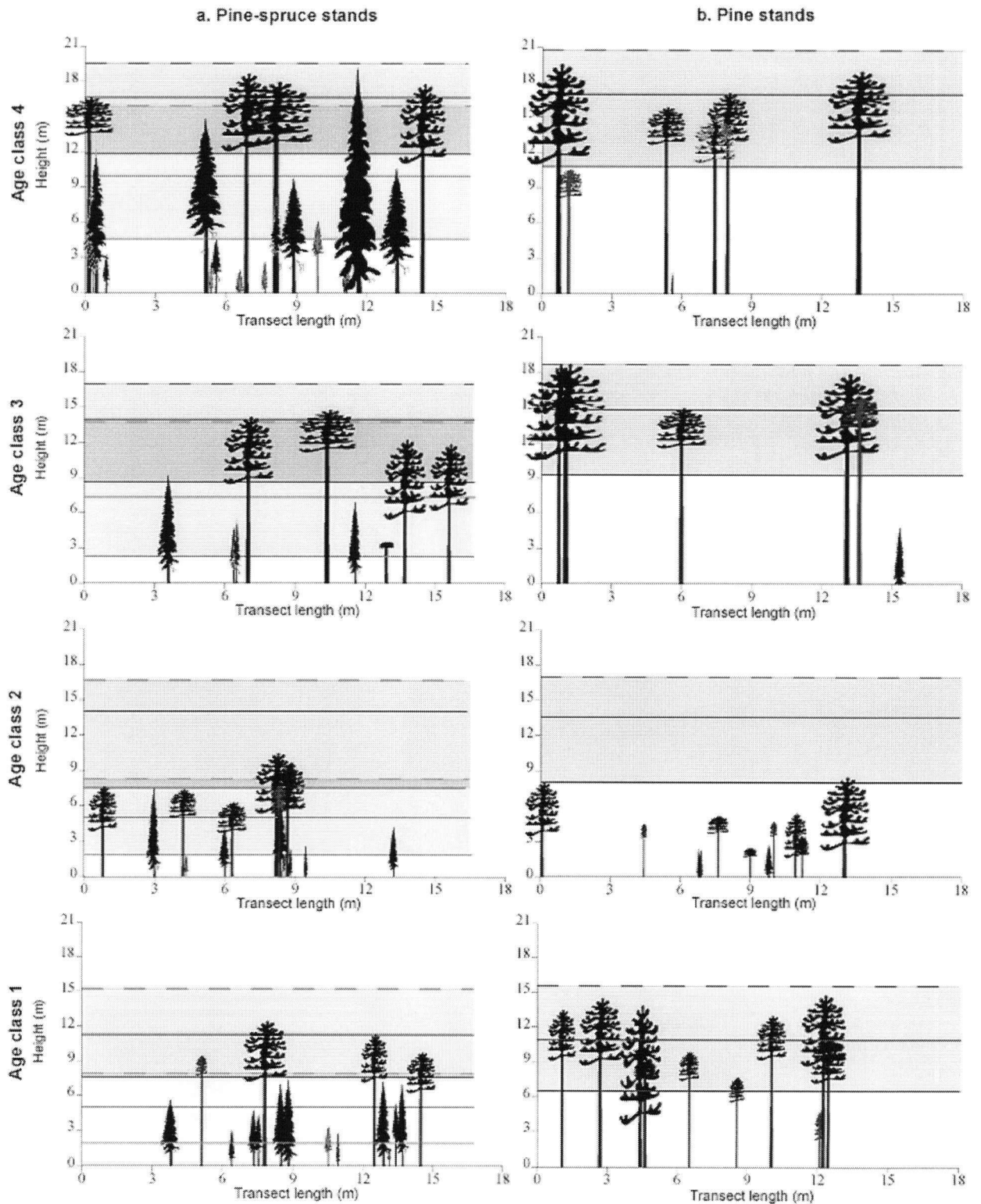


Figure 22. Vertical structure of (a) pine-spruce stands and (b) pine stands across age classes. The dashed lines are average top heights, the upper plain lines are average total heights and the lower plain lines are average height to live crown of pine (upper position, grey) and spruce (lower position, light grey).

4.3 Stand Growth

Diameter and height growth are dependent on many factors such as site quality, density and interaction with other tree species. In order to compare growth between species, these factors should be fixed and controlled as much as possible. It was already established that study sites were of similar quality. The effect of density is believed to be minimized in the case of dominant trees and the growth conditions are optimal. Although the effect of density on dominant height has already been established earlier (see also Smithers 1961), there is the possibility of an effect of species composition. Determining the growth of pine in the presence/absence of black spruce will help our understanding of stand dynamics. It may also help in the design of appropriate silvicultural methods.

4.3.1 Height Growth

The models using the Chapman-Richards function adequately fitted the average height growth curves ($R^2 > 0.98$ and $0.08 < \text{SEE} < 0.12$) for largest-diameter pine trees and spruce trees. These curves were compared in order to discern height growth patterns. Similar trends in height growth for pine and spruce were expected in the same stand type regardless of age class. This hypothesis was corroborated for spruce whose height growth was consistent across age classes in the pine-spruce stands. Pine height growth, however, was highly variable, and on average, slightly higher in pine stands than in pine-spruce stands (Figure 23, Appendix 1).

Height growth of spruce was fairly constant, nearly linear, and showed no evidence of reduced growth in the older stands (Figure 23c). Some differences were observed between height growth curves of spruce derived from different age classes. However, the heights estimated from different growth curves were always less than 2 m apart for a given age during the time span considered (Figure 23c). Further, the difference observed might be an artefact of the reduced sample size within each age class.

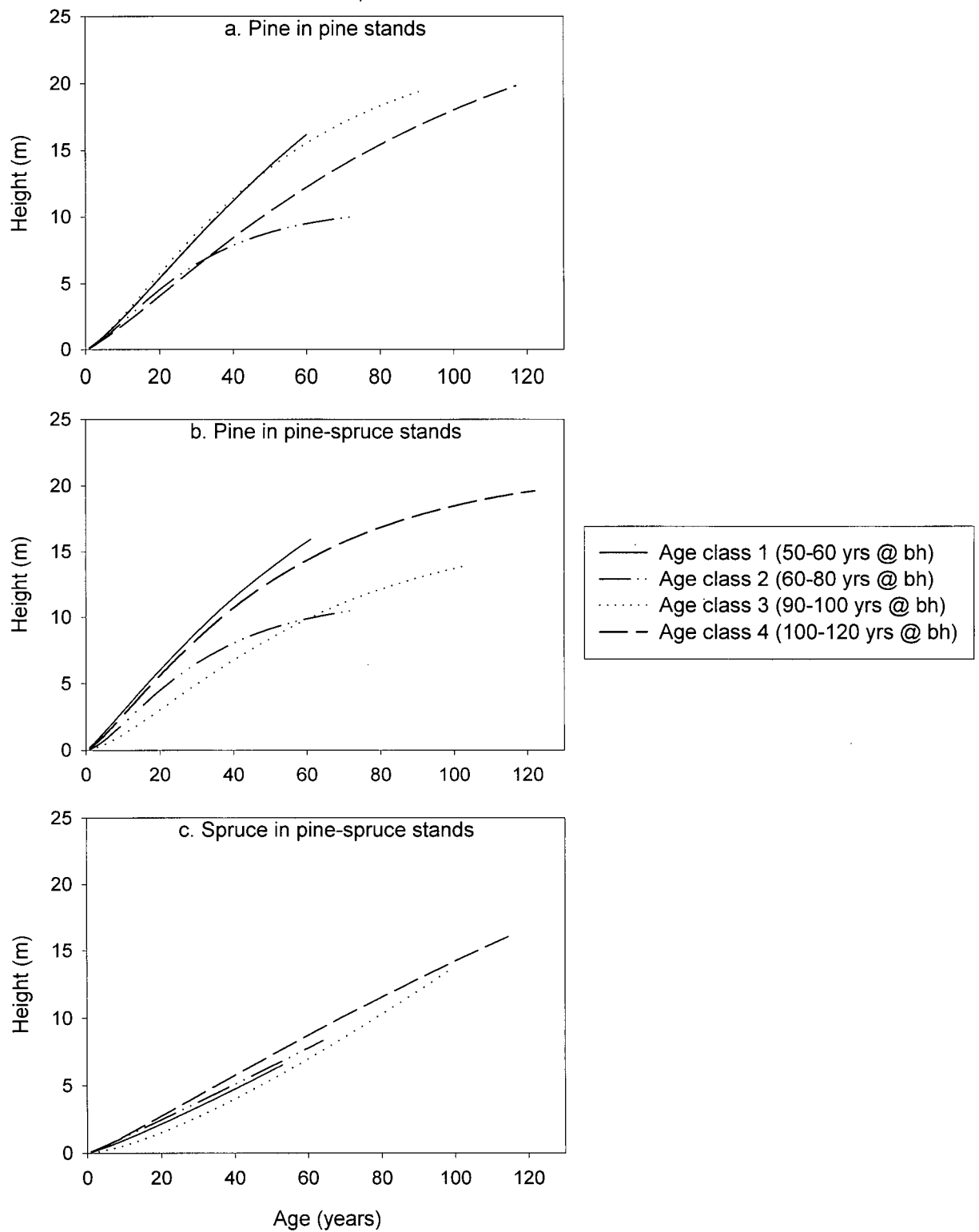


Figure 23. Average height growth curves for (a) dominant pine trees in pine stands; (b) dominant pine in pine spruce stands and (c) largest-dbh spruce trees according to age classes. All curves were based on 3 trees per age class.

Differences were also observed between pine height growth curves between stand types and age classes. However, within a given age class, pine in pine stands and pine in pine-spruce stands displayed similar curves. It appeared that the observed variability between pine curves of each stand type was primarily due to the differences among age classes with each age class displaying a specific height growth pattern (Figures 23a,b). In the age class 1 and 4 stands, pine, regardless of stand type, grew faster than in the age class 2 and 3 stands. One possible explanation could be that the different burns at the origin of each age class occurred in stands in different development stages. The resulting variations in initial density among stands (Horton 1956) could have impacted the growth of the trees to different extent (Smithers 1961, Brisco 2001). It is possible that the height growth curves were different due to the impact of varying density levels among stands of different age classes. However, the observed difference are more likely due to the small sample size (only 3 trees per category) rather than to the age class factor. Curve level is the expression of the relationship between site conditions and the tree species. It can be affected by stocking density and stem distribution (stand structure). Curve shape is mainly a function of the intrinsic growth trend of the species over time. Since insufficient data is available in the present study, the greatest emphasis in comparing growth of pine and spruce should be placed on curve shape.

The comparisons between average height growth curves for dominant pine trees and the largest-dbh spruce trees based on all stands versus average height growth curves for age classes 1 and 2 indicated no apparent differences in height growth pattern of the dominant pine trees and the largest-dbh spruce trees between stand types (Figure 24, Appendix 1). However, the curves based on all stands showed a slightly higher height growth of pine in the pine stands than in the pine-spruce stands (Appendix 1, Figure 24). Although the height growth of the largest-dbh spruce trees was inferior compared to pine, the average curves for spruce have not shown any indication of decrease in older ages as the pine curves did. These growth trends were weak, and despite the variability among age classes, the pine height growth curves were very similar between stand types within a given age class. This leads to the conclusion that pine height growth is more affected by intraspecific than by interspecific competition (see also Horton 1956).

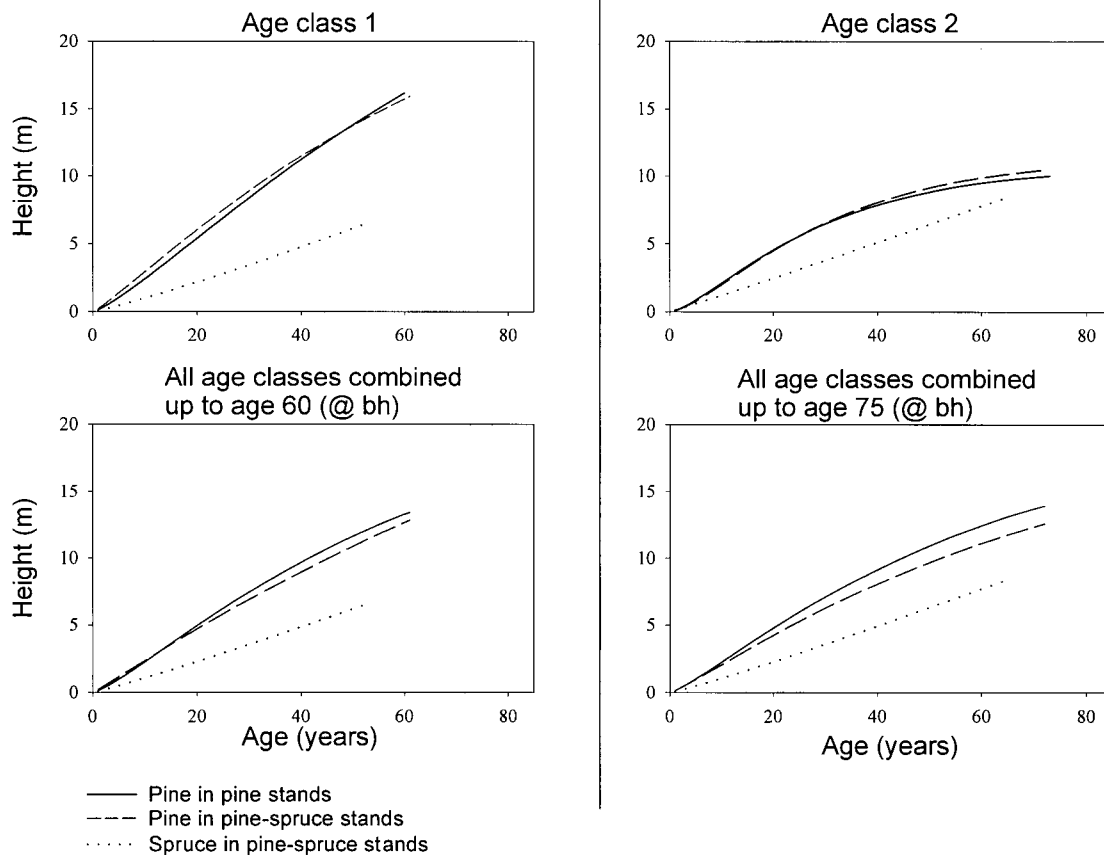


Figure 24. Average height growth curves for dominant pine trees and the largest-dbh spruce trees based on age class 1 and 2 stands (the upper row; curves were based on 3 trees each) and all stands with the cut-off of 60 and 75 years (@ bh) (the lower row; curves based on 12 and 9 trees respectively).

At 100 years (@ bh), the pine dominants, regardless of stand type, reached approximately a height of 18 m, and the spruce dominants reached a height of approximately 15 m. At this age, the height growth increment of dominant pine trees began to decrease whereas that of the largest dbh spruce trees did not. These results are consistent with our current understanding: lodgepole pine height growth is faster than that of black spruce (Horton 1956; Morris et al. 1988) but exhibits a decline earlier (see Clyde and Titus 1987). Black spruce height growth is slow but steady and levels off at exceptionally advanced ages (Horton and Lees 1961; Smith 1984).

4.3.2 Diameter Growth

The diameter growth curves were fitted using a cubic polynomial model with a R^2 above 0.99. A similar pattern of basal area over age curves was expected for dominant pine trees

regardless of stand type and age class, and for the largest dbh spruce trees regardless of age class. Contrary to expectations, there were differences between the average curves for each study species in relation to stand type and age class (Figure 25, Appendix 2). Visual comparison of the curves suggests that the age for a rapid increase in radial growth increases with increasing age class; i.e., from approximately 40 years @bh (age class 1-2 stands) to 50-60 years @bh (age class 3-4 stands). The explanation offered for these discrepancies is the difference in the history of stand density (Smithers 1961) and the small sample size (see also the height growth section). The same caution as previously expressed should be use in the examination of the results.

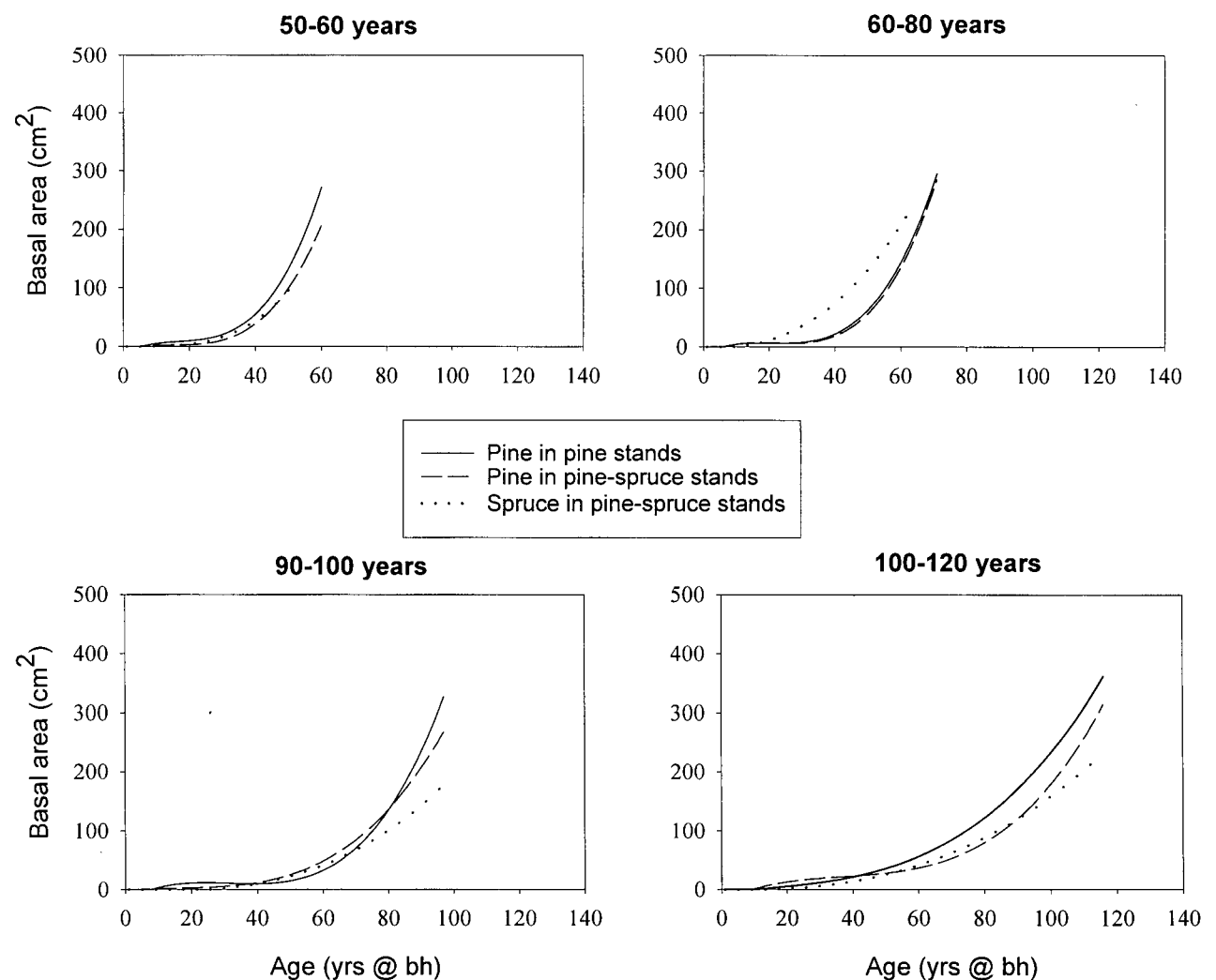


Figure 25. Average diameter growth curves for dominant pine trees and the largest-dbh spruce trees according to stand type and age class (each curve based on data from 3 trees).

The diameter growth curves for dominant pine trees in age classes 1 and 2 were distinct from the age class 3 and 4 curves. However, visual observation of the curves show that the pine curves are similar between stand types within an age class (Figure 25). Comparison of the diameter growth up to 60 years for pine based on the age class 1 stand data indicated a weak difference between stand types (Figures 25 and 26). The same pattern was observed when using the data from all stands up to 60 years (Figure 26). The radial growth of dominant pine trees was slightly higher in pine stands than in pine-spruce stands, and that of the largest dbh spruce trees was only slightly lower than that of pine.

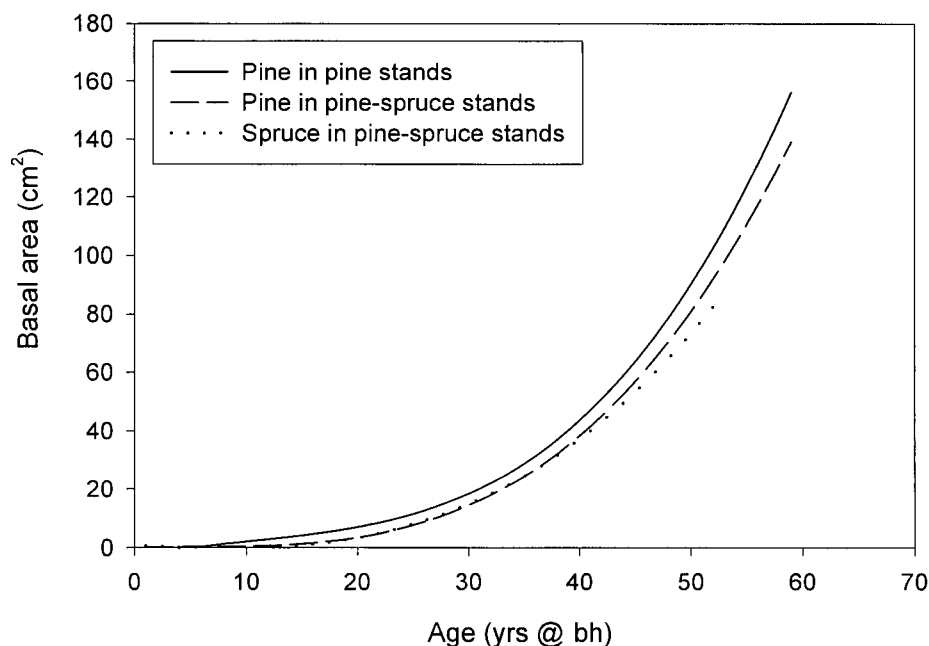


Figure 26. Average basal area cumulative growth curves ($n=12$ for each curve) derived from all stands up to the age of 60 (@ bh) for dominant pine trees and the largest-dbh spruce trees by stand type. R^2 for all curves are >0.99 .

All curves between age and diameter were concave with a relatively long juvenile phase (zone of accelerated growth). Based on the pine chronosequence developed by Brisco (2001) for the same study area, it is reasonable to expect the future basal area growth of pine to maintain the increasing trend observed in this study for approximately 80 years from now. Brisco (2001) found

that the radial increment of pine does not slow before the senescent phase onset at breast-height age 200 years.

Pine diameter growth was not affected by the presence of spruce. Again, one can conclude that interspecific competition is not the cause of variability in basal area growth (Horton 1956). In addition, pine diameter-growth curves were very similar to those of spruce. Several explanations are possible. Some authors have shown that black spruce, given appropriate light and space, could grow as fast as lodgepole pine or aspen (Horton and Lees 1961; Armson 1975). Since only the largest black spruce trees were selected for stem analysis, it is possible that they have grown with sufficient light and space conditions. Another explanation for the similarity between pine and spruce basal area growth is the typical slow diameter growth of pine (Smithers 1961), which generally shunts more of its resources to height growth (improved light interception), whereas black spruce allocates more photosynthates to lateral growth in low light. Because the lower branches on shade-tolerant tree species retain foliage longer (Larson 1963), relative diameter increment is greater and is maintained at a higher level for a longer period of time than that of lodgepole pine.

From the study of height growth of dominant trees, it appears that black spruce remains in the lodgepole pine understory for approximately 100 years. However, the differences in curve shape confirm one of the hypotheses: that black spruce will top lodgepole pine at later stages of development. The basal area growth of dominant pines and spruces were not very different. The examination of lodgepole pine growth between stand types also illustrated the sensitivity of the species to density (i.e., lodgepole pine is more sensitive to intraspecific than to interspecific competition). Lodgepole pine growth was not impeded by black spruce, but rather by its own density.

4.3.3 Volume Growth

Volume growth between study stands was compared in order to determine whether mixed-species stands are more productive than single-species stands. The analyses focused on net stand volume and merchantable volume.

Stand density is one of the main factors affecting tree growth and thus it was important to consider stand volume jointly with stand density, particularly where lodgepole pine is concerned. All study stands were fully stocked according to the density management diagram developed for lodgepole pine by Farnden (1996) (see also Figure 17). Nonetheless, density was highly variable among study stands (Figure 27), which could potentially affect stand volume. This variability has been noted in the literature concerning the Upper Foothills (Horton 1956; Smithers 1956, 1961; Horton and Lees 1961; Johnstone 1976).

Generally, density decreased and mean stand basal area and volume increased with age (Table 14; Figures 27 and 28). The mean total number of stems per hectare was higher in pine-spruce stands than in pine stands, regardless of age class (Table 2, Figure 27a). However, the number of pines per hectare was not significantly different between stand types at any age (Figure 27b), although always lower in pine-spruce stands. It follows that mixed-species stands of pine and spruce have higher densities (Figure 27a) simply because they carry spruce trees on top of the average pine density of pure pine stands.

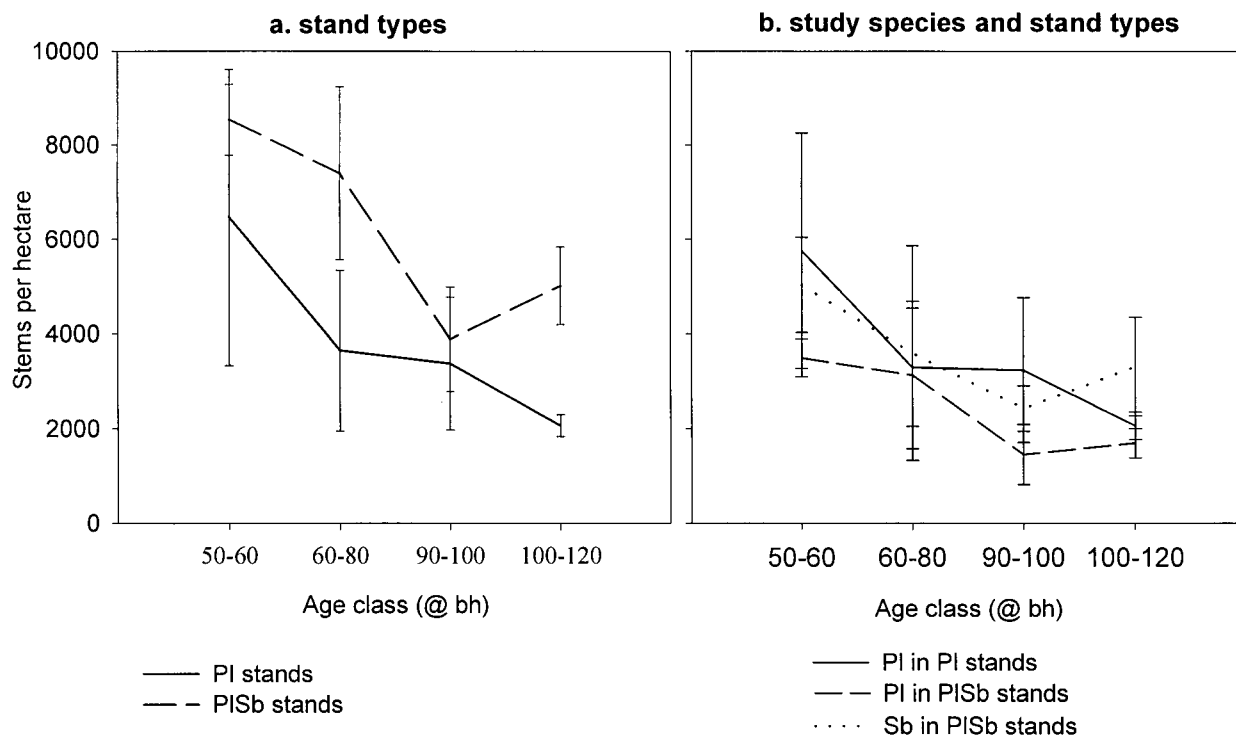


Figure 27. Stand density (stems per hectare) and standard deviations for (a) stand types and (b) study species in stand types.

The small differences in stand basal area and volume between age class 2 and 3 in pine-spruce stands (Table 14) were attributed to pine mortality (Figure 27b; see also stand structure section). From density information alone, it was not clear if pine self-thinning occurred between age class 2 and 3 pine stands or if it occurred earlier. However, the previous examination of stand structure suggested that pine self-thinning in pure stands did occur between age classes 2 and 3. The sharp decrease in density between age classes 1 and 2 was likely an artefact of the sample variability (Table 14, Figure 27b, note the large standard deviations). The increase of spruce stems per hectare in age class 4 did not refute the possibility of spruce self-thinning occurring between age class 3 and 4, but positively validated the previous deduction that new spruce cohorts established after pine mortality between age classes 2 and 3.

Table 14. Means and standard deviations (in parentheses) of selected stand characteristics for pine in pine (PI) stands and pine and spruce in pine-spruce (PISb) stands by age class.

Stand type/ Age class	Mean number of stems per hectare	Mean volume (m ³ ha ⁻¹)	Mean stand basal area (m ² ha ⁻¹)	Mean merchantable volume (m ³ ha ⁻¹)
PI (n=3) Age class 1	6467 (3134)	217 (52)	40.6 (6.4)	131 (63)
PISb (n=3) Age class 1	8533 (750)	202 (25)	42.2 (5.7)	135 (32)
PI (n=4) Age class 2	3650 (1698)	281 (125)	43.8 (10.7)	253 (110)
PISb (n=3) Age class 2	7400 (1833)	255 (92)	45.7 (5.9)	192 (83)
PI (n=3) Age class 3	3379 (1403)	287 (60)	42.8 (4.7)	242 (99)
PISb (n=3) Age class 3	3889 (1102)	252 (71)	43.6 (11.1)	239 (74)
PI (n=4) Age class 4	2066 (229)	309 (76)	39.9 (8.5)	269 (79)
PISb (n=4) Age class 4	5017 (822)	396 (39)	59.8 (1.1)	313 (44)

Stand volumes are presented in Figure 28. The regression models (Equation [15] and [16]) were significant ($p < 0.001$) and demonstrated strong evidence that age, proportion of spruce and density were related to stand net volume (Table 15, Figure 28). Normality, observation independence, autocorrelation, and homoskedasticity assumptions were checked and found satisfactory.

[15]
$$\text{Stand net Volume} = -210.4 + 2.711(\text{Stand Age}) - 462.2(\text{PPspruce}) + 22.49(\text{RD}) + 2.507(\text{Stand Age} * \text{PPspruce})$$

$R^2 = 0.73$ $\text{Adjusted } R^2 = 0.68$ $\text{Root MSE} = 49.44$ $\text{Coefficient of variation} = 17.61$

[16]
$$\text{Stand net Volume} = -238.2 + 2.301(\text{Stand Age}) - 305.7(\text{PPspruce}) + 0.161(\text{SDI}) + 0.828(\text{Stand Age} * \text{PPspruce})$$

$R^2 = 0.85$ $\text{Adjusted } R^2 = 0.82$ $\text{Root MSE} = 37.07$ $\text{Coefficient of variation} = 13.21$

With R^2 , the coefficient of determination; adjusted R^2 , the coefficient of correlation adjusted for the number of variables; Root MSE, the square root of the mean square error.

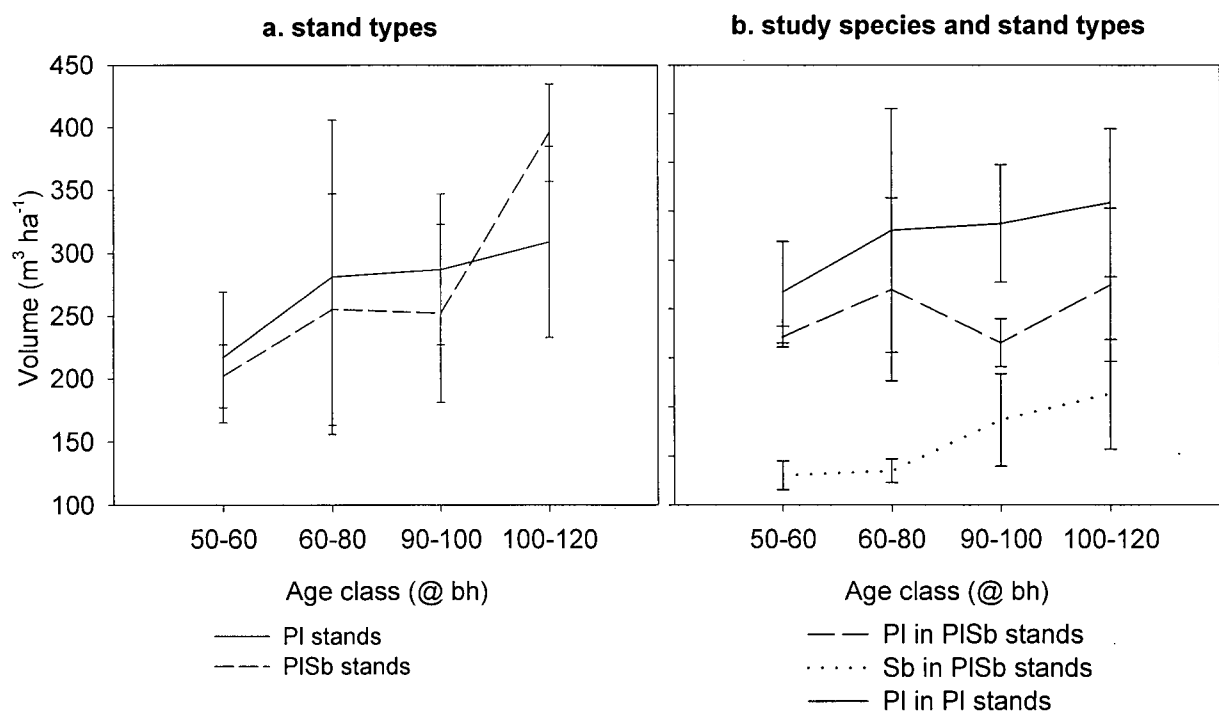


Figure 28. Mean stand volumes and standard deviations (a) for stand types and (b) study species in stand types.

Both regression analyses explained over 70% of the observed variability in stand net volume. The model using SDI instead of RD was slightly better. These models can be interpreted as follows, as a rule, as the stand ages, net stand volume increases; as density increases, net stand volume increases (Curtis et al. 1997). However, in the case of the present study, a large sample bias might have affected these relationships. The maximum density encountered in the present study was 10,000 sph, which may be below the threshold at which net volume starts decreasing. The presence of spruce in the stand initially leads to a decrease in volume, but at advanced ages, the presence of spruce improves stand volume.

The interaction term was not significant in the models (Table 15), but could be expected to be so, given the ecology and succession pattern of pine and spruce. The failure of regression analysis to convey a more biologically accurate prediction might have several causes. The first one is related to the nature of regression: the theoretical mean value of the observations lies exactly on the regression line. Fifty percent of the study stands were pure pine stands and fifty percent were stands with a spruce component ranging from 15 to 45% of the total stand basal area. The regression analysis is thus likely to be biased towards pine stands. The second explanation is related to the effect of data on the regression: as the sample stands covered only a time segment between 50 and 120 years, they could not provide data covering the whole chronosequence. The third explanation for the shortcomings of regression analysis is a failure to satisfy the primary assumption that there is a linear relationship between predicted variable and predictor variables (Neter et al. 1996). For these different reasons, it might be more reliable to use age classes and stand types and to compare different groups with an analysis of covariance (ANCOVA) (Neter et al. 1996).

Table 15. Results from the analysis of variance (Equation [13]) modelling the regression of gross stand volume from stand age, spruce proportion of stand basal area, and relative density. 'Age' represents age class, 'Type' represents stand type, Age x PPspruce represents the interaction term between these variable, RD is the relative density index (after Curtis 1982) and SDI is the stand density index after Reineke (1933), df are degrees of freedom, SS are sums of squares, MS are mean squares, F is the test statistic of the F test, and P>F is the likelihood that an equivalent amount of variation in stand volume would be explained by random chance in the population.

<i>Using RD as a density index</i>						<i>Using SDI as a density index</i>					
Source	df	SS	MS	F	P>F	Source	df	SS	MS	F	P>F
Age	1	38591	38591	15.79	0.0006	Age	1	30197	30197	21.97	0.0001
PPspruce	1	6787	6787	2.776	0.1098	PPspruce	1	2928	2928	2.131	0.1585
Age* PPspruce	1	1766	1766	0.722	0.4045	Age* PPspruce	1	186.9	186.9	0.136	0.7158
RD	1	58170	58170	23.80	0.0001	SDI	1	81719	81719	59.47	0.0000
Error	23	53782	2243			Error	23	30233	1374		
Total	27	201640				Total	27	201640			

The necessity of including density as a predictor of stand net volume resulted in the use of ANCOVA using a density index as covariate. Pine density did not significantly differ between PI stands and PISb stands. It was therefore believed that part of the effect attributed to the stand density index was in fact due to the mixed-stand factor. Since the ratio of spruce to pine stem density was fairly constant throughout the mixed-species stands (average spruce sph/pine sph = 1.79 with a standard error of 0.1), I used density indices calculated on the basis of pine alone. This would account for the variability in density encountered among stands and would assess the full influence of the mixed-stand factor on the predicted variable.

All the assumptions of the ANCOVA were satisfied. Significant differences were detected for stand gross volume among stand types and age classes ($\alpha = 0.05$) (Table 16). The age class x stand type interaction was not significant, which allowed for meaningful comparisons of both age class and stand type means. The overall models (Equations [17] and [18]) were strongly significant ($p \leq 0.000$) and of good fit, suggesting that stand type and age class explained much of the observed variation in stand gross volume and that differences between stand density explained much of the remaining variation.

The interpretation of the models suggested that for a given pine density and age, the presence of 15 to 40% of spruce basal area resulted in an increase in net stand volume. However, both models suggested that the younger the stands were, the smaller the contribution of spruce to

stand volume. While the regression concluded there was a negative effect of spruce presence on the stand, the ANCOVA tended towards a positive effect on the presence of spruce. As in the case of regression, the ANCOVA assumes a linear relationship between the predictor and the predicted variables. Despite the use of classes rather than continuous variables, the sampling was limited in the range of species composition and the range of stand ages covered. This might have resulted in apparent linearity where there is non-linearity. Pukkala et al. (1994) found that mixed-species stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) exhibited a non-linear increase in volume depending on the relative presence of each species. The contrasting effect of regression and ANCOVA are possibly explained by the limitations of the data set.

[17]
$$\text{Stand Net Volume} = 24.81 + 119.8(\text{PISb}) - 175.3(\text{Age class 1}) - 84.67(\text{Age class 2}) - 55.50(\text{Age class 3}) - 43.62(\text{PISb} \times \text{Age class 1}) - 81.84(\text{PISb} \times \text{Age class 2}) - 31.23(\text{PISb} \times \text{Age class 3}) + 28.75(\text{RDpine})$$

$R^2 = 0.66$ $\text{Adjusted } R^2 = 0.51$ $\text{Root MSE} = 61.61$ $\text{Coefficient of variation} = 21.95$

[18]
$$\text{Stand Net Volume} = -72.83 + 126.1(\text{PISb}) - 150.2(\text{Age class 1}) - 88.08(\text{Age class 2}) - 60.90(\text{Age class 3}) - 41.80(\text{PISb} \times \text{Age class 1}) - 64.54(\text{PISb} \times \text{Age class 2}) - 1.294(\text{PISb} \times \text{Age class 3}) + 0.214(\text{SDlpine})$$

$R^2 = 0.82$ $\text{Adjusted } R^2 = 0.74$ $\text{Root MSE} = 44.89$ $\text{Coefficient of variation} = 15.99$

With R^2 , the coefficient of determination; $\text{adjusted } R^2$, the coefficient of correlation adjusted for the number of variables; Root MSE , the square root of the mean square error.

Table 16. Results from the ANCOVA (Equation [14]) modelling gross stand volume as a function of age class, stand type, and relative density. 'Age' represents age class, 'Type' represents stand type, Age x Type represents age class x stand type interaction, RD is the relative density index (after Curtis 1982), df are degrees of freedom, SS are sums of squares, MS are mean squares, F is the test statistic of the F test, and P>F is the likelihood that an equivalent amount of variation in stand volume would be explained by random chance in the population.

Using RD as a density index						Using SDI as a density index					
Source	df	SS	MS	F	P>F	Source	df	SS	MS	F	P>F
RD	1	45353	45353	11.16	0.0003	SDI	1	74394	74394	36.91	0.0000
Age	3	101976	33992	8.956	0.0001	Age	3	97694	32565	16.16	0.0000
Type	1	21762	21762	5.737	0.0047	Type	1	35258	35258	17.49	0.0006
AgexType	3	5831	1944	0.512	0.4480	AgexType	3	5118	1706	0.846	0.4864
Error	19	68320	3796			Error	19	36280	2016		
Total	27	201640				Total	27	201640			

The analysis of variance, contrary to ANCOVA or regression does not assume the nature of the statistical relationship between predicted and predictor variables. Therefore, I compared the stands using an ANOVA with age classes and stand type as the predictor variables. The overall model was marginally significant ($p= 0.078$) and the predicted variables were only weakly related to the terms of the model (Table 17). This is probably due to the strong effect of density on stand volume.

Table 17. Results from the analysis of variance (Equation [15]) modelling gross stand volume as a function of age class and stand type. 'Age' represents age class, 'Type' represents stand type, Age x Type represents age class x stand type interaction, df are degrees of freedom, SS are sums of squares, MS are mean squares, F is the test statistic of the F test, and $P>F$ is the likelihood that an equivalent amount of variation in stand volume would be explained by random chance in the population.

Source	df	SS	MS	F	P>F
Age	3	63944	21215	3.659	0.0310
Type	1	12072	12072	2.345	0.1431
AgexType	3	19839	6613	1.135	0.36
Error	19	110678	5825		
Total	27	201667			

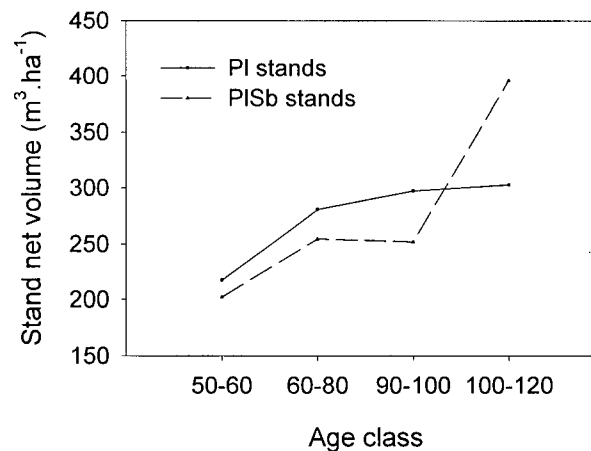


Figure 29. Least square mean net volume response across stand types for each age class after ANOVA.

In age classes 1 to 3, the net volume of pine stands was, on average, $25 \text{ m}^3 \text{ ha}^{-1}$ greater than in pine-spruce stands, but in age class 4 (>100 years @ bh) the pine-spruce stands clearly outperformed the pine stands (Figures 28 and 29, Table 14). However, these results should be viewed

with some caution as there is a large uncertainty associated with the small sample sizes. The mean net stand volume of the age class 4 pine-spruce stands was $87\text{m}^3 \text{ ha}^{-1}$ or 28% higher than of the age class 4 pine stands. While stand density declined in age class 4 pine stands, it increased in age class 4 pine-spruce stands (Figure 27) with increased spruce recruitment. Spruce trees mainly contributed to this increase and whether this notable rise in stand gross volume was a result of spruce regeneration can be partly determined by examining the merchantable volumes of pine and pine-spruce stands across time.

The difference between pine and pine-spruce merchantable stand volumes was not as large as the differences for net stand volume (Figure 30). The ANCOVA was performed as was previously described. The overall model was significant ($p < 0.05$) and explained 50 to 67% of the variation in merchantable volume. This analysis showed that merchantable volume was affected by age and pine density index with SDI performing better than RD. The presence of spruce increased the merchantable volume for a given density, but the younger the stand, the lower the contribution of spruce (Equations [19] and [20]). A given area in pine-spruce stands supports more trees, and as such, supports a higher merchantable volume than pine stands. However, stand type only marginally contributed to merchantable stand volume overall (Table 18) and over the time span considered in the present study, the presence of spruce was not a major contributor to merchantable volume due to its slow growth, despite its contribution to density. Pine density and age were the determinants of stand merchantable volume. Again, these results should be viewed with some caution due to a large uncertainty of the small sample sizes.

$$[19] \quad \text{Merchantable Volume} = 83.02 + 70.77(\text{PISb}) - 183.8(\text{Age class 1}) - 44.77(\text{Age class 2}) - 33.54(\text{Age class 3}) - 8.628(\text{PISb} \times \text{Age class 1}) - 91.53(\text{PISb} \times \text{Age class 2}) - 3.794(\text{PISb} \times \text{Age class 3}) + 18.15(\text{RDpine})$$

$$R^2 = 0.52 \quad \text{Adjusted } R^2 = 0.32 \quad \text{Root MSE} = 74.59 \quad \text{Coefficient of variation} = 32.70$$

$$[20] \quad \text{Merchantable Volume} = -45.46 + 80.67(\text{PISb}) - 179.4(\text{Age class 1}) - 58.62(\text{Age class 2}) - 46.76(\text{Age class 3}) + 4.364(\text{PISb} \times \text{Age class 1}) - 70.91(\text{PISb} \times \text{Age class 2}) + 39.49(\text{PISb} \times \text{Age class 3}) + 0.173(\text{SDIpine})$$

$$R^2 = 0.68 \quad \text{Adjusted } R^2 = 0.53 \quad \text{Root MSE} = 61.61 \quad \text{Coefficient of variation} = 27.00$$

With R^2 , the coefficient of correlation; *adjusted* R^2 , the coefficient of correlation adjusted for the number of variables; *Root MSE*, the square root of the mean square error.

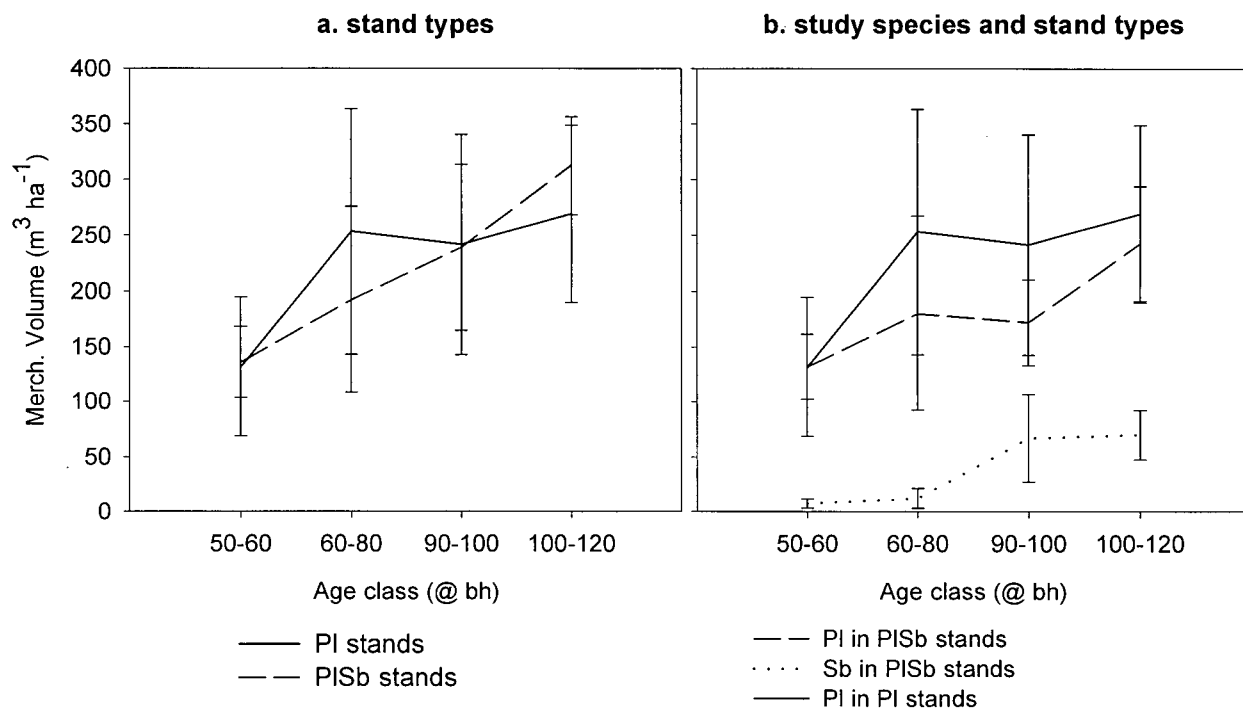


Figure 30. Mean merchantable volumes and standard deviations in (a) stand types and (b) study species in stand types.

Table 18. Results from the ANCOVA (equation [15]) modelling gross stand volume as a function of age class, stand type and relative density. 'Age' represents age class, 'Type' represents stand type, Age x Type represents age class x stand type interaction, df are degrees of freedom, SS are sums of squares, MS are mean squares, F is the test statistic of the F test, and P>F is the likelihood that an equivalent amount of variation in stand volume would be explained by random chance in the population.

<i>Using RD as a density index</i>						<i>Using SDI as a density index</i>					
Source	df	SS	MS	F	P>F	Source	df	SS	MS	F	P>F
RD	1	16891	16891	3.035	0.0985	SDI	1	48733	48733	12.84	0.0021
Age	3	95087	31696	5.696	0.0064	Age	3	108820	36273	9.556	0.0005
Type	1	6719	6719	1.207	0.2863	Type	1	19565	19565	5.154	0.0357
AgexType	3	9757	3252	0.584	0.6329	AgexType	3	10570	3523	0.928	0.4473
Error	19	100170	5565			Error	19	36280	2016		
Total	27	211913				Total	27	201640			

5 CONCLUSIONS

Climatic and edaphic conditions of the study stands were similar; i.e., all stands were influenced by the same regional climate and were associated with fresh sites. The vegetation and soil analyses as well as analyses of pine site index all suggested that the stands were associated with sites of similar site quality and had very comparable growing conditions. It was recognized that these analyses were based on a limited sample size. However, these analyses failed to disprove dissimilarity and the vegetation, site and soil characteristics were consistent among stands. Similar site qualities limited some of the shortcomings of building a chronosequence.

Pine growth was not affected by the presence of spruce in pine-spruce stands across time. The mean dbh, height, and height to live crown of all pine were not significantly different among stand types. The self-thinning of pine appears to have occurred between age classes 2 and 3, but for spruce between age classes 3 and 4. Spruce trees were notably shorter than pine trees in the younger pine-spruce stands, but the difference between mean heights of pine and spruce decreased with increasing age. Consequently a two-storied canopy developed with pine in the upper canopy. However, in age class 3 and 4 stands the strata occupied by pine and spruce overlapped, as increasing numbers of spruce trees ingressed into the upper canopy layer. The height growth of pine was faster than that of spruce, but slower after age 100. This accounted for the two-storied canopy of lodgepole pine-black spruce stands.

The height and diameter growth of the largest-dbh pine trees was not noticeably affected by the presence of spruce, which indicated that competition with spruce was minimal. However, the height and growth patterns for dominant pine trees were not consistent among age classes, which was attributed to differences in the history of density among stands. In contrast to pine, the tallest spruce trees displayed a very consistent height growth pattern. Note that these conclusions are based on a small number of largest-dbh trees and should be viewed with some caution. More extensive sampling including trees from different canopy positions will be required to establish whether pine growth is similar between stand types.

Volume comparisons showed differences between age classes and stand types. The younger pine stands had a greater volume than pine-spruce stands. This difference was not significant when stands were compared using regression analysis, ANCOVA and ANOVA. However, the oldest pine-spruce stands had a greater gross volume ($87 \text{ m}^3 \text{ ha}^{-1}$ or 28%), as well as higher merchantable volume ($44 \text{ m}^3 \text{ ha}^{-1}$ or 16%) than pine stands. In the oldest age class, for equivalent pine stem density, pine-spruce stands yielded more volume, which could be attributed to a decrease in pine growth but not in spruce growth. However, the small sample size and high variability associated with density also calls for caution when interpreting the stand volume analyses.

In summary, stand structure and stand growth differs between pine and pine-spruce stands primarily as a result of intrinsic species growth patterns and density, rather than by interspecific competition. Productivity between stand types did not follow the same pattern through time. Volume yield, a measure of productivity, is a function of many different parameters among which, age, species composition and density are some of the most important. As the effect of these factors also differs between species, linear statistical methods may fail to capture the dynamics of mixed-species stand development.

6 MANAGEMENT IMPLICATIONS

It should be made clear that the following sections deal with speculations and implications that can be drawn from my findings. Note that these are not intended as recommendations to industry *per se*, rather these are intended as hypothetical scenarios. Given my data, these ideas could not be adequately addressed and would require further testing. However, the results of my research and those of previous studies provide reasonable grounds for extension and extrapolation beyond my findings.

6.1 Increased Volume Production of Natural Mixed-Species Stands

This study showed that the development of pine-spruce stands is probably related to the specific responses of each species to density, as well as their intrinsic growth rates. When the management objective is timber production and harvesting is planned for the period beyond 100 years (@ bh), it is suggested that unmanaged, fire-origin, even-aged pine-spruce stands on "d" (Labrador tea-mesic) ecosites would provide greater net stand volume and greater merchantable volume than pure pine stands. Extrapolation of the height, diameter, and volume growth for pine and spruce in pine-spruce stands beyond the age of 120 years (@ bh) suggests that the volume of pine-spruce stands will continue to increase. Although this conjecture is based on the analyses of a limited sample size, it is supported by the chronosequence study of Brisco (2001) in the same study area.

According to Brisco (2001), there was no substantial decrease in pine site index with increasing age, and the number of pine trees stabilized to fewer than 2,000 stems per hectare by age 150 (@ bh) (compared to about 1,800 stems per hectare in the age class 4 stands in the present study). However, the radial increment of pine decreased around 200 years (@ bh). The density of the spruce component in the stand canopy reached a maximum of about 3,000 stems per hectare at age of 100 years (@ bh) (compared to about 3,200 stems per hectare in age class 4 pine-spruce stands of this study). In Brisco's study, spruce heights increased more rapidly than pine,

overtopping pine by the age of 200 (years @ bh), and stabilizing at about 22 m at an age of 200 years (@ bh) (see also Horton 1956; Horton and Lees 1961).

In the present study, dominant spruce trees (mean top height = 15.3 m) have not yet approached the height of dominant pine trees (mean top height = 19.7 m). In view of the complementary results of this study and Brisco (2001), an increase in timber production in pine-spruce stands on d ecosites could be expected up to the age of 200 (years @ bh), as height and radial growth of both pine and spruce may continue without a substantial decrease (Figure 31). However, further testing of volume in advanced age classes is required to validate this hypothesis. If increased volume in pine-spruce stands is established, capture of the increased volume of pine-spruce stands would imply a longer rotation than 80 years and would require (i) determining what will be the best end product for spruce timber, and (ii) determining the economic feasibility for required changes in the present harvesting and wood processing technologies.

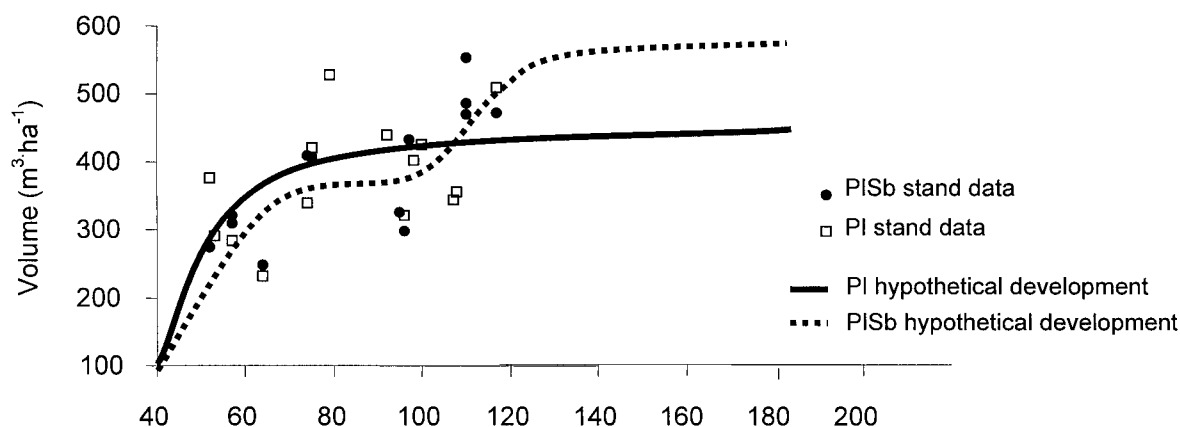


Figure 31. Hypothetical development of stand volume with time (dotted line - PISb stands, plain line - PI stands; dots represent actual data point from the sampled stands). This figure is not based on an existing model, rather on a priori expectations

6.2 Increase Volume Production Through Silviculture

It may be possible to increase timber production of pine-spruce stands on d-ecosites in managed stands prior to 100 (@ bh) by eliminating excessive initial stand density. However, it is difficult to predict how much earlier this gain would occur due to uncertainties about the development

of the spruce component. Clearly, establishment of an operational trial would be desirable for inquiring into this issue. After harvesting unmanaged stands, both pine and spruce should be established at the same time either naturally or by planting to the desired stocking standards. The target standard for pine in the Boreal White and Black Spruce zone of BC is 1,200 well-spaced seedlings per hectare. However, there is uncertainty about the desired stocking standard for the spruce component. Using the relative proportion of spruce and pine in the age class 4 pine-spruce stands in relation to the stocking target for pine, it appears that the desired number of spruce seedlings is in the range from 1,200 to 2,000 per hectare. In view of the fact that the establishment of pine regardless of regeneration method is expected, relying on timely natural regeneration of spruce could be risky and often not feasible (especially in the absence of seed source) and therefore, is not recommended. Spruce could be established by planting following a spatial pattern that would provide for the minimum growth suppression by pine (Figure 32). Such a pattern, referred to as a systematic-individual tree distribution pattern, was previously applied for establishment of mixed-species stands of shade-tolerant western red cedar and shade-intolerant black cottonwood (McLennan 1990). In this operational trial, results indicated that mixed-species stands yielded increased net volume compared to single species stands over a 20-year period.

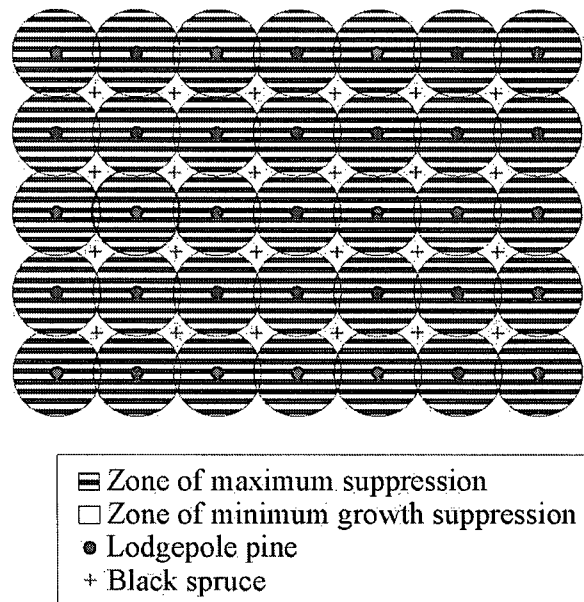


Figure 32. Hypothetical projection of the zone of minimum growth suppression for black spruce under the canopy of lodgepole pine (adapted from McLennan, 1990).

6.3 Age-Class Goals and Age-class Imbalance

On Weldwood land, the forest age-class structure is complicated by a strong imbalance, which impedes harvest planning. The current age-class distribution in the Upper Foothills is skewed, with the younger age classes having less area than other age classes. Consequently, the company is likely to harvest older stands for the coming years. The present study indicated that lodgepole pine and black spruce mixed-species stands are likely to yield a high volume of timber beyond 100 years. Provided with further evidence of this increased yield, Weldwood may be able to lower the cap presently imposed on pine-spruce stand yields by Alberta Forest Services. As part of the biodiversity/conservation requirement of the new legislation in Alberta (AFCS 1997), forest companies are asked to maintain a variety of stands with different age-classes. Whether it is to offset the age-class imbalance or whether it is to provide older stands for conservation purposes, pine-spruce stands could allow the harvest of significant volumes with long rotations.

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APPENDICES

6.4 Appendix 1. Height growth tables for dominant pine trees and largest-dbh spruce trees

Appendix 1a. Average height growth (m) of dominant pine trees and the largest spruce trees in the age class 1 stands (cut-off at 60 yrs @ bh).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	1.03	1.36	0.44
10	2.40	2.92	0.97
15	3.88	4.49	1.54
20	5.39	6.01	2.14
25	6.90	7.48	2.77
30	8.37	8.88	3.41
35	9.81	10.20	4.07
40	11.20	11.45	4.74
45	12.53	12.63	5.42
50	13.80	13.73	6.11
55	15.02	14.76	
60	16.17	15.73	

Appendix 1b. Average height growth (m) of dominant pine trees and the largest spruce trees in the age class 2 stands (cut-off at 75 years @ bh).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.84	0.76	0.57
10	2.09	1.98	1.19
15	3.36	3.26	1.82
20	4.54	4.48	2.46
25	5.57	5.58	3.11
30	6.47	6.53	3.76
35	7.22	7.36	4.42
40	7.86	8.05	5.09
45	8.39	8.64	5.76
50	8.82	9.13	6.43
55	9.18	9.54	7.11
60	9.48	9.87	7.79
65	9.72	10.15	8.01
70	9.92	10.37	
75	10.13	10.88	

Appendix 1c. Average height growth (m) of dominant pine trees and the largest spruce trees in the class 3 stands (cut-off at 95 years @ bh).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	1.03	0.43	0.21
10	2.52	1.18	0.56
15	4.13	2.07	1.00
20	5.73	3.02	1.51
25	7.28	3.99	2.07
30	8.75	4.95	2.67
35	10.13	5.88	3.31
40	11.40	6.77	3.99
45	12.57	7.62	4.70
50	13.65	8.41	5.44
55	14.63	9.15	6.20
60	15.52	9.84	6.98
65	16.33	10.48	7.78
70	17.06	11.07	8.60
75	17.72	11.62	9.44
80	18.32	12.11	10.29
85	18.85	12.57	11.16
90	19.33	12.99	12.04
95		13.38	12.93

Appendix 1d. Average height growth (m) of dominant pine trees and the largest spruce trees in the class 4 stands (cut-off at 115 years @ bh).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.79	1.13	0.57
10	1.83	2.59	1.25
15	2.93	4.11	1.98
20	4.06	5.59	2.72
25	5.18	7.01	3.48
30	6.29	8.33	4.24
35	7.37	9.57	5.00
40	8.42	10.70	5.76
45	9.43	11.74	6.51
50	10.40	12.69	7.26
55	11.34	13.56	8.00
60	12.23	14.35	8.73
65	13.08	15.06	9.45
70	13.90	15.71	10.17
75	14.67	16.29	10.87
80	15.41	16.82	11.56
85	16.11	17.29	12.24
90	16.78	17.72	12.91
95	17.41	18.11	13.57
100	18.01	18.45	14.22
105	18.58	18.77	14.86
110	19.12	19.05	15.49
115	19.63	19.30	16.10

Appendix 1e. Average height growth (m) of dominant pine trees and the largest-dbh spruce trees up to 60 years (@ bh) based on all-stands (cut-off at 50 years @ bh for spruce).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.98	1.16	0.50
10	2.27	2.36	1.07
15	3.61	3.54	1.66
20	4.95	4.70	2.27
25	6.23	5.82	2.90
30	7.46	6.90	3.54
35	8.61	7.94	4.18
40	9.68	8.95	4.84
45	10.68	9.92	5.50
50	11.60	10.86	6.17
55	12.46	11.76	
60	13.24	12.63	

Appendix 1f. Average height growth (m) of dominant pine trees and the largest-dbh spruce trees up to 75 years (@ bh) based on all-stands (cut-off at 60 years @ bh for spruce).

Age (@ bh)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	1.01	0.96	0.49
10	2.26	2.06	1.05
15	3.53	3.16	1.65
20	4.78	4.24	2.27
25	5.98	5.28	2.91
30	7.11	6.26	3.57
35	8.17	7.20	4.24
40	9.16	8.08	4.92
45	10.08	8.91	5.60
50	10.93	9.70	6.30
55	11.71	10.43	7.00
60	12.43	11.11	7.71
65	13.10	11.75	
70	13.71	12.35	
75	14.00	12.93	

6.5 Appendix 2. Basal area growth tables for dominant pine trees and largest-dbh spruce trees

Appendix 2a. Average basal area growth (cm²) based on age class 1 (50 - 60 years @ bh) stands for dominant pine trees and largest-dbh spruce trees by stand type.

Age (yrs)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.00	0.41	0.00
10	5.10	2.26	0.50
15	7.78	2.61	1.55
20	9.70	3.07	3.86
25	13.12	5.27	8.35
30	20.34	10.83	15.93
35	33.64	21.37	27.52
40	55.30	38.52	44.02
45	87.60	63.90	66.34
50	132.83	99.13	95.40
55	193.26	145.83	.
60	271.18	205.64	.

Appendix 2b. Average basal area growth (cm²) based on age class 2 (60 - 80 years @ bh) stands for dominant pine trees and largest-dbh spruce trees by stand type.

Age (yrs)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.00	0.00	0.00
10	4.33	4.44	0.12
15	6.30	6.83	4.04
20	6.38	6.79	11.00
25	6.28	6.13	21.27
30	7.70	6.64	35.11
35	12.35	10.13	52.79
40	21.95	18.38	74.57
45	38.21	33.21	100.72
50	62.82	56.41	131.51
55	97.51	89.78	167.19
60	143.98	135.12	208.05
65	203.95	194.22	.
70	279.11	268.90	.

Appendix 2c. Average basal area growth (cm²) based on age class 3 (90 - 100 years @ bh) stands for dominant pine trees and largest-dbh spruce trees by stand type.

Age (yrs)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.00	0.04	0.00
10	3.13	1.23	0.00
15	8.51	1.97	0.00
20	11.02	2.62	0.00
25	11.53	3.54	0.00
30	10.91	5.11	1.83
35	10.04	7.67	5.00
40	9.80	11.60	9.40
45	11.05	17.26	15.13
50	14.67	25.02	22.28
55	21.54	35.23	30.95
60	32.52	48.27	41.24
65	48.49	64.49	53.26
70	70.33	84.26	67.08
75	98.91	107.95	82.82
80	135.09	135.92	100.57
85	179.76	168.53	120.43
90	233.79	206.15	142.50
95	298.05	249.13	166.87

Appendix 2d. Average basal area growth (cm²) for age class 4 (100 - 120 yrs @ bh) stands for dominant pine trees and largest-dbh spruce trees by stand type.

Age (yrs)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.00	0.00	0.00
10	0.00	0.88	0.00
15	2.43	7.73	0.00
20	5.16	12.77	1.08
25	8.23	16.41	3.03
30	11.84	19.05	5.74
35	16.20	21.10	9.28
40	21.50	22.97	13.71
45	27.95	25.05	19.09
50	35.75	27.76	25.47
55	45.11	31.51	32.92
60	56.21	36.68	41.49
65	69.28	43.71	51.26
70	84.50	52.97	62.26
75	102.08	64.90	74.58
80	122.22	79.88	88.25
85	145.12	98.32	103.36
90	170.98	120.64	119.94
95	200.02	147.22	138.08
100	232.41	178.49	157.81
105	268.38	214.85	179.21
110	308.12	256.70	202.33
115	351.83	304.44	227.23

Appendix 2e. Average basal area growth (cm²) based on the stands of all age classes up the age of 60 years (@ bh) for dominant pine trees and largest-dbh spruce trees by stand type.

Age (yrs)	Pine in pine stands	Pine in pine-spruce stands	Spruce in pine-spruce stands
5	0.01	0.01	0.00
10	0.57	0.37	0.04
15	2.57	1.58	0.72
20	6.24	3.84	3.02
25	12.16	7.80	7.71
30	20.61	14.42	14.88
35	30.10	22.39	24.92
40	43.34	37.46	37.13
45	64.09	60.37	53.57
50	86.47	80.72	73.22
55	122.22	108.22	.
60	174.40	148.77	.