WOOD QUALITY OF TREMBLING ASPEN (*Populus tremuloides* Michx)
AND WHITE SPRUCE (*Picea glauca* (Moench) Voss) IN THE BOREAL MIXEDWOOD FOREST

by

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Abstract

The boreal forest is the most widespread forest type in Canada, with a large percentage represented by mixedwood forests of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx). It serves as not only a vast ecological reserve, but also as the supply source for forest-based industries. A better understanding of the interactions between the different species and their affects on productivity and wood quality traits helps create a more efficient industry that better utilizes the available resources, and concurrently preserves as much forest of ecological reserves and societal vistas. In this study, three sites composed of trembling aspen and white spruce, with varying compositions (one composed of mainly aspen, one of mainly spruce, and a mixed site with both species) were compared to determine how the presence of one species affects the growth and wood quality traits of the other. Four main wood quality traits were examined: wood density, microfibril angle (MFA), fibre traits (fibre length, fibre width and fibre coarseness) and cell wall chemistry. Along with site comparisons, social classes were determined for each site in an attempt to provide a more in-depth comparison across sites.

Wood density showed very little variation among sites for both species, with only significant variations occurring between social classes. The aspen site showed statistically lower MFAs than the aspen from the mixed site, however, no differences were observed between the spruce from the mixed and spruce sites. Fibre length, width and coarseness were higher in the pure species sites for both trembling aspen and white spruce. In terms of cell wall composition, there were no differences in carbohydrate contents across sites for both species. Lignin content did vary, with the aspen site possessing higher lignin content than the mixed site, while for spruce the spruce site showed a lower lignin content. Overall, the use of social classes did not
refine the characterization of site, producing similar results to those obtained when comparing trees by site, regardless of class.
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To my father (in memoriam)
Chapter 1: Introduction

The boreal forest is the most widespread forest type in Canada (Figure 1). It is composed of species such as balsam poplar, white birch, jack pine, blacks spruce and balsam fir. In addition, a large percentage is also represented by mixedwood forests of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx).

Figure 1. Forest Regions of Canada. Boreal forest regions represented by the 3 shades of green. Source: Natural Resources Canada – Canadian Forest Services (2009)

A number of studies have attempted to understand the effects of single and mixed species stands dynamics of the boreal forest. However, most of these studies focused on identifying the effects
of species distribution on productivity (such as yields in basal area), nutrient cycling, and rotation lengths (Kelty, 1992; Man & Lieffers, 1999; MacPherson, 2001; Green, 2002; Chen, 2003; Kelty, 2006; Filipescu, 2007; Comeau, 2009; Cortini, 2012). Over the past few years, wood attributes have emerged as an added characteristic of interest. This initial interest was focused on the white spruce wood quality, as traditionally aspen has attracted little commercial interest compared to white spruce. As such, the desire to promote white spruce silvicultural operations and regeneration focused on the establishment and growth of relatively pure stands of white spruce. Stuart and Smith (1995) called this an “attempt to unmix the mixedwood forests”. However, over time aspen fibre has become economically important due to recent advances in pulping and strand-board technology, adding incentives to examine the productivity of this mixedwood species (Man and Lieffers, 1999). In addition, aspen and the other *Populus spp.* have been identified as key potential tree crops for biofuels applications.

The objective of this thesis is to elucidate the effects of the ecological combining ability of trembling aspen and white spruce specific to wood quality of both species. Although some wood quality characteristics are inherit to a particular species, the same traits are also influenced by tree growing conditions. Through the analysis of wood quality traits such as wood density, microfibril angle, fibre traits and cell wall chemistry, this study attempts to elucidate what effects the presence or absence of one species has on the wood quality of the other.

### 1.2 Mixed species vs. single species stands

There has been much debate over what is the best way to reforest an area that has been cleared, either by autogenic disturbance (such as fire, landslides, wind throw, etc.) or allogenic activities (clearcut, thinning, etc.). Among the many considerations that have to be taken into account
when reforesting and managing the landbase is the use of a monoculture or a mixed species plantation. Both have their advantages and disadvantages, and it is hard to distinguish which is the better of the two without *a priori* knowledge of the long term priorities of the stand. For example, is the long term priority wild life management, biodiversity, carbon sequestration, water quality, desirable wood traits or productivity?

The reasons why monocultures are favored over mixed species stands are well understood and documented – mainly the ability to concentrate all site resources on the growth of one species with the most desirable characteristics. However, the use of mixed species stands may generate long term benefits. The goal of using mixed species is to strategically combine particular species to produce specific interactions that will increase stand-level productivity or individual tree growth rates. Other objectives might include the harvest of products from different species on different rotations, reducing the potential risks of changing markets, reducing potential insect or disease impacts, or any combination thereof (Kelty, 2006).

Whenever natural regeneration occurs, the resulting forest will be composed of several species. Thus, one might consider that mixed species stands better mimic the complex interactions and processes of natural regeneration, forest succession and site related attributes, and therefore the most productive choice. According to Smith (1986), “the most successful mixed plantings are stratified mixtures composed of faster growing shade intolerant species above slower starting shade tolerant species”. As the faster, shade intolerant trees establish, they alter the stand in ways which allow tolerant trees to develop. This type of forest succession model follows the ideals of relay floristics, where one species changes the condition in a way that favors the establishment of another species.
There are other reasons for using mixed species stands over single species stands. For example, it is possible to shorten rotation lengths, increase basal area, as well as minimize the expense involving clear cutting, planting, and competition control (Lieffers, 1996; Greene et al., 2002; Comeau et al., 2009). When compared to single species stands, mixed stands may have a higher, equal or lower productivity; for example, differential resource use among the species in the mixture may lead to a higher productivity (Assman, 1970; Smith, 1986; Vandermeer, 1989). However, the mixture may exhibit equal or lower productivity if the total resources are divided among the composing species (Kelty, 1992; Smith et al., 1997).

There is, however, much controversy regarding the most appropriate strategy for reforestation. Although the use of mixed species stands seems to closely resemble the natural regeneration process and forest succession, it does not necessarily follow that mixed species stands are more productive. Chen et al., (2003) stated that “there is no solid evidence that mixed species stands are more productive than single species stands”. On the other hand, according to Comeau et al., (2009), “experiments on agricultural plants suggest that productivity gains may be obtained in mixed species stands because they have different patterns of resource use (competition reduction), and may utilize resources more fully and in a non-competitive way.”

Unfortunately, studies on forest ecosystems and their productivities are difficult to undertake due to the fact that the ideal scenario would be even-aged, mixed and single species stands grown under the same biogeoclimatic conditions (soil conditions, nutrients, climatic patterns, water regime, etc.). This approach, however, is impractical and nearly impossible to accomplish since differences in sites qualities (macro and micro) will always be present. And, it is well known that the effect of one species on the productivity of another species is directly related to the site index (Smith, 1986). Filipescu and Comeau (2007) found that the relationship
between spruce growth and aspen competition are site-specific in stands that are less than 20 years of age. However, species mixtures with apparent ecological combining ability may not always produce higher yields, as inappropriate species proportions and densities, spatial arrangements or site conditions where resource limitations is not overcome by the chosen species may impact the efficacy of the combining ability (Kelty, 1992). Due to the lack of appropriate sites in which these studies may be conducted, it is feasible to study existing stands with these qualities and compare pure stands of species with their mixtures (Green et al., 2002). One must identify and study existing natural stands to better elucidate the effects of mixed species when compared to pure stands of a desired species (Brown, 1992; Burkhart & Tham, 1992; MacPherson et al., 2001).

1.2.1 Trembling aspen and white spruce stands

The boreal mixedwood forest is the most widespread forest type in Canada (Rowe, 1972) with a substantial portion being composed of trembling aspen and white spruce. Following a disturbance these stands are initially dominated by aspen, and with time the extent of white spruce recruitment in the understory varies with spruce seed source and seedbed conditions (Lieffers et al., 1996). Once established, spruce will eventually overtop and dominate the aspen. The practicality of an approach to manage stands allowing the development of mixtures of spruce and aspen is partially dependent on the ability of such stands to produce large quantities of aspen and spruce fibre (MacPherson et al., 2001). Over the years there have been some controversies over whether or not a mixed white spruce/trembling aspen stand would be more productive than a pure stand of either species.
Kabzems and Senyk (1967) reported higher annual wood increments for an 80-year old mixed aspen-spruce stand than a 90-year old spruce stand (1.33m\(^3\)/ha vs. 1.05m\(^3\)/ha, respectively). When comparing aspen stands with and without a spruce understory, MacPherson et al., (2001) found that the mixed plots contain approximately 10% more biomass than pure aspen stands. When comparing the productivity of the aspen alone, the pure aspen plots possessed 12.9% more biomass than the aspen in the mixed plots. Conversely, the authors were unable to produce statistical evidence that the addition of a spruce understory was the main cause of the observed reduction in the aspen productivity in the mixed plots. The study concluded that “there was a clear increase in total biomass and periodic annual increment in the mixed species plots, confirming the superior productivity of mixedwood stands.”

Day and Bell (1988) have also shown that fully stocked and tended plantations of white spruce have much higher productivity than unmanaged stands of spruce in association with aspen. However, no comparison was made of mixed and pure stands under the same treatment regime.

1.3 Ecological combining ability of trembling aspen and white spruce

In order for a stand composed of mixed species to manifest in high productivity as a result of the interactions between the species, two basic principles must occur: competitive reduction and facilitative production (Harper, 1977; Vandermeer, 1989; Kelty, 2006). When one, or ideally both, of these principles occur, then the stand as a whole will benefit greatly and productivity levels will increase. Whenever the mix of two or more species results in both competitive reduction and facilitative production, the species are considered to have an “ecological combining ability” (Harper, 1977).
Competitive reduction takes place when two species that occupy the same niche (i.e. a forest stand) have different needs, and therefore compete less with each other for resources (Vandermeer, 1989; Kelty, 1992). Since each species require different resources, the individual species will not be competing and as such the entire stand will be more efficient since a wider range of resources are concurrently being utilized. The key concept to achieve this efficiency, however, is to combine species that differ in characteristics such as shade tolerance, height growth rate, crown structure (particularly leaf area density), foliar phenology and root depth and phenology (Kelty, 2006).

Facilitative production occurs when one species positively affects the growth of a second species (Vandermeer, 1989; Man & Lieffers, 1999). This improvement in development occurs due to enhanced environmental and nutritional conditions that only take place in the presence of the second species. These enhanced conditions will result in benefits such as increased growth, reduced mortality, and higher nutrient availability. Trees that create these favorable conditions for another species are called “nurse trees”. The greatest use of facilitative production in forestry has been through the combination of nitrogen fixing tree species (species with root symbionts that fix atmospheric nitrogen) and non-fixing tree species, resulting in active growth of valuable timber species that show substantial growth responses to increased nitrogen availability (Kelty, 2006).

1.3.1 Competition reduction in trembling aspen / white spruce stands

Competition reduction through differential use of resources may be associated with partitioning of both above-ground (mainly light) and below-ground (nutrients and water) resources (Man & Lieffers, 1999). These interactions can potentially increase productivity as there are reduced
crown (shade tolerance separation, physical separation of canopies, phenological separation and successional separation) and root (physical separation of roots, phenological separation, and successional separation) competition interactions.

As a consequence of the differences in shade tolerance of aspen and white spruce, during the early stages of development aspen and white spruce are generally stratified. Aspen will occupy the upper canopy, while spruce is found in the lower canopy. Comparatively, the foliage of shade-tolerant species has a lower compensation and saturation points for photosynthesis, but higher light use efficiency than shade-intolerant foliage. Due to morphological and physiological adjustments, shade-tolerant trees have an enhanced ability to fix carbon at low light conditions. (Boardman, 1977). Therefore, a stand composed of a shade-intolerant species in the upper canopy and a shade-tolerant species in the lower canopy uses a greater portion of the available light compared to a monoculture of a single shade intolerant species (Kelty, 1992). Following this line of reasoning, mixed stands of aspen in the main canopy and white spruce in the understory should have higher light use efficiency than a pure aspen or white spruce stand. However, there will be increasing resource requirements of the understory white spruce as it grows, especially once it becomes co-dominant with aspen, at approximately 70-years of age (Man & Lieffers, 1999).

The physical separation of canopies may also create interactions that are likely to generate competitive reduction. Inter-crown friction by tree sway in response to wind can cause the loss of leaves and even branches, for example. This effect is heightened in areas dominated with mono-layered forests with trees in similar sizes, such as a monoculture (Putz et al., 1984). Therefore, a mixed aspen-spruce canopy can, in essence, reduce the amount of leaf loss due to wind and tree sway.
In aspen-dominated boreal mixedwoods, a substantial amount of light is transmitted to the understory trees in spring and autumn when overstory aspen is leafless (Constabel and Lieffers, 1996). Understory spruce is photosynthetically active during these periods, and therefore able to use this light resource (Man & Lieffers, 1999). This phenological separation leads to more light being utilized throughout the spring and autumn.

As previously discussed, following a natural or man-made disturbance, shade-intolerant trees will be the first to establish, and these trees will gradually tend to be replaced by shade-tolerant trees over time. An aspen stand achieves full leaf coverage in 5 to 15 years, after which leaf area declines as the stand matures (Peterson & Peterson, 1992). In Alberta, volume production peaks at around 50-80 years for aspen stands and at 90-150 years for white spruce stands (Man & Lieffers, 1999). A stand dominated by aspen in the early stages and then shifting to spruce should have higher overall volume production than stands of either species alone. The same authors note that this objective may require harvesting of the aspen before the spruce is mature, however.

In terms of reduced root competition, soil resources (water and nutrients) can be partitioned through root stratification (different rooting depths and structures), differential nutrient requirements, and different root activity (Man & Lieffers, 1999). Root excavations in Alberta have clearly shown different rooting patterns between aspen and spruce: white spruce possesses fine roots that are generally within the first 50 cm of the soil, while many aspen fine roots can reach depths of 100 cm (Strong & La Roi, 1983). Despite the information on the fine root structure, it has not been shown if this vertical separation is important in reducing the competition for nutrients and/or increasing the total productivity of the mixed stand.
1.3.2 Facilitative production in trembling aspen / white spruce stands

Facilitative production can be defined as the improved growth of one species as a direct influence of another species. This improvement may be a result of improved environmental conditions for growth, improved growth quality, and reduced growth loss due to pest attacks, competition and wind throw (Vandermeer, 1989). Man & Lieffers (1999) identified the following interactions between aspen and white spruce which might lead to facilitative production: improved litter decomposition and nutrient cycling, amelioration of environmental extremes, control of competitors, reduction of pest attacks, and increase of wind stability.

In the boreal forests, stands that are dominated by conifers inherently display a slow rate of litter decomposition and a slower nutrient cycle due mainly to the low soil temperature, the high carbon to nitrogen ratio, or inhibitory effect of conifer litter on microbial activity (Prescott et al., 1989). The presence of a hardwood with a high nutrient content in its litter, and low or no concentration of inhibitors to microbial activity should improve soil quality provided when nutrients are in short supply (Man & Lieffers, 1999). Aspen has the ability to capture soil nutrients and recycle it to the litter, as the leaves of aspen contain high nutrient concentrations and are easier to decompose than spruce foliage (Peterson & Peterson, 1996). According to the authors, the rapid growth of juvenile aspen in the early stages of stand development may be beneficial in capturing and eventually cycling nutrients that might otherwise be lost due to leaching.

Another attribute that aspen can have in improving growth of white spruce is to serve as shelter trees. A shelter tree is a rapid growing pioneer species planted first to aid the growth of a high value late successional species. White spruce, as a late successional tree, is sensitive to
environmental extremes, especially in its juvenile stage. Aspen shelter trees reduce frost frequency and severity while increasing relative humidity (Man & Lieffers, 1999). The authors found that white spruce seedlings under an aspen canopy maintain healthy growth while similar seedlings growing in open conditions show reduced shoot growth and needle discoloration, especially in spring and fall when night frosts are more frequent.

An aspen overstory will also reduce the frequency of plants that compete with white spruce seedling. Plants such as red raspberry (*Rubus idaeus*) and bluejoint reedgrass (*Calamagrostis Canadensis*) compete significantly with white spruce in clear cut areas (Lieffers et al., 1996). However, the presence of an aspen overstory is very effective in controlling competitors while allowing the establishment of the shade-tolerant spruce (Man & Lieffers, 1999). Finally, a mixed species stand of aspen and white spruce has higher wind stability than a monoculture or either species. There is very little wind throw of white spruce under the shelter of aspen stands when compared to pure spruce stands. On the other hand, white spruce left after the removal of overstory aspen is particularly susceptible to blow down (Brace Forest Services, 1992). If the intent is to remove the aspen from a mixed species stand prior to the removal of white spruce, special measures should be taken to reduce the effects of blow down, such as leaving a few shelter trees in the stand.

### 1.4 Wood quality traits

Wood properties are a result of the combination of three characteristics: macroscopic morphology, wood anatomy and chemical composition (Pereira et al, 2003). The macroscopic morphology of wood consists of the presence, extend and distribution of different types of wood tissue, such as reaction wood, growth rings, juvenile wood, and knots. The anatomical aspects
include the types of cells and biometry, as well as the proportions of each comparatively. The chemical composition of wood, the cell wall components and extraneous materials, also has a direct influence on the properties of wood. These characteristics and their relationships to each other establish the overall wood quality of a tree, stem, or piece of lumber.

Wood quality may be defined in the broad sense as the combination of all wood characteristics that affect the recovery chain and the final value of the end product. Mitchell (1961) defined wood quality as “the resultant of physical and chemical characteristics possessed by a tree or a part of a tree that enable it to meet the property requirements for different end products”. Several wood characteristic can be influential in determining the wood quality of a stem, such as wood density, earlywood to latewood ratio, and presence of knots, to name a few. In addition to growth rates, measuring wood quality traits such as wood density, fibre length, fibre coarseness, microfibril angle and cell wall chemistry may be a valuable tool when selecting superior clonal material (Mansfield and Weinseisen, 2007). For this study, wood quality of each species is expressed as a function of wood density, microfibril angles, fibre traits (mainly length, width and coarseness) and cell wall chemistry.

1.4.1 Wood Density

Wood density has long been considered the most important factor affecting wood quality (Zobel, 1961; Yanchuk et al., 1983; Bamber and Burley, 1983; Butterfiend, 2003). Through an estimate of wood density, one can learn a great deal about the nature of the wood sample. This makes wood density an excellent trait to predict end use characteristics of wood (Jozca and Middleton, 1995; Morreira, 1999; Pot et al., 2002; De Araujo, 2008). Wood density is relatively easy to determine and is well correlated to many other physical properties, including strength, stiffness
and performance in many uses. Density also affects the shrinking and swelling behavior of wood, although this relationship is not as direct as in the case of strength properties (Saranpaa, 2003). Wood density is also a useful indicator of pulpwood quality because of its relationship to fibre properties, such as cell wall thickness (Da Silva Perez et al., 2003). It is generally the main wood quality attribute considered by industry, since higher values are correlated to stronger woods and higher pulp yields.

Although there is great variation in wood density among species, among individuals of the same species, and within different areas of the same tree, the density of solid wood itself (i.e. the cell wall material of fibres and tracheids) is considered to be relatively consistent for all species - 1.5 g/cm$^3$. Therefore, wood density may be considered as a measure of the total amount of cell wall substance in a set volume of wood (Burger and Ritcher, 1991). Wood with thicker cell walls has a higher density than the same volume of wood with thinner cell walls. Cell wall thickness is species related, but variations between early and latewood fibres, and between corewood and outerwood cells from the same position between each growth ring can often be very significant. Latewood cells frequently have much thicker walls than earlywood cells and the early wood cells of the outerwood rings may have thicker walls than those in the corewood (Butterfield, 2003). For hardwoods, vessel diameter and frequency tend to be inversely proportional to wood density. Thus, wood that has a relatively high fibre to vessel ratio yields more dense wood than one with a lower ratio (Savidge, 2003).

As discussed, density is highly regarded as the most significant factor in the assessment of wood quality. According to Bamber and Burley (1983) "of all the wood properties, density is the most significant in determining end use as it has considerable influence on wood strength, machinability, conversion, acoustic properties, wearability, paper yield properties and probably
many other”. This consideration of density as the over-riding determinant of wood quality is the consequence of two factors: firstly it is valid as a generalization, and secondly it is a relatively cheap and easy parameter to measure (Walker and Wollons, 1998). However, the same authors state that density on its own is not a self-sufficient index of wood strength. According to Araujo (2007), the macroscopic structures of wood and its chemical composition should also be taken into account when considering the mechanical properties of wood. Therefore, it is important to complement the insights that wood density creates with additional wood quality traits.

1.4.2 Microfibril Angle

Of the three layers that compose the secondary cell wall, the S₂ layer is the thickest (from 3 to 15 times thicker than the S₁ and S₃ layer combined). The S₂ layer carries most of the axial loading in fibres with the S₂ mean microfibril angle having an inverse relationship to the axial stiffness of the cell (Butterfield, 2003). Microfibril angle (MFA) is an estimate of the mean angle of the cellulose microfibrils of the S₂ layer of the cell wall relative to the longitudinal orientation of the fibre.

MFA is significantly influenced by physiological age (Donaldson, 2008). It is now accepted that the large microfibril angles common to the first few growth rings of a vertical stem are the major cause of low stiffness in the juvenile wood, or corewood. Corewood is generally described as the wood of the first few growth rings that shows the juvenile characteristics of short fibre lengths and large microfibril angles (Walker and Butterfield, 1996). Once established, these large angles appear to take several years to decline before cells of high stiffness are produced. Over time, the mean microfibril angle declines with radial growth of the stem, unless reaction wood is formed as a result of asymmetric stem loading caused by lateral branches or
other forces such as a strong prevailing wind from one direction or tree inclination (Butterfield, 2003).

The orientation of the microfibrils contributes to the physical properties of both sawn lumber and processed fibre. The Cave (1986) relationship, which states that cell wall stiffness increases 5-fold with a downward shift from 40 to 10 in mean microfibril angle, is now accepted (Butterfield, 2003). MFA has a great impact on how the fibre, and consequently the wood, will perform in strength, shrinking and swelling tests (Jozsa and Middleton, 1995). Together with wood density, MFA shows a strong relationship to modulus of elasticity (MOE) and longitudinal shrinkage (Donaldson, 2008). Evans and Ilic (2001), found that MFA together with wood density accounted for approximately 96% of the variation in longitudinal modulus of elasticity in *Eucalyptus delegatensis*, with the MFA alone accounting for 86% of the variation. The same authors concluded that the influence of MFA on wood stiffness was significantly greater than that of wood density.

It is therefore clear that microfibril angle is an important wood quality trait. According to Butterfield (2003) “selecting clonal plantlets that have smaller microfibril angles in their first growth rings would clearly provide the timber industry with trees of superior wood quality, as MFA always gets lower with increasing distance from the stem centre.” However, the measurement of MFA in the field or at the mill site is difficult and costly. Therefore, insights that might be made into which stand composition tends to produce stems with the lower inherent microfibril angles will go a long way towards generating better use of the available forest resources.
1.4.3 Fibre traits

Fibre traits, in particular fibre length and coarseness, are attributes of primary importance to the pulp and paper industry, since they have a direct influence on pulp and paper quality, with fibre length, fibre diameter and cell wall thickness contributing the greatest influence (Seth, 1990a; Seth 1990b; Mansfield and Weinseisen, 2007). Fibre length impacts interfibre bonding and tear strength is proportional to fibre length (Seth and Page, 1988). Fibre wall thickness also plays an important role in determining wood quality for the pulp industry. Thin walled cells contribute to burst and tensile strength since they are more flexible and as such collapse during sheet formation, generating a more compact network in paper. On the other hand, thicker walled cells contribute favourably to tear strength, breaking length, bulk and absorbance properties, but are less conformable than thinner cell-walled fibres (Da Silva Perez and Fauchon, 2000). Coarseness, which expresses the amount of cell wall per unit length of fibre, is important in determining paper strength (Seth, 1990b). Fibres possessing a high coarseness will produce a paper with higher porosity, while low coarseness leads to a greater collapse of fibers, resulting in improved paper density and optical properties.

Fibre frequency, together with fibre wall thickness (which may be expressed in coarseness), also has a direct influence on wood density and degree of shrinkage, and indirect influence on the mechanical properties of wood (Burger and Richter, 1991). Shimoyama (1990) reported a 0.60 coefficient of correlation between wood density and fibre wall thickness in *Eucalyptus saligna*, *Eucalyptus urphyla* and *Eucalyptus grandis*. Similarly, it has been shown that wood density may serve as an indication of fibre wall thickness in Eucalyptus (Barrichelo and Brito, 1976; Barrichelo, 1979; Dias and Da Silva, 1985).
1.4.4 Cell Wall Chemistry

The chemical components of wood can be classified as the extractive and the structural components. The extractives are non-structural elements that are contained in the cell lumen, cellular voids and channels, as well as in resin canals and some parenchymous tissues, such as rays. They are largely soluble and may be removed from wood by use of solvents with adequate polarity, without drastically changing the cellular structural characteristics of the wood (Pereira et al., 2003). On the other hand, the structural components of wood can generally be classified into cellulose, hemicelluloses and lignin, which together make up the structure of the cell wall itself (Burger and Ritcher, 1991). Wood may therefore be defined in chemical terms as a three dimensional biopolymer composite composed of an interconnected network of cellulose, hemicellulose and lignin with minor amounts of extractives and inorganics.

On a dry weight basis, all wood cell walls consist mainly of carbohydrate-based polymers (between 65-75%) that are combined with lignin (18-35%) (Rowell et al., 2005). The chemical composition of wood ranges broadly between 40-50% cellulose, 20-30% hemicellulose, 20-35% lignin and 0-10% extractives, with a small extent (<1%) of inorganic compounds, commonly referred to as the ash (Pereira et al., 2003; Carvalho et al., 2009). The major carbohydrate portion of wood is composed of cellulose and hemicellulose polymers with minor amounts of other carbohydrates derived from starch and pectin (Stamm, 1964 in Rowell et al., 2005).

1.4.4.1 Cellulose

Cellulose is the most abundant organic chemical found on earth and is the main component of wood and the skeletal polysaccharide of wood cell walls. It is a long chain polymer of β-D-
glucose molecules linked together by β-(1-4) glycosidic bonds (Wise and Jahn, 1952; Fengel and Wegener, 1983; Goldstein, 1993; Sjostrom, 1993). Two adjacent glucose molecules bind by eliminating one molecule of water between their hydroxylic groups at carbon 1 and carbon 4, thereby making the units known as cellobiose, which constitute the repeating chemical entities in the cellulose polymer (Wise and Jahn, 1952; Fengel and Wegener, 1983; Carvalho et al., 2009).

The cellulose molecule is therefore composed of repeating cellobiose residues, in a long chain containing several thousand of anhydroglucose units, with a molecular formula of \((C_6H_{10}O_5)_n\) (McGinnis and Shafizadeh, 1993). The number of glucose units in a cellulose molecule is known as its degree of polymerization. In wood, the degree of polymerization ranges from 9,000 – 10,000, and possible as high as 15,000 (Fengel and Wegener, 1983; McGinnis and Shafizadeh, 1993; Pereira et al., 2003; Rowell et al., 2005). The supramolecular structure of cellulose is characterized by a highly ordered arrangement with densely packed molecules, building up a fibrous-like rod structure called a microfibril. This structure is based on the alignment of cellulose chains parallel to each other and in the same direction, building up planar layers (Pereira et al., 2003; Carvalho et al., 2009).

1.4.4.2 Hemicellulose

Hemicelluloses are strongly associated with cellulose and contribute to the structural nature of the tree, functioning as supporting material in the cell walls (Sjostrom, 1993). They are non-cellulosic polysaccharides that consist of various compounds of different chemical composition and molecular structures (Fengel and Wegener, 1983). Hemicelluloses are comprised of more than one type of sugar unit and are sometimes referred to by the sugars they contain (Rowell et al., 2005). The most important hemicelluloses in wood cell wall are xylans and glucomannans.
Other hemicelluloses may be present, usually in low proportions, although in more significant amounts in some species (Pereira et al., 2003).

Hemicelluloses differ from cellulose in many aspects. They are heteropolymers composed of two or more monomers. Their molecular structure consists of a linear backbone chain with short side branching of monomeric units. The degree of polymerization is much lower (up to about 200) than that of cellulose, and they are not crystalline (Sjostrom, 1993; Rowell et al., 2005). Hemicelluloses do not have a uniform molecular composition and within each type of hemicellulose the monomeric composition, degree of polymerization and the extent of substitution and branching may vary with species and wood type (Fengel and Wegener, 1983; Sjostrom, 1993; Pereira et al., 2003).

Hardwoods and softwoods differ in the amounts and types of hemicelluloses they contain. In hardwoods, the predominant hemicelluloses are xylans (between 15-30%) accompanied in much lower amount by glucomannans (1-2%). In softwoods, the main hemicelluloses are galactoglucomannans (about 20%) with smaller amounts of xylans (5-10%) (Goldstein, 1993; Pereira et al., 2003).

### 1.4.4.3 Lignins

Lignin is the third major component of the cell wall, serving as a cement between wood fibers, as a stiffening agent within fibres, and as a barrier to the enzymatic degradation of the cell wall (Goldstein, 1993). Lignins are amorphous, highly complex, aromatic polymers composed of phenylpropane units (Fengel and Wegener, 1983; Rowell et al., 2005; Carvalho et al., 2009). Lignin consists of a complex arrangement of substituted phenolic units, leading to a complicated structure that can only be defined by the frequency of occurrence of the various linkages (Goldstein, 1993). Lignin is distributed throughout the cell wall, with the highest concentration
in the middle lamella. However, due to the difference in volume between the middle lamella and the secondary cell wall, about 70% of the total lignin is found in the secondary cell wall (Rowell et al., 2005).

In general, the lignin content found in softwoods (25-35%) is greater than the hardwoods (18-25%) (Carvalho et al., 2009). Softwood lignins are mainly a polymerization product of coniferyl alcohol and are called guaiacyl lignin, while hardwood lignins are mainly syringyl-guaiacyl lignin, consisting of copolymer monolignols derived from coniferyl and sinapyl alcohols (Fengel and Wegener, 1983; Pereira et al., 2003; Rowell et al., 2005).

The chemical components and their assembly in the cell wall are directly related to the properties of wood, and their effects may be either positive or negative, depending on the final product. In timber, the role of lignin is associated with compressive strength while cellulose is associated with tensile and bending strength, and changes in their proportions effect physical properties (Pereira et al., 2003). However, the same authors state that most of the variation found in solid timber is related to the presence of different types of wood, such as juvenile wood or reaction wood, where the largest differences regarding the cell wall structural components take place.

As with timber products, the chemical composition of wood has a direct influence on its utility for pulping. The amount of cellulose is positively correlated with pulp yield, whereas lignin is negatively correlated (Amidon, 1981 in Pereira et al., 2003). It is common knowledge that hardwoods are easier to pulp chemically than softwoods, and this is attributed to the differences in lignin monomer composition, where lignin rich in syringyl lignin is easier to chemically pulp (Stewart et al., 2009). The delignification rate does not depend on the
accessibility to lignin but rather on its chemical structure, and it is directly proportional to the syringyl to guaiacyl ratio (Pereira et al., 2003).

1.5 Research Objective

The main objective of this research is to elucidate the effect(s) of the ecological combining ability of white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) on growth and wood quality traits grown in the Canadian boreal forest.
Chapter 2: Materials and Methods

2.1 Sample collection

Between July and August of 2009, a total of 100 increment cores were collected from each of the three different sites in the boreal mixedwood forests of central Alberta, for a total of 300 samples. These sites were selected based on basal area and species distribution. This approach permitted for the identification of an aspen dominated site (aspen site), an aspen-spruce mixed site (mixed site), and a spruce dominated site (spruce site). Specifically, the aspen and spruce sites had over 70% of their basal area composed of aspen and spruce trees, respectively while the mixed site was composed of a 70% and 30% split of aspen and spruce, respectively. The sample sites are part of the Permanent Sample Plots established in Alberta for long-term evaluation, which included PSP 430 for the aspen site, PSP 434 for the mixed site, and PSP 379 for the spruce site. All three sites are located in the Central Mixedwood Natural sub region, inside the Boreal Forest Natural region of Alberta, and all sites are classified as mesic on the moisture scale, and modal on the soil nutrient scale.

The aspen site (PSP 430) is located near Lac la Biche, AB (Long: 111.56 Lat: 54.86 Elevation: 643 m). Its total area, including the buffer zone is 156m x 156m (2.428ha), while the sample plot itself is located in the centre consisting of an area of 32.2m x 31.8m (0.1024ha). According to the Alberta Vegetation Inventory (AVI) system of overstory classification, this PSP is classified as C19aw9sw1. Specifically, this designation means the site has a C class density (51-70% of above canopy light blocked by overstory), with an average tree height of 19m for the leading species (aspen), and that aspen occupies 90% of the total crown canopy, while spruce occupies 10%.
The mixed site (PSP 434) is also located in the Lac la Biche, AB region (Long: 111.42 Lat: 54.87 Elevation: 672 m). The site is represented by a total area is 200m x200m (4ha) with the sample plot located in the centre consisting of an area of 31.6m x 32.2m (0.1018ha). Its AVI classification is C20aw9sw1 – C class density (51-70% of above canopy light blocked by overstory), 20m average tree height of the leading species (aspen), 90% of total crown canopy occupied by aspen, and 10% of total crown canopy occupied by spruce.

The spruce site (PSP 379) is located near Athabasca, AB (Long: 113.44 Lat: 55.34, Elevation 664m). Its total area is 150m x 150m (2.25ha) with the sample plot located in the centre with an area of roughly 31.68m x 31.65 (0.1003ha). This PSP has an AVI classification of C29sw9aw1 – C class density (51-70% of above canopy light blocked by overstory), with an average tree height of 29 m for the leading species (spruce), with 90% of total crown canopy occupied by spruce, and 10% of total crown canopy occupied by aspen.

Table 1 shows the site attributes for each PSP used for sample collection. Note that the percentage of aspen and spruce is relative to the crown canopy occupied by each species. However site selection was determined based on basal area and not crown canopy.

<table>
<thead>
<tr>
<th>Site</th>
<th>PSP</th>
<th>% Canopy Closure</th>
<th>Avg Tree Height</th>
<th>Aspen %</th>
<th>Spruce %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen</td>
<td>430</td>
<td>51-70</td>
<td>19</td>
<td>90</td>
<td>10</td>
</tr>
<tr>
<td>Mixed</td>
<td>434</td>
<td>51-70</td>
<td>20</td>
<td>90</td>
<td>10</td>
</tr>
<tr>
<td>Spruce</td>
<td>379</td>
<td>51-70</td>
<td>29</td>
<td>10</td>
<td>90</td>
</tr>
</tbody>
</table>
Ideally, samples would have been collected from trees located inside each of the Permanent Sample Plots (PSP). However, since these plots are for permanent data collection and research, we were unable to obtain samples from trees located directly inside the PSPs. As such, a system was established which allowed us to identify trees located in the PSP’s buffer zone of similar size and proximity to those that would have been ideally sampled inside the PSP (Figure 2).

Initially, trees were measured for height and diameter at breast height (DBH) inside the PSP, and candidate trees were identified based on DBH estimates. Next, we found trees inside the buffer zone which had DBH and height measurements similar to the desired trees from inside the PSP. In each case a tree was then identified as the main tree for that sampling group, and an 8m radius around the candidate tree was created and all trees of the desired species inside this 8m radius circle were then measured for DBH and height (as well as photographed). Based on this data, the 10 trees with the DBH values closest to that of the candidate tree were selected for sampling. These 10 trees were then increment cored with a 10 mm increment core borer at DBH on the north profile of the tree. This process was repeated ten times for each site, for a total of approximately 300 cores. Figure 2 illustrates the sampling process, where $X_a$ is the initial candidate tree located inside the permanent sample plot, $X_b$ indicates the tree in the buffer zone with similar DBH and height to $X_a$, and $x$ represents trees selected for increment core sampling inside the 8m radius.

In addition to these cores, 20 extra increment cores were collected for instrument calibration. All trees sampled for this purpose were randomly selected, being 5 aspen trees from the aspen site, 5 aspen and 5 spruce trees from the mixed site, and 5 trees from the spruce site, for a total of 10 increment cores per species.
Figure 2. Representation of sampling process, where $X_a$ is the candidate tree inside the permanent sample plot, $X_b$ is the tree in buffer zone with similar characteristics to $X_a$, and $x$ represents trees selected for sampling. Not to scale.

All DBH measurements were made using a diameter tape, while tree height measurements were recorded using a Vertek III and a T3 Transponder. This equipment uses ultrasonic signals to obtain exact measurements of distance. Heights are then calculated trigonometrically based on distance from tree, air temperature and angle variables.
2.2 Tree volume

The volume of each tree employed in this study was calculated using the diameter at breast height (D) and tree height (H), employing the volumetric equations provided by the BC Ministry of Forests (British Columbia Forest Inventory Division, 1976) specific to these species, grown on a defined site, based on the Forest Inventory Zone (F.I.Z.), as follows:

Trembling Aspen:

\[
\log V = -4.538904 + 1.83441 \log D + 1.208970 \log H
\]

S.E. = ±8.2%
No. of Trees = 1077
F.I.Z. = K,L

White Spruce:

\[
\log V = -4.379777 + 1.783940 \log D + 1.146280 \log H
\]

S.E. = ±8.0%
No. of Trees = 3018
F.I.Z. = K,L

where, the volume of each tree (V) is expressed in cubic meters, diameter at breast height in centimeters, and height in meters.
2.3 Wood density

All increment core samples were allowed to air dry for a week. Once dry, each increment core was cut to a 1.68 mm thickness using a twin blade pneumatic precision saw. The sawn samples measured approximately 1.68 mm in width by 10 mm in height, and only varying according to each tree’s diameter. The side slabs generated from the sawing operation were saved and subsequently used for wood chemistry and fibre properties testing. The density samples were then soxhlet extracted with acetone at 70°C overnight.

Each of the 10 extra samples obtained for instrument calibration were similarly sawn, but then edge sanded to obtain parallel edges. Samples were then soxhlet extracted and dried in a 105°C oven overnight. Next, the samples were cooled in a desiccator and their dry weights were obtained using a precision scale. The samples were then allowed to reach air moisture equilibrium in a humidity control chamber set at 12%. Measurements for height, length and width were then taken three times for each sample using calipers, and an average for each measurement was obtained. With both average volumes and dry weights in hand, density values for the test samples were calculated in g/cm³, and converted to kg/m³. Volume at 12% humidity equilibrium and oven dry weights were utilized for these calculations as per the protocol for the X-ray densitometer (Quintek Measurement Systems). These samples were then scanned using X-ray densitometry. The program allows the operator to then enter the measured sample density in kg/m³, and a mass absorption coefficient (cm²/g) is created for that sample. Once all 20 mass absorption coefficients were collected, averages were then obtained for each species.
With the mass absorption coefficient calculated, each sample was scanned using X-ray densitometry (Quintek Measurement Systems) from bark to pith, and an average sample density for each sample was obtained.

### 2.4 Cellulose microfibril angle (MFA)

Employing the sample precision cut samples used for density determination, microfibril angle measurements were obtained. For the spruce samples, measurements were taken every five growth rings, starting from the pith. The same could not be done for the aspen samples, as the growth rings were not visible to the naked eye. Therefore, measurements were taken every 1 cm starting at the pith. Microfibril angles were estimated by x-ray diffraction using a Bruker D8 Discover X-ray diffraction unit fitted with an area array detector. The x-ray source was fitted with a 0.5mm collimator and the scattered photons were collected by a general area detector diffraction system. The theta angle set for both the X-ray source and the detector was 0°. The microfibril angles for aspen and spruce were then estimated by use of the following equations:

Aspen: \[ \text{MFA} = 0.9583(T) - 3.8364 \]

Spruce: \[ \text{MFA} = 0.9455(T) - 4.192 \]

where T is the measure of the width of the (002) diffraction arc.
2.5 Fibre traits

One of the residual slabs generated during increment core processing was manually cut into smaller pieces of approximately 10mm x 3mm x 3mm using a razor blade. These pieces were then digested in Franklin solution (1 part Glacial Acetic acid:1 part 30% hydrogen peroxide) at 70°C for forty-eight hours. After digestion, the remaining material was rinsed thoroughly with tap water. The material was then placed into a Waring blender with water and gently stirred for approximately 15 minutes to break up the fibrous materials into individual fibers. Once the fibers had been dissociated small amounts of the solution were then run on the Fiber Quality Analyzer (Optest Equipment) to collect measurement of fibre length and fibre width. The aspen samples were also tested for vessel element length, vessel element width and number of vessel elements per meter of fibre.

The remaining suspension was vacuum filtered through a 100 mm filter paper to remove the water, and dried overnight at 105°C. Subsequently, a small portion from each sample was removed and precision weighed to attain 1.2 – 2.4 mg for aspen, 3.2 – 5.8 mg for spruce. This weighed fibrous material was then again placed in the blender and gently stirred for approximately 30 min to break up the dried fibre into individual fibres. The entire solution was then used to collect coarseness measurement on the same Fiber Quality Analyzer (Optest Equipment).

2.6 Cell wall chemistry

Due to the large number of samples, only 30 representative samples from each site were randomly selected for cell wall chemistry analysis. Therefore, 30 aspen samples from the aspen site, 15 aspen and 15 spruce samples from the mixed site, and 30 spruce samples from the spruce
site were employed for cell wall chemistry evaluation. This was achieved using the second residual slab of the density sample that remained after sawing. These samples were ground in a Wiley Mill to pass through a 0.40 mm mesh (40 mesh). The samples were then Soxhlet extracted in 70°C acetone overnight.

A modified Klason technique was employed to determine the lignin and carbohydrate content of each sample. Initially, 200mg of each sample were hydrolyzed using 72% H$_2$SO$_4$ for two hours, being mixed every ten minutes. This solution was then transferred into serum bottles, to which 112mL of distilled water were added. The bottles were then sealed and autoclaved at 121°C for one hour. The acid insoluble lignin content was determined gravimetrically by vacuum filtering the solution through pre-weighed, medium coarseness sintered glass crucibles. The acid soluble lignin portion was determined by measuring the absorbance of the acid hydrolysate at 205 nm on a Varian Cory 50 BIO UV-Visible spectrophotometer using the following formula:

\[
\% \text{Soluble Lignin} = \frac{(A_{205} / 110) \times \text{Dilution Factor} \times 115 \times 100}{\text{(g of tissue)} \times 1000}
\]

where $A_{205} =$ absorbance of acid hydrolysate at 205 nm.

The hydrolysate was then filtered through a 4 mm Chormspec syringe filter (nylon; 0.45 µm). The carbohydrate contents of each sample were then determined using an anion exchange high-performance liquid chromatography (Dx-600; Dionex, Sunnyvale, CA, USA) equipped with an ion exchange PA1 (Dionex) column, a pulsed amperometric detector with gold electrode, and a SpectraAS3500 auto injector (Spectra-Physics).
2.7 Social classes

The initial plan was to divide samples from each stand into diameter classes in order to facilitate comparisons between classes from different stands. However, this approach proved to be inefficient due to the large differences in diameters between each of the stands. To overcome this situation, individuals from each stand were separated into dominant and co-dominant social classes based on DBH values of the entire stand. As such, individuals with a DBH that ranged from the median to the 3\textsuperscript{rd} quartile of the whole stand were classified as co-dominant. Individuals whose DBH surpassed the 3\textsuperscript{rd} quartile were classified as dominant. This approach allowed for comparisons not only between sites, but also different social classes from different sites within each species (Tables 2 and 3).

<table>
<thead>
<tr>
<th>Site</th>
<th>Total</th>
<th>Dominant</th>
<th>Co-Dominant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen</td>
<td>99</td>
<td>66</td>
<td>33</td>
</tr>
<tr>
<td>Mixed</td>
<td>50</td>
<td>14</td>
<td>36</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Site</th>
<th>Total</th>
<th>Dominant</th>
<th>Co-Dominant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce</td>
<td>100</td>
<td>52</td>
<td>48</td>
</tr>
<tr>
<td>Mixed</td>
<td>50</td>
<td>24</td>
<td>26</td>
</tr>
</tbody>
</table>
2.8 Statistical Analysis

For each wood traits quantified, comparisons between the mean values and their variations were made to determine if significant differences occurred between trees from the species-specific site and those from the mixed site. In order to compare the different wood traits quantified across sites, each tree had a mean value calculated for each of the fibre traits analyzed. The variations in means from each site were then used to calculate if statistical differences occurred.

The null hypothesis was that tree volume, wood density, microfibril angle, fibre length, fibre width, fibre coarseness (as well as vessel length, width and vessels per meter for trembling aspen), carbohydrate content and lignin content would be the same for all trees of the same species, regardless of site of origin. The α level was determined at 0.05 for all tests (95% confidence level). Analyses of variance were calculated for each of the wood traits. Differences between means were tested using Student t-tests. The same tests were executed in order to compare the social classes across sites.
Chapter 3: Results

3.1 DBH and tree volume

3.1.1 Trembling aspen tree volume

Table 4 shows the mean DBH, height and volume for the trembling aspen trees located in the pure aspen and the mixed sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen Site (PSP 430)</td>
<td>99</td>
<td>17.60</td>
<td>18.00</td>
<td>0.198*</td>
</tr>
<tr>
<td>Mixed Site (PSP 434)</td>
<td>50</td>
<td>21.19</td>
<td>19.93</td>
<td>0.312*</td>
</tr>
</tbody>
</table>

As discussed in the methods chapter, trees in both stands were grouped into dominant and co-dominant social classes to permit a better comparison between the stands. Tables 5 and 6 show the mean values for diameter, height and volume of the different social classes in both stands:

<table>
<thead>
<tr>
<th>Social Class</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Vol. (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant</td>
<td>66</td>
<td>19.2</td>
<td>19.4</td>
<td>0.324*</td>
</tr>
<tr>
<td>Co-Dominant</td>
<td>33</td>
<td>14.7</td>
<td>15.4</td>
<td>0.146*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Social Class</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Vol. (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant</td>
<td>14</td>
<td>26.0</td>
<td>22.5</td>
<td>0.662*</td>
</tr>
<tr>
<td>Co-dominant</td>
<td>36</td>
<td>19.3</td>
<td>18.9</td>
<td>0.313*</td>
</tr>
</tbody>
</table>
### 3.1.2 White spruce tree volume

Trees originating from the pure spruce site were much larger than those of the mixed site. The trees in the mixed site, which were younger, were comparatively smaller than the older trees in the spruce site, once again demonstrating that the sites represent different stages of forest succession. The following tables show the mean values for DBH, height and volume of the trees in each site (Table 7), and those segregated by social classes (Table 8 and Table 9).

**Table 7.** Mean DBH, height and volume for all white spruce trees in the pure stand (PSP 379) and the mixed stand (PSP 434). * indicates significant differences ($\alpha=5\%$)

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Volume (m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce Site (PSP 379)</td>
<td>100</td>
<td>31.88</td>
<td>27.27</td>
<td>0.941*</td>
</tr>
<tr>
<td>Mixed Site (PSP 434)</td>
<td>50</td>
<td>16.58</td>
<td>14.87</td>
<td>0.149*</td>
</tr>
</tbody>
</table>

**Table 8.** Mean DBH, height and volume for white spruce trees in each social class in the spruce site (PSP 379). * indicates significant differences ($\alpha=5\%$)

<table>
<thead>
<tr>
<th>Social Class</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Vol. (m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant</td>
<td>57</td>
<td>35.6</td>
<td>29.5</td>
<td>1.215*</td>
</tr>
<tr>
<td>Co-dominant</td>
<td>48</td>
<td>27.5</td>
<td>24.6</td>
<td>0.615*</td>
</tr>
</tbody>
</table>

**Table 9.** Mean DBH, height and volume for white spruce trees in each social class in the mixed site (PSP 434). * indicates significant differences ($\alpha=5\%$)

<table>
<thead>
<tr>
<th>Social Class</th>
<th>n</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Vol. (m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant</td>
<td>24</td>
<td>19.7</td>
<td>16.7</td>
<td>0.218</td>
</tr>
<tr>
<td>Co-Dominant</td>
<td>35</td>
<td>14.0</td>
<td>13.3</td>
<td>0.091</td>
</tr>
</tbody>
</table>
3.2 Wood density

3.2.1 Aspen wood density

Figure 3 shows the mean density for the trembling aspen trees grown on the pure aspen and the mixed sites, regardless of social class. Although the average wood density on the mixed site was slightly lower (451.6 kg/m$^3$) than the pure site (459.0 kg/m$^3$), there were no significant differences between sites ($\alpha = 5\%$).

![Aspen Mean Density (kg/m$^3$)](image)

**Figure 3.** Mean wood density (kg/m$^3$) for trembling aspen trees in aspen site (PSP 430) and the mixed site (PSP 434). Error bars indicate standard deviation.

To better illustrate the variation in wood density between sites, the trees were again grouped by social classes (Figure 4). Using this class system, it was apparent that there were statistically significant differences ($\alpha = 5\%$) between the dominant trees in the aspen site and the dominant trees in the mixed site. Specifically, the trees originating from the pure aspen site displayed higher density than the samples originating from the mixed site. However, no significant differences were apparent between the co-dominant trees on the same sites.
3.2.2 White spruce wood density

Similar to the findings with the trembling aspen, there were no significant differences between the mean wood densities of white spruce trees (Figure 5) grown on the pure spruce (PSP 379) and in the mixed sites (PSP 434). However, the trees from the mixed site tended to be lower (383.85 kg/m$^3$ vs. 427.18 kg/m$^3$).

When the trees were compared by social classes, both classes show significant differences between sites (Figure 6). The mean density was lower for both dominant and co-dominant trees originating from the mixed site.
**Figure 5.** Mean wood density (kg/m$^3$) for white spruce trees in the spruce site (PSP 379) and the mixed site (PSP 434). Error bars indicate standard deviation.

**Figure 6.** Mean density (kg/m$^3$) for spruce trees in spruce site (PSP 379) and mixed site (PSP 434) by social classes. Star indicates significant differences ($\alpha=5\%$).
3.3 Microfibril angle

3.3.1 Trembling aspen MFA

The microfibril angle (MFA) was measured for all trees at breast height, and recorded at several distances from the pith in order to better understand changes in MFA as a function of cambial age. For the trembling aspen samples (Table 10), measurements were taken every centimeter starting at the pith, as accurate growth rings could not be discerned. As expected, a higher MFA was apparent near the pith, which decreased with age, and then eventually stabilized. This plateau occurred much earlier for the trees originating from the pure aspen site (4 cm distance from pith) than for those in the mixed site, which appeared to be still declining. However, when compared at any given distance from the pith, the mean MFA in the mixed site was larger than that of the pure aspen site (Table 10).

Table 10. Mean microfibril angle (degrees) at given distances from pith for trembling aspen trees from the aspen site (PSP 430) and the mixed site (PSP 434)

<table>
<thead>
<tr>
<th>Distance (cm)</th>
<th>Aspen Site</th>
<th>Mixed Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>28.59</td>
<td>29.46</td>
</tr>
<tr>
<td>1</td>
<td>23.84</td>
<td>26.28</td>
</tr>
<tr>
<td>2</td>
<td>20.50</td>
<td>23.25</td>
</tr>
<tr>
<td>3</td>
<td>18.47</td>
<td>21.30</td>
</tr>
<tr>
<td>4</td>
<td>17.90</td>
<td>20.27</td>
</tr>
<tr>
<td>5</td>
<td>17.79</td>
<td>19.83</td>
</tr>
<tr>
<td>6</td>
<td>17.53</td>
<td>19.45</td>
</tr>
<tr>
<td>7</td>
<td>17.64</td>
<td>19.23</td>
</tr>
<tr>
<td>8</td>
<td>17.76</td>
<td>19.30</td>
</tr>
<tr>
<td>9</td>
<td>17.45</td>
<td>19.60</td>
</tr>
<tr>
<td>10</td>
<td>-</td>
<td>19.55</td>
</tr>
<tr>
<td>11</td>
<td>-</td>
<td>18.71</td>
</tr>
<tr>
<td>12</td>
<td>-</td>
<td>18.74</td>
</tr>
<tr>
<td>13</td>
<td>-</td>
<td>17.49</td>
</tr>
</tbody>
</table>
When grouped into social classes, the same pattern persists. This is illustrated for both the dominant and co-dominant classes in Figures 7 and 8. The dominant trees in the pure aspen site have a higher MFA than dominant trees in the mixed site only in the first centimeter from the pith. After that, trees from mixed site posses a higher angle, following the trend noted above.

**Figure 7.** Mean microfibril angle (degrees) at given distances from pith for all dominant trembling aspen trees in aspen site (PSP 430) and mixed site (PSP 434)

**Figure 8.** Mean microfibril angle (degrees) at given distances from pith for all co-dominant trembling aspen trees in aspen site (PSP 430) and mixed site (PSP 434)
3.3.2 White spruce MFA

Since growth rings were easily discernible in the spruce samples, measurements of MFA were taken every five years of growth, starting from the pith. As trees from the pure spruce stand (PSP 379) were much larger and older than those from the mixed site, measurements for trees from the mixed site range from 1 to 50 years, whereas those of trees from the spruce site range from 1-130 years. Table 11 depicts the mean MFA, at five year intervals, starting from the pith for all white spruce trees from each site.

Generally, trees from both sites had similar MFAs in first ten years of growth. As the trees aged, trees from the mixed site (PSP 434) showed a more rapid decline and consequently lower MFA estimated than those from the pure spruce site at similar ages. Trees from the mixed site also reach a plateau at a younger age than those from the spruce site.
Table 11. Mean microfibril angle (degrees) at given ages for white spruce trees from the spruce site (PSP 379) and the mixed site (PSP 434)

<table>
<thead>
<tr>
<th>Age (Years)</th>
<th>Spruce Site</th>
<th>Mixed Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>32.17</td>
<td>32.28</td>
</tr>
<tr>
<td>5</td>
<td>29.78</td>
<td>29.69</td>
</tr>
<tr>
<td>10</td>
<td>25.45</td>
<td>24.30</td>
</tr>
<tr>
<td>15</td>
<td>22.06</td>
<td>21.86</td>
</tr>
<tr>
<td>20</td>
<td>21.54</td>
<td>18.45</td>
</tr>
<tr>
<td>25</td>
<td>20.54</td>
<td>16.74</td>
</tr>
<tr>
<td>30</td>
<td>18.90</td>
<td>17.35</td>
</tr>
<tr>
<td>35</td>
<td>18.03</td>
<td>17.13</td>
</tr>
<tr>
<td>40</td>
<td>18.87</td>
<td>16.85</td>
</tr>
<tr>
<td>45</td>
<td>17.06</td>
<td>17.55</td>
</tr>
<tr>
<td>50</td>
<td>17.01</td>
<td>16.22</td>
</tr>
<tr>
<td>55</td>
<td>16.45</td>
<td>-</td>
</tr>
<tr>
<td>60</td>
<td>16.31</td>
<td>-</td>
</tr>
<tr>
<td>65</td>
<td>16.68</td>
<td>-</td>
</tr>
<tr>
<td>70</td>
<td>16.72</td>
<td>-</td>
</tr>
<tr>
<td>75</td>
<td>16.06</td>
<td>-</td>
</tr>
<tr>
<td>80</td>
<td>16.30</td>
<td>-</td>
</tr>
<tr>
<td>85</td>
<td>16.47</td>
<td>-</td>
</tr>
<tr>
<td>90</td>
<td>16.58</td>
<td>-</td>
</tr>
<tr>
<td>95</td>
<td>17.03</td>
<td>-</td>
</tr>
<tr>
<td>100</td>
<td>17.09</td>
<td>-</td>
</tr>
<tr>
<td>105</td>
<td>17.94</td>
<td>-</td>
</tr>
<tr>
<td>110</td>
<td>18.35</td>
<td>-</td>
</tr>
<tr>
<td>115</td>
<td>17.99</td>
<td>-</td>
</tr>
<tr>
<td>120</td>
<td>16.53</td>
<td>-</td>
</tr>
<tr>
<td>125</td>
<td>17.17</td>
<td>-</td>
</tr>
<tr>
<td>130</td>
<td>17.42</td>
<td>-</td>
</tr>
</tbody>
</table>

When divided into social classes, the same patterns emerged (Figures 9 and 10). Due to the large difference in ages between trees originating from the different sites, the figures only show the data collected from the first 50 years.
**Figure 9.** Mean microfibril angle (degrees) at given ages for all dominant white spruce trees in spruce site (PSP 379) and mixed site (PSP 434)

**Figure 10.** Mean microfibril angle (degrees) at given ages for all dominant white spruce trees in spruce site (PSP 379) and mixed site (PSP 434)
3.4. Fibre traits

3.4.1 Trembling aspen fibre traits

All fibre traits showed significant differences when comparing samples from the pure aspen site to those originating from the mixed site. Fibres from the pure aspen site were longer (Figures 11) and wider (Figures 12) than those from the mixed site. Fibre coarseness also followed a similar trend (Figures 13). Vessel element measurements also show significant differences between sites. Consistent with the fibre traits, vessel element characteristics from the pure aspen site were larger than those from the mixed site, by all metrics (Figure 14, 15 and 16).

![Aspen Fibre Length (mm)](image)

**Figure 11.** Mean fibre length (mm) of trembling aspen trees from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference (α=5%)
Figure 12. Mean fibre width (µm) of trembling aspen trees from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$)

Figure 13. Mean fibre coarseness (mg/m) of trembling aspen trees from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$)
Figure 14. Mean vessel element length (mm) of trembling aspen from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$).

Figure 15. Mean vessel element width (µm) of trembling aspen from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$).
Once again, the trees were divided into social classes based on DBH values of the stand as a whole. When comparisons were made based on this criterion, the fibre traits remained significantly different (Figures 17, 18 and 19). Fibres originating from the co-dominant trees in the pure aspen site had higher mean values than fibres derived from dominant trees. However, this trend was inverted in the mixed aspen site, where the dominant trees possessed the longer fibres. There was no significant difference between sites for dominant class. Trees from the dominant social class had wider fibres when compared to trees of the co-dominant class on the same site. When comparing sites, the aspen site had higher values regardless of social class. The dominant class also showed higher coarseness values than the co-dominant class on both sites. There were no significant differences between sites when comparing social classes.
Figure 17. Mean fibre length (mm) of trembling aspen from aspen site (PSP 430) and mixed site (PSP 434) per social class. Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$).

Figure 18. Mean fibre width (µm) for trembling aspen from aspen site (PSP 430) and mixed site (PSP 434) per social class. Error bars indicate standard deviation. Star indicates significant difference ($\alpha=5\%$).
3.4.2 White spruce tracheid traits

Fibre traits from the pure spruce site possessed longer (Figures 20) and wider tracheids (Figure 21). As such, they are also coarser in nature (Figure 22). The data for spruce tracheids traits were also separated by social classes for both sites. As with the aspen data, fibre properties from both sites and classes are displayed on the same graphs (Figure 23, 24 and 25). On the pure spruce site, co-dominant trees showed higher mean tracheid lengths. However, this is not the case in the mixed site, where the dominant trees had the longer tracheid traits. When comparing the same social class between sites, the spruce site had higher value for both classes (Figure 23).
Similar to tracheid length, when comparing the same social class between the different sites, the pure spruce site showed a higher tracheid width for both classes. However, no differences were apparent in dominant class between the sites. In addition, tracheids from the dominant class in the mixed site were wider than those originating from co-dominant trees from the spruce site (Figure 24). Tracheid coarseness (Figure 25) also showed significant differences when comparing social classes between sites. The spruce site showed higher coarseness values regardless of social class. On both sites, the dominant class had a higher coarseness value.

**Figure 20.** Mean tracheid length (mm) for white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference between sites ($\alpha=5\%$).
Figure 21. Mean tracheid width (µm) for white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference between sites (α=5%).

Figure 22. Mean tracheid coarseness (mg/m) for white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant difference between sites (α=5%).
Figure 23. Mean tracheid length (mm) for white spruce from spruce site (PSP 379) and mixed site (PSP 434) per social class. Error bars indicate standard deviation. Star indicates significant differences between sites (α=5%).

Figure 24. Mean tracheid width (µm) for white spruce from spruce site (PSP 379) and mixed site (PSP 434) per social class. Error bars indicate standard deviation. Star indicates significant differences between sites (α=5%).
3.5 Cell wall chemistry

3.5.1 Trembling aspen cell wall chemistry

The initial comparison made for trembling aspen was between trees originating from the aspen site (PSP 430) and trembling aspen from the mixed site (PSP 434). There were no significant differences between sites for carbohydrate content. Lignin content on the other hand was higher in trees originating from the aspen site (Figure 26). When the trees were divided into social classes the same trend persisted; no significant changes for carbohydrate content, and lignin always showed differences between sites. In addition, the pure aspen site always had lower carbohydrate contents and higher lignin contents for both social classes. It is clear that dividing the samples into sub-groups based on social class had no effect on the results when comparing the pure aspen stand to the mixed stand.
**Figure 26.** Cell wall carbohydrate and lignin contents (percentage) for trembling aspen trees from aspen site (PSP 430) and mixed site (434). Error bars indicate standard deviation. Star indicates significant differences between sites (α=5%).

**Figure 27.** Cell wall carbohydrate and lignin contents (percentage) for dominant trembling aspen trees from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant differences between sites (α=5%).
3.5.2 White spruce cell wall chemistry

Similar to trembling aspen, the initial comparison between sites for white spruce trees showed no significant difference in carbohydrate content. There was however, a significant difference in lignin content between the pure spruce and the mixed site. And, a similar trend was observed for lignin but not in carbohydrate contents, when the samples are divided into social classes.

Figure 28. Cell wall carbohydrate and lignin contents (percentage) for co-dominant aspen trees from aspen site (PSP 430) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant differences between sites (α=5%)
**Figure 29.** Cell wall carbohydrate and lignin contents (percentage) for white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant differences between sites ($\alpha=5\%$)

**Figure 30.** Cell wall carbohydrate and lignin content (percentage) for dominant white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant differences between sites ($\alpha=5\%$)
Figure 31. Cell wall carbohydrate and lignin content (percentage) for co-dominant white spruce from spruce site (PSP 379) and mixed site (PSP 434). Error bars indicate standard deviation. Star indicates significant differences between sites ($\alpha=5\%$).
Chapter 4: Discussion

4.1 Site comparison and social classes

As seen in tables 4 and 7, significant differences in tree volume were apparent for the both trembling aspen and white spruce originating from the pure sites when compared to trees from the mixed site. The aspen site (PSP 430) had the smallest mean volume, as expected since it is a younger site. In contrast, the aspen trees from the mixed site possessed a much larger volume, consistent with the age of the strand/trees. These findings were also mirrored in the white spruce comparison, as the difference in stand developmental age is particularly visible, since growth rings can be easily identified in these samples. Individuals from the mixed site had an average age of approximately 50 growth rings at breast height, while those from the pure spruce site averaged around 120 rings.

Thus, based on age alone, we inferred that we are dealing with sites that are at different stages of development. This supports the notion of a “relay floristics” succession model (Egler, 1954), where following a disturbance, fast growing shade intolerant species occupy the newly opened growing space. These species, overtime, alter site conditions in such a way that slower, shade tolerant species can establish themselves and eventually dominate. Following this model, it is evident that the aspen site (PSP 430) is the youngest of the 3 sites since it is heavily dominated by aspen (>70% of its basal area), which is a fast growing shade intolerant species. On the other hand, the spruce site is the oldest stand where white spruce, a shade tolerant and slower growing tree, dominates the basal area, and only a few large aspen trees remain. The mixed site represents a midpoint between these two different stages of forest succession. An observer might be tempted to regard the three sites as different successional stages of a single stand, turning the
main focus of this research into the comparison of wood quality at different stages of stand development. However, since data is not available on what these stands were like in the past, it is impractical to assume that they share sufficient characteristics to group them into one single forest stand.

Trees with larger diameters are expected to have different juvenile to mature wood ratios than trees with smaller diameters, and therefore they are expected to show differences in wood quality traits. As a consequence of the differences in age and stand development, social class was employed as a means of comparison. Through this segregating, patterns emerge which show how these effects have a larger or smaller influence on the wood quality traits in question.

4.2 Tree Volume

4.2.1 Trembling aspen

Due to the clear differences in tree diameter and height, tree volumes were significantly different between the two sites. Trees originating from the aspen site have a considerably smaller mean volume than those from the mixed site (0.198 m$^3$ vs. 0.312 m$^3$). Furthermore, when comparisons were made by contrasting trees categorized by social class on the different sites, the variation in tree volume was even greater. The mean volume for the dominant class originating from the mixed site was more than double the mean volume of dominant trees from the aspen site. A similar estimation was apparent for the co-dominant class.

As expected, the dominant class had a larger tree volume than co-dominant class in both the mixed and the aspen sites (Tables 2 and 3). This observation was largely related to the fact that volume is a function of diameter and height, both of which were larger on the mixed site. It
was apparent that the presence of spruce trees in the mixed site had little to no effect on the differences in volume between the social classes for aspen trees in the aspen and mixed sites.

4.2.2 White spruce

The difference in tree volume between the mixed and the pure spruce site was even greater than compared to the difference between mixed and pure aspen: 0.149 m$^3$ in the mixed site compared to 0.941 m$^3$ in the all spruce site. This observation again supports the claim that differences exist in stand development. Dominant trees from the older and more developed spruce site have a mean volume over five times greater than the dominant trees from the mixed site. The same is true for trees from the co-dominant class. This implies that the near absence of aspen in the spruce site has no significant effect on spruce volume when comparing the same social class from both sites. In fact, the mean volume for the co-dominant class in the spruce site is much greater than the mean volume for the dominant trees on the mixed site (0.615 m$^3$ vs. 0.218 m$^3$). However, there does seem to be a larger difference in volume between dominant and co-dominant trees on the spruce site.

4.2.3 Considerations regarding tree volume

Tree volume seems to vary largely due to tree age and stand developmental status, rather than due to the presence of or absence of one species. This, however, does not limit the importance of knowing the tree volume, and indirectly, wood volume per site. Although other wood quality attributes are important, volume remains the vital criteria in making the decisions of when and where to harvest. This notion implies that even though a particular site offers trees with ideal wood quality traits, if the wood volume is low, it may be more viable to allow the site to mature in order to obtain a greater abundance of higher quality wood.
4.3 Wood density

4.3.1 Trembling aspen

Aspen wood density ranged from 338.54 kg/m$^3$ to 581.40 kg/m$^3$ with a mean value of 456.51 kg/m$^3$ for all aspen trees. These findings are consistent with previously published values (Yanchuk et al., 1983; Karki, 2001; Avramidis and Mansfield, 2005; Mansfield and Weineisen, 2007). There were no significant differences in wood density when comparing sites. This observation implies that the presence of white spruce in the mixed stand had no effect on the overall wood density of trembling aspen.

However, this is not the case when comparing trees by social class between sites. Although the co-dominant class showed no differences in wood density, there was a difference when comparing the dominant trees from each of the sites. The dominant trees originating from the aspen site had a significantly higher mean density than those from the mixed site (463.23 kg/m$^3$ vs. 438.12 kg/m$^3$, respectively). This is an interesting result, as it demonstrates that the younger and smaller dominant trees from the aspen site have a higher density than the older, more mature trees from the mixed site.

One possible explanation for this observation is that the dominant trees in the aspen site have only the co-dominant aspen trees to compete with, and as such have much more resources available to them, leading to a higher wood density. In contrast, on the mixed site, the dominant aspen trees have to compete not only with the co-dominant aspen for resources, but also the white spruce that now occupies a portion of the available growing space. This limits the available resources to the dominant aspen trees, including light and nutrients, and ultimately leads to a lower wood density. Since the co-dominant trees from the aspen site are already suppressed by
the dominant aspen, the presence of spruce in the mixed site has little effect on resources availability, and thus does not impact the wood trait in these trees.

4.3.2 White spruce

White spruce wood density varied from 326.12 kg/m$^3$ to 519.98 kg/m$^3$, with a mean density of 412.11 kg/m$^3$. These results are in accordance with previously published values for white spruce (Micko et al., 1981; Taylor et al., 1982; Corriveau et al., 1987). When comparing sites, there were no significant differences between trees originating from the spruce site and the mixed site. Despite being statistically similar, trees from the mixed site had an overall lower mean density than trees from the spruce site (383.85 kg/m$^3$ vs. 427.18 kg/m$^3$, respectively). As previously discussed, the trees from the pure spruce site are much older than those from the mixed site, and this difference in age contributes to the explanation of the observed difference. The mature wood in the older trees represents a larger percentage of the total wood. In addition, the smaller growth rings of the older spruce site trees lead to a smaller earlywood to latewood ratio, which could also contribute to the overall increased wood density. Although these differences are not statistically significant between sites, it does account for the higher density in the trees from the spruce site.

Although the comparison of trees originating from the spruce and mixed sites showed no difference, statistical variation is apparent when comparing social classes. Trees from both the dominant and co-dominant class showed higher mean wood density in trees originating from the spruce site. This again follows the general trend that white spruce trees from the pure spruce site have a higher wood density than those from the mixed site, regardless of social classes.
When comparing different social classes from the same site, trees from the co-dominant class have a higher mean density than those from the dominant class in both sites. This comparison indicates that the presence of aspen in the mixed site had no significant apparent effect on the differences in wood densities between social classes.

4.3.3 Considerations regarding wood density

Wood density is considered by many as the single most important wood quality trait, as it is contributes significantly to the physical and mechanical properties of wood. Therefore, it is understandable why any difference in wood density between the single species and mixed species site would be of industrial importance. Unfortunately, when comparing trees sites, there were no significant differences between the single species and mixed species sites for both trembling aspen and white spruce. This observation suggests that the presence or absence of one species has little effect on the overall wood density of the other species. Therefore, when forest managers make decision on factors such as which site to harvest, the best time for harvesting, or the final use of the timber from each type of site, wood density should not a factor that should be taken into consideration if the trees have not first been sub-divided into social classes.

If, however, data is available which permits the segregation into social classes, then predictions of wood density can be made, in particular for white spruce. Although there were no significance differences when comparing all spruce from the mixed and spruce site, when the estimates were sub-divided into social class, the pure spruce site showed a significantly higher wood density than that of the mixed site for both dominant and co-dominant social classes. In contrast, the dominant trembling aspen trees from the pure aspen site had statistically higher
wood density than those from the mixed site. Since the same did not occur with the co-dominant trees, it brings into question the validity of qualifying the aspen trees by social class.

4.4 Microfibril angle (MFA)

While density, fibre traits and cell wall chemistry generated a single value that is used to represents the entire tree, the microfibril angle estimates were measured at several points across the diameter of the tree. This method facilitates a mechanism which allows for a comparison of trees from the different sites at the same stage of development. For both trembling aspen and white spruce, the microfibril angle at the pith was high and decreased with distance from the pith, eventually reaching a relatively constant value.

4.4.1 Trembling aspen

The MFA of trembling aspen was measured at 1cm increments from pith to bark. Due to the inherent differences in tree diameter, the trees from the mixed site generated more values than the smaller trees from the pure aspen site. However, since the MFA tended to stabilize once a region of mature wood was deposited (Table 10), it is feasible to compare the differences between sites for the first 10 increments.

Using this approach, it was apparent that the trees from the mixed site had a higher MFA than the trees from the pure aspen site at any given distance from the pith. The mean MFA for the trees originating from the mixed site at the first point of measurement (near the pith) was less than one degree higher than that of trees from the aspen site (29.49° vs. 28.59°). As the distance from the pith increased, so did the difference between in MFA from the mixed and aspen sites, reaching a maximum difference of 2.83° at 3cm from the pith, with a mean difference of 2.05°.
To better illustrate the differences in MFA between sites, both the mean MFA for the entire tree as well as the MFA estimate of each tree’s final growth year were applied to a t-student test in order to determine if any differences exist. There were significant differences ($\alpha=5\%$) between them; the mixed site exhibiting higher values for both mean MFA and final MFA ($19.75^\circ$ vs. $20.89^\circ$, and $18.01^\circ$ vs. $18.94^\circ$, respectively). Clearly, the mixed site has a propensity to deposit wood cells that characteristically displayed higher MFA values than the trees originating from the pure aspen site.

Separating the trees into dominant and co-dominant classes and comparing classes across sites produced similar results. The mixed site had higher MFA values than the pure aspen site in both classes, with the only change occurring with the dominant aspen, where the aspen site showed a higher value for the angle measured near the pith. From that point on, the mixed site shows a higher MFA at any distance from the pith. Again, when comparing mean MFA values and the final MFA values by class between the sites, the trees from the mixed site showed significantly higher MFA ($\alpha=5\%$). This suggests that adopting categorization by social class may not be efficient when the microfibril angle is being considered, since the results are similar to those obtained by site comparisons.

4.4.2 White spruce

Unlike the trembling aspen, the MFA estimated for the white spruce trees, taken at the pith and then at every 5 years, showed very little differences between sites. When comparing the first 50 years of growth of trees originating from the pure spruce and the mixed site, there were no significant differences between them. Although the spruce site had a slightly smaller initial MFA, the first 20 years showed practically no differences. From then on the MFA of the mixed
site drops below that of the spruce site, reaching a maximum difference of 3.80° at age 30. After which, the difference between sites once again decreased, remaining at less than a degree difference until age 50.

Similar to the trembling aspen, the mean MFA for the entire tree as well as the final MFA value for each tree were compared in an attempt to identify potential differences between sites. The pure spruce site showed a slightly higher estimate for both mean tree MFA and final MFA (22.52° vs. 20.96° and 17.54° vs. 17.38°, respectively), however, the differences were not statistically significant (α=5%).

The use of social classes to compare sites produced similar results. For both the dominant and co-dominant classes, the mixed site showed a slight reduction in MFA. In the dominant class, this reduction occurs from the 5th year onward, with the mixed site only showing a higher MFA at year 45. The mixed co-dominant class only started to show smaller MFA estimates than the co-dominant spruce at approximately year 15, remaining below the co-dominant spruce site for the remaining years. When comparing the mean tree MFA and the final MFA both the dominant and the co-dominant classes show no significant differences between sites.

Overall, the differences in white spruce MFA between the mixed and spruce sites were insignificant, for both site vs. site comparison, as well as social classes comparisons.

4.4.3 Considerations regarding microfibril angle

Overall, the microfibril angle only showed significant changes between sites in trembling aspen trees. There were no significant differences in MFA for white spruce when comparing sites, or when comparing social classes across sites. Therefore, it is apparent that the presence or absence of trembling aspen has little effect on the microfibril angle of white spruce.
Trembling aspen trees from the mixed site showed a higher MFA than those from the aspen site. However, a lower MFA is considered a more desirable trait, therefore making the aspen wood from the pure aspen site a more attractive choice, especially for the lumber sector. As discussed in the introduction, MFA has been linked with longitudinal shrinkage, modulus of elasticity and modulus of rupture, and has been shown to be at least as important as density for the prediction of the strength and the stiffness of solid wood of some tree species (Jozsa and Middleton, 1995; Evans and Ilic, 2001; Downes et al., 2002; Donaldson, 2008).

Evans and Ilic (2001) reported that MFA together with wood density accounted for 96% of the variation in the modulus of elasticity for *E. delegatensis*, with MFA alone accounting for 86% of the variation. As shown, wood density of trembling aspen had very little variation between sites and social classes, only showing statistical differences when comparing the dominant social class across sites. On the other hand, MFA varied significantly in all comparisons, both between sites and between social classes. This makes MFA a valuable measurement in comparing aspen resources, since it can be used to infer differences in wood and fiber stiffness and shrinkage between the sites, as well as between social classes.

**4.5 Fibre Traits**

Fibre traits showed significant differences by stand and among social classes for both species.

**4.5.1 Trembling aspen**

Comparing aspen by site showed significant differences for all fibre traits measured: fibre length, fibre width, vessel element length, vessel element width, vessels per meter, and fibre coarseness.
These differences suggest that the presence of white spruce in the mixed site has an effect on fibre quality traits of trembling aspen.

Fibre length for trembling aspen had a mean value of 0.868 mm for all trees from both aspen and mixed aspen site combined, which are similar estimates to those previously published for trembling aspen (Yanchuk et al., 1984; Yanchuk and Micko, 1990; Mansfield and Weineisen, 2007). The trembling aspen trees from the aspen site had a significantly higher mean fibre length than the trees from the mixed site (0.897 mm vs. 0.804 mm). The same pattern was observed when comparing fibre widths of trees from both sites. The fibre coarseness values also indicated that trees from the pure aspen site possess significantly higher mean coarseness values than those from the mixed site (0.136 mg/m vs. 0.124 mg/m). It is therefore apparent that trees from the pure aspen site have longer and wider fibres, and that these fibres have thicker cell walls, as implied by coarseness. Consistent with the fibre measurements, all vessel estimates were significantly greater in cells originating from the aspen site compared to the mixed site (Figures 14, 15 and 16).

Although all fibre traits showed significant differences between the two sites, when the trees were divided into social classes, some traits show similar values in the same social class for both sites (Figure 17). Fibre length had a higher mean value in trees from the aspen site when comparing co-dominant classes. However, there was no significant difference in fibre length when comparing the dominant trees. Therefore, the significance in fibre length that occurs when comparing trembling aspen trees between sites is a function of the large differences apparent in the co-dominant classes.
Comparing the fibre widths of each social class follows a similar trend to comparisons made by site, where trees from the aspen site have wider fibers than those from the mixed site (Figure 16). These estimates are consistent for both dominant and co-dominant classes, and in both cases there are significant differences between sites.

Although there was a significant difference in fibre coarseness between sites, when the trees were divided into social classes no such difference emerge (Figure 19). The dominant trees from the aspen site have a higher mean coarseness than dominant trees from the mixed site, but this difference is not significant at 5%. The same trend occurs with the co-dominant trees from each site. Therefore, the significant difference in coarseness between sites only occurs when comparing all trees from each site, regardless of class. Once the data is broken up into smaller subsets (social classes), these differences are not retained.

4.5.2 White spruce

Similar to the trembling aspen, the white spruce from the mixed and pure spruce site showed differences in all fibre traits. Tracheid lengths varied between 1.469mm and 2.641mm with a mean value of 2.081mm for all white spruce trees, regardless of site. These values are consistent with estimates previously published (Taylor et al., 1982; Beaulieu, 2003). Tracheids originated from the spruce site possessed a higher mean (2.154 mm) than those from the mixed site (1.931mm). According to Sanio’s Law, “the tracheid increases in size from within outwards, throughout a number of annual rings, until they have attained a definite size, which remains constant for the following annual rings” (Bailey and Sheppard, 1915). Since trees from the spruce site possess, on average, over twice as many growth rings as those from the mixed site, it is expected that the samples from the pure spruce site will possess a larger proportion of
Tracheids that have already reached their defined size. As a result, the mean tracheid length value of the entire tree will be higher.

Tracheid width for all trees varied from 31.5 µm to 42.5 µm with a mean value of 37.82 µm regardless of site. When comparing the different sites, tracheid width followed the same trend as length, where the tracheids from the pure spruce site were wider than those from the mixed site (38.1 µm vs. 37.2 µm). Although the mean values were close, there was a significant difference between the sites. Coarseness of all white spruce trees independent of site, varied from 0.102 mg/m to 0.258 mg/m with a mean value of 0.152 mg/m. As expected, coarseness also showed the similar pattern, where tracheids from the pure spruce site possess a higher mean coarseness than those from the mixed site (0.164 mg/m vs. 0.130 mg/m). And, coarseness was significantly different.

When grouping the samples by social classes in an attempt to eliminate the effect of age, clear trends became apparent regarding values for length and width. For both dominant and co-dominant classes, the tracheids from the spruce site had longer lengths than tracheids from the same class in the mixed site (Figure 23). However, tracheids from dominant trees had a mean shorter length than those from the co-dominant trees, on the pure spruce site. This was not the case in the trees originating from the mixed site. This suggests that as the stand advances from a mixed composition to one dominated by white spruce, the co-dominant white spruce trees will have longer tracheids that will eventually surpass the tracheids lengths of the dominant class as succession progresses.

Tracheids width variation by the social class showed that the tracheids from the pure spruce site had a higher mean value than those from the mixed site when comparing the same
social class (Figure 24). Dominant trees from the pure spruce site were wider than the dominant trees from the mixed site, however, there was no significant difference between them. When comparing co-dominant trees, the difference was statistically significant, however.

Grouping the trees into social classes had no effect on white spruce coarseness. Comparing social classes between sites produced the same results as when comparing all trees from each site regardless of class. Tracheids from the spruce site always showed a higher mean value than coarseness estimates from the mixed site, and in all cases there were significant differences between the samples.

### 4.5.3 Considerations regarding fibre traits

It is imperative to determine what the final use for the wood from each site is in order to reach decisions as to which of the two sites is the most efficient for each species. However, as a general rule, longer and wider fibres are of greater interest, in particular to the paper and pulp industry, as fibres possessing these characteristics generate higher quality paper products (Seth 1990a; Seth 1990b). If indeed longer and wider fibres are desired, the aspen trees from the aspen site possess the better properties, as they show significantly longer fibre length, and greater fibre width and fibre coarseness. In contrast, if spruce is the species of interest, then the trees originating from the pure spruce site have the higher quality fibres. As with the trembling aspen, the white spruce trees from the spruce site show significantly longer tracheid lengths, and have larger width and higher coarseness values than trees from the mixed site.

Fibre coarseness is a valuable tool when trying to specify the value of wood for pulp and paper since it takes into consideration length, width and cell wall thickness. As discussed, the ideal coarseness will depend on the final use of the paper which is being produced. A lower
coarseness will generate higher fibre collapse, producing a paper with improved density and optical properties (Mansfield and Kibblewhite, 2000). Fibres with high coarseness will generate paper with a higher porosity. If the industry in question is seeking fibres with a higher coarseness, then they should prioritize sites where the species in question is dominant and not from the mixed site.

The mixed site shows the least favourable fibre traits for both trembling aspen and white spruce. However, because these stands offer a greater diversity in timber options (since it is composed of two species), decision makers would have to take into consideration if the decreased fibre quality in the mixed species is substantial enough to offset other potential advantages of harvesting from a mixed species stand.

When considering social classes applied to trembling aspen, trees from the co-dominant class show a bigger difference in fibre quality traits between the two sites. The co-dominant class shows differences in length and width, while the dominant class differs only in width. There are no differences between sites in coarseness values for both social classes. There is therefore no strong indication that a particular social class will be better than its equivalent in the mixed or pure site.

With respect to white spruce, trees from the pure spruce site show better traits than those from the mixed site for both dominant and co-dominant social classes. Tracheid length and coarseness are significantly higher in both classes in the spruce site, with tracheid width also being higher for the co-dominant trees. These trends follow the same pattern when comparing all spruce trees without separating them into social classes, where the trees from the spruce site posses significantly higher tracheid length, width and coarseness.
Therefore, classification by social classes for both trembling aspen and white spruce is not beneficial, in terms of fibre traits. However, based on the data obtained, when harvesting from either a mixed site or a site where the species in question is dominant, trees in the dominant social class will have higher coarseness values than trees from the co-dominant class. This is true for both trembling aspen and white spruce. This information can be used to improve the final usage of each class within a site, thus adding to the productivity and value of the site.

4.6 Cell Wall Chemistry

4.6.1 Trembling aspen

The mean carbohydrate and lignin content of the xylem of the trembling aspen samples, regardless of site, was 75.3% carbohydrates and 21.9% lignin. These values are in accordance to previously published values for cell wall composition of trembling aspen (Stewart et al., 2006; Mansfield and Weineisen, 2007)

As shown (Figure 26) there were no significant differences in carbohydrate content of the aspen, regardless of site. This observation suggests that the presence of white spruce has little or no effect on the carbohydrate content of the xylem of aspen. However, there was a reduction in lignin content in the aspen trees from the mixed site (20.4% vs. 22.6%). Lignin is a major obstacle in the production of pulp and paper, and trees possessing lower lignin content are beneficial in pulp production. However, this lower lignin content is offset by the poorer fibre traits observed in aspen trees from the mixed site compared to those from the aspen site.

When separating the trees into social classes, a similar trend showing lower lignin content in the mixed site occurs for both dominant and co-dominant social classes (Figures 27 and 28).
The lower lignin content apparent by social classes on the aspen site compared to the mixed site are larger than the difference between all trees from each site, regardless of class: 22.3% to 19.9% for dominant trees, and 23.4% to 20.8% for co-dominant trees. Despite these differences, there were still no significant changes in carbohydrate content between sites when comparing social classes.

4.6.2 White spruce

The chemical analyses of the xylem of the white spruce were similar to that of the trembling aspen. The total carbohydrate and lignin content for all spruce trees, regardless of site or class, was 70.9% and 26.0%, respectively. These values are also similar to previously published cell wall chemistries in white spruce (Rowell et al., 2005; Willfor et al., 2005). Softwoods tend to have higher lignin content than hardwoods, varying from 25-30% (Pereira et al., 2003).

Not unlike trembling aspen, there were no significant differences in carbohydrate content between the spruce and the mixed site. However, once again there was a difference in the lignin content, where the mixed site showed a statistically higher amount of lignin than the spruce site (26.9% vs. 25.6%). This difference in lignin content, together with improved fibre quality traits (i.e. tracheid length and coarseness) makes the spruce trees from the spruce site a better candidate for paper and pulp applications.

Sub-dividing the sites into dominant and co-dominant classes had no effect on cell wall chemistries. For both dominant and co-dominant classes there were no significant differences in carbohydrate content. In addition, the spruce site had lower lignin content than the mixed site for both classes. The dominant trees from the spruce site had the lowest lignin content (25.1%),
while the co-dominant trees from the mixed site had the highest content (26.9%). As with the trembling aspen, dividing the sites by social classes showed no advantage.

4.6.3 Considerations regarding cell wall chemistry

For both species and social classes, the presence or absence of one species seems to have no significant effect on the levels of carbohydrate in the cell wall. However, it does influence the lignin content, since both species showed significant differences between the species specific site and the mixed site.

For the trembling aspen, the mixed site had the lowest observed estimates of cell wall lignin. In contrast, the spruce site had the lowest lignin content for the spruce. As discussed, following the notion of a relay floristics forest succession, the aspen site is at a younger stage than the mixed site, which in turn will one day progress into the spruce site. The tree volume data not only supported this idea of forest succession, but also showed that trees from the aspen site were younger than those from the mixed site, with the trees from the spruce site being the oldest. The visible growth rings on the spruce increment cores also supported this observation. As such, it is possible to conclude that the older the site, the lower the lignin content for both trembling aspen and white spruce.

When comparing social classes between sites, both dominant and co-dominant classes showed the same pattern as comparing sites independent of social class for both species. It is therefore irrelevant to wood chemistry to divide the sites into social classes.
4.7 Trembling aspen in single species and mixed species stands

There are several differences between the aspen trees from the aspen site and the mixed site when taking volume and wood quality traits into consideration. Table 12 shows the significant differences that were observed between the pure aspen and the mixed site for trembling aspen:

<table>
<thead>
<tr>
<th>Wood Trait</th>
<th>Aspen Site (PSP 430)</th>
<th>Mixed Site (PSP 434)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volume</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wood Density</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fibre Length</td>
<td>↑</td>
<td>↓</td>
</tr>
<tr>
<td>Fibre Width</td>
<td>↑</td>
<td>↓</td>
</tr>
<tr>
<td>Fibre Coarseness</td>
<td>↑</td>
<td>↓</td>
</tr>
<tr>
<td>Mean MFA</td>
<td>↓</td>
<td>↑</td>
</tr>
<tr>
<td>Final MFA</td>
<td>↓</td>
<td>↑</td>
</tr>
<tr>
<td>Carbohydrate Content</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lignin Content</td>
<td>↑</td>
<td>↓</td>
</tr>
</tbody>
</table>

It is impractical to suggest that one site produces better wood than the other, since desired wood quality traits vary according to the final use of the wood. However, some general observations can be made based on the summary table above.

Due to the difference in volume, and presumably age, it is expected that the younger trees from the aspen site posses a higher juvenile to mature wood ratio than the more mature trees from the mixed site. Juvenile wood from hardwoods are characterized by possessing lower wood density, larger microfibril angles, and shorter fibres (Zobel and Sprague, 1998). It would
therefore be expected that trees from the aspen site should have, at least to some degree, lower wood density, smaller fibres, and larger MFAs. However, when compared to the mixed site, these trees show no significant difference in wood density, and have significantly longer fibers with smaller MFAs.

Although tree volume drastically changes from one site to the other, this is primarily due to the difference in age between trees, and not necessarily due to the influence of the presence or absence of white spruce. Therefore, it is not practical to make volume based harvesting decisions or processing purposes only taking into consideration the species composition of each site.

For the lumber and structural wood industry, of all the traits measured, wood density is the best indicator of wood quality. There were observable variations in wood density, making it hard to draw conclusions on the best site based on this fundamental wood quality trait. Although higher density wood is often sought after due to its direct influence on wood strength and performance, low density wood also has its qualities and should not be overlooked. Low density wood may be valued in such industries as OSB manufacturing where lower density chips provide improved aspect ratio and absorption. Semple et al., (2007) found that boards made from low density hybrid poplar clones were similar or better in properties than those made from the mill run commercial aspen furnish, and complied with minimum strength standards. The authors found that a low density clone (328 kg/m³) produced greater mat volume for its weight and subsequently compacted into higher density boards.

In addition to wood density, the microfibril angle of the S₂ is a critical factor in determining the mechanical properties of wood (Jozsa and Middleton, 1995; Evans and Ilic, 2001; Downes et al., 2002; Butterfield, 2003; Mansfield et al., 2009). A smaller MFA has been
associated with improved flexural properties, and as such lower MFA values are desired for the lumber industry. The aspen site showed significantly lower MFA values, making the wood from this site a better candidate for lumber and structural wood purposes.

For the pulp and paper industry, a higher density wood is often desired, as it will generate higher pulp yields. Since there were no significant differences in the wood density between the two sites, other parameters must be used to determine which site will produce better feedstocks. As discussed in the introduction, fibre length is directly linked to interfibre bonding, and as such influences the tensile strength of paper. Higher coarseness, which expresses fibre wall thickness, will generate higher tear strength, breaking length, bulk and absorbance properties (Seth 1990a; Seth 1990b; Da Silva Perez and Fauchon, 2003). The wood from the pure aspen site possesses longer fibre lengths and increased fibre coarseness, and as such would be a better candidate for pulp and paper use. Another fundamental trait for pulp purposes is the lignin content. As discussed, the removal of lignin in the production of pulp is one of the most costly steps, and as such wood with lower lignin contents is more suitable for chemical pulp production. Even though the aspen site showed better fibre traits, its trees contained significantly higher lignin concentrations. The mixed site, on the other hand, had trees with lower lignin content but proper fibre traits. Therefore, decisions need to be made based on final product quality or yield improvements.

4.7.1 The use of social classes applied to trembling aspen

Although dividing the trees from each site into social classes based on DBH values did disclose some interesting observations, the overall trends when comparing similar social classes across sites made few differences. Wood density in the dominant class was significantly higher in trees
originating from the pure aspen site than in the mixed site. However, this difference was not apparent in the co-dominant class or when comparing sites. On the other hand, the significant differences in fibre length from the aspen and mixed site were not expressed in the dominant class. Coarseness showed no significant differences in both classes despite being of importance when comparing sites. With respect to tree volume, fibre width, vessel element length, vessel element width, vessels/m, mean MFA, final MFA, carbohydrate content and lignin content, both the dominant and co-dominant classes showed the same significant differences as when comparing all trees on each site.

The trees were classified into social classes based on their DBH. Trees showing DBH values between the midpoint to the 3rd quartile were considered co-dominant trees, while trees with DBH values between the 3rd quartile and the maximum value classified as dominant. In order to subdivide the trees in each site into such social classes, it is necessary to measure the DBH of all trees on the site, a process which is very time consuming and potentially costly. Since the vast majority of the quality traits studied showed no differences between the comparison of sites and the comparison between the same social class between sites, it is fair to conclude that the time and resources required to categorize the trembling aspen trees into social classes is not worth the limited benefits it would produce.
4.8 White spruce in single species and mixed species stands

Significant results were also obtained when comparing the wood quality traits of white spruce trees from the mixed and pure spruce sites, as shown by Table 13.

Table 13. Significant differences in white spruce between spruce site (PSP 379) and mixed site (PSP 434) for various wood quality traits

<table>
<thead>
<tr>
<th>Wood Trait</th>
<th>Spruce Site (PSP 379)</th>
<th>Mixed Site (PSP 434)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volume</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wood Density</td>
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<td></td>
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<td>Fibre Length</td>
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<td>Fibre Width</td>
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<td>Fibre Coarseness</td>
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<td>Mean MFA</td>
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The large difference in tree volume between the pure spruce and mixed site is primarily a function of the large differences in tree age between the two sites. Trees from the mixed site were on average 50 years of age, while some of the trees originating from the spruce site were well over 120 years of age. This difference in age seems to be the main cause of this large disparity between tree volumes, and the presence or absence of aspen has little to no effect on tree volume.

Similar to the findings of aspen, for the lumber and structural wood industry, wood density is the main trait. However, no significant differences were apparent between sites despite
the difference in age and, presumably, differences in juvenile to mature wood ratio. Again, like trembling aspen, it is therefore impossible to determine which site had better wood quality based solely on wood density. Microfibril angle can also be used as an indicator of how well the wood might perform in physical and mechanical tests, with a lower MFA being preferred. Once again, there were no significant differences between the two sites. The lack of statistically significant difference between the two sites makes it difficult to draw conclusions for the lumber industry, based on these traits. The choice between sites therefore must be made based on other parameters, such as accessibility, harvesting time, tree volume, volume per hectare, annual increment.

In contrast, for pulp and paper purposes, the data suggests that the white spruce from the pure spruce site possesses both better traits and lower lignin contents. Tracheid length, width and coarseness are all significantly higher in the spruce site. The lower lignin content also suggests that the wood from the spruce site would be better suited for pulp production than the wood from the mixed site. However, one must consider that the spruce site is around 70 years older than the mixed site, and as such, it might not be economically sound to wait this extended period for only incremental improvements. On the other hand, if a forest manager has access to both forest types, it would be sound to harvest the site with higher spruce basal area first and allow the mixed species site to mature.

Overall, the spruce site shows better quality traits than the mixed site. All tracheid traits are significantly improved, as is tree volume. Lignin content is lower, which can be seen as a positive trait, especially to the pulp industry. All other traits (wood density, mean MFA, final MFA and carbohydrate content) show no significant differences among the sites. However, it is important to stress that the spruce site is a much older site.
4.8.1 The use of social classes applied to white spruce

The use of social class to sub-divide each site again showed interesting results. Although some traits behaved differently when compared by social classes, the majority showed the same pattern as when comparisons were made by site.

When comparing all individuals from the spruce site to those of the mixed site, there were no significant differences in wood density. However, once social class was introduced, both the dominant and the co-dominant class showed a significant increase in wood density in trees originating from the pure spruce site. Together, this implies that the overall wood quality of the trees from the spruce site is superior.

In addition to wood density, tracheid widths showed a difference when social classes were applied. When comparing sites, tracheid width, together with length and coarseness, increased on the spruce site. However, when comparing the dominant class between the two sites, there was no statistical difference in tracheid widths, while this difference does occur in the co-dominant class.

Despite difference occurring in wood density of social classes across sites and change in tracheid width in the dominant class, most traits showed similar trends when compared by site. Due to the amount of time and resources which must be spent to classify all the trees into social classes, it would not seem beneficial to attempt this action on a commercial scale.
4.9 Limitations and future work

It is necessary to point out some of the limitations of this study, most of which stem from restrictions of accessibility. In addition, some future work is proposed to help overcome these limitations and to better justify the conclusions regarding wood quality between the different sites.

Although the method used for sampling guaranteed a large number of trees of both species from the sites, only a single location was sampled for each site type. Thus, despite having a large number of individuals in the study, they may not represent the natural variation of wood traits in trembling aspen and white spruce of the boreal mixedwood forests of Canada. A more effective sampling method might have been to sample fewer trees from more sites. Such a strategy would guarantee a better representation of the different stands and therefore reveal a greater diversity in the wood traits of trembling aspen and white spruce.

The method of sample collection suggested above is particularly important when considering trembling aspen trees, as aspen regeneration can proceed by ramet formation, and ultimately may generate clonally propagated stems. Thus, the employed sampling methodology may indeed have captures samples that originate from a single individual. Although different stems will grow at dissimilar rates and generate different wood traits (due to environmental differences), such phenotypic variability will be reduced because stems may share a common genetic background. Increasing the number of sites used for sampling would greatly reduce the possibility of having stems of the same genotype, or employing a large geographic area to collect samples may minimize the impact of clonality.
Another aspect which must be addressed is the fact that the trees employed in the comparison of sites were of different ages and stages of development. Age differences can affect wood traits, including juvenile to mature wood ratio, proportion of early to latewood, and width of growth ring, to name a few. Specifically, for the white spruce, trees from the mixed site showed an average of around 50 growth rings, while trees from the pure spruce site possessed as many as 130 growth rings. The same difference in development occurs for the trembling aspen trees. Although the aspen growth rings are not visible to the naked eye, the large differences in average tree diameter between trees from the aspen site and trees from the mixed site also suggest a difference in stage of development. Since most wood quality traits were generated from the entire increment core, comparing trees of substantially different ages will impact the overall wood quality, and as such the conclusions drawn based on site.

One way to overcome the differences in age and development would be to compare the same number of growth rings from each tree across sites. For instance, in the case of white spruce, the traits could be re-analyzed to only consider the first 50 growth rings of each tree, regardless of how many rings are in each individual core. Such an approach would limit the dissimilarities generated by the differences in stage of development. This is easily done for the white spruce, where growth rings are visible and therefore can be easily counted. In contrast, with the trembling aspen, where growth rings are not visible, other techniques for tree aging would be required, such as using x-ray densitometry to try and identify growth rings or the use of microscopy to establish age based on visual year transitions characteristic of growth rings.
Chapter 5: Conclusion

Comparing the different wood traits for both species across the sites has produced some interesting results regarding wood quality traits. However, it is still not possible to establish if one site/stand produces better wood than the other, since in order to draw such a conclusion one must first know which traits are desirable, and this is inheritably linked to its industrial use. In addition, one must consider if the main focus is on one particular species or if trembling aspen and white spruce are both of interest. In terms of wood quality, four main traits were analyzed: wood density, microfibril angle, fibre quality traits, and cell wall chemistry. These four characteristics did not all demonstrate an individual desired forest prescription (species composition), once again highlighting the importance of defining what parameters are desirable in order to select which site produces a better wood.

Wood density, considered by many the most important factor affecting wood quality, is a highly valued trait for both lumber and paper and pulp industries, since higher wood densities are often highly correlated to better physical properties of solid wood and higher pulp yields. Unfortunately, there were no significant differences in wood density when comparing the mixed site to the single species site, for both trembling aspen and white spruce. For trembling aspen, the trees from the mixed site had a higher wood density than those from the aspen site. On the other hand, the spruce from the mixed site had lower wood density than trees from the spruce site. However, none of these differences in wood density were statistically significant, despite the clear differences in tree volume between the sites. Although there were some differences between sites when social classes were used, the overall trend in this study shows that one must take other factors into account when determining wood quality tendencies.
Since wood density showed very little variation between the different sites for both species, MFA becomes a secondary determinant which may be used to establish the potential difference in wood quality between sites. Being able to harvest trees that posses a lower MFA would produce wood of higher quality, since MFA has been shown to influence important physical characteristics, including modulus of elasticity and shrinkage. The trembling aspen trees from the aspen site posses significantly lower MFAs than the trees from the mixed site, making them a better alternative for harvesting, in particular for the lumber industry. The white spruce however, showed no significant differences in MFA between sites, making it clear that, as with wood density, other factors must be taken into account to determine which site produces a higher quality wood. For both species, the use of social classes added little value to the results, since comparing the same classes across sites produced virtually identical results to simply comparing all trees in each site.

Although fibre traits have been shown to influence physical characteristics of wood that are important to the lumber and timber industries, it is the pulp and paper industry which is more affected by differences in fibre traits. Three main fibre traits were analyzed for both species: fibre length, fibre width and fibre coarseness. In addition, vessel measurements (vessel element length, vessel element width, and vessels per meter) were also obtained for the trembling aspen. For both species, the mixed site produced wood with lower fibre quality traits than the single species stand. The pure species stands produced fibres that were significantly longer, wider and with a higher coarseness. This observation clearly shows that the mixed site possesses trees with less desirable fibre traits, and as such will produce wood with a lower quality. However, one must keep in mind the differences in tree volume, and consequently, basal area of each site. Once
again, the use of social classes as a means to compare the different sites produced very similar results to when comparing site versus site.

Wood chemistry, in particular the carbohydrate and lignin contents, also produced interesting results for both species. The carbohydrate content did not vary significantly between the mixed site and the pure species site for both trembling aspen and white spruce. However, the lignin content did show significant differences between sites. As discussed, lignin is associated with cell wall stiffness and with reducing enzymatic degradation of the cell wall. On the other hand, lignin is a major obstacle to be overcome in the chemical pulp industry. Therefore, a lower or higher lignin content will be favorable depending on the industry in question. For trembling aspen, the trees from the mixed site show a significantly lower lignin content. The opposite is true for the white spruce, where trees in the mixed site show a significantly higher content. The use of social classes once again only confirmed these results and produced no different trends between sites and classes.

In summary, for the trembling aspen, the mixed site shows a higher tree volume, lower quality fibre traits, a larger microfibril angle, and lower lignin content than the pure aspen stand. For white spruce, the mixed site has a lower tree volume, lower fibre quality traits, and a higher lignin content. As an overall conclusion, one might consider the trees from the pure species stand generally have higher wood quality traits than comparable trees from mixed sites. However, it is not possible to make a definitive statement without knowing which factors are the most desirable and what industrial use the resource is intended to supply.
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