*Forests* **2015**, *6*, 1628-1648; doi:10.3390/f6051628

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*forests*

**ISSN 1999-4907**

www.mdpi.com/journal/forests

*Article*

# Variation in Trembling Aspen and White Spruce Wood Quality Grown in Mixed and Single Species Stands in the Boreal Mixedwood Forest

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Academic Editors: Phillip Comeau and Eric J. Jokela

*Received: 8 January 2015 / Accepted: 6 May 2015 / Published: 12 May 2015*

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**Abstract:** The Canadian boreal forest is largely represented by mixed wood forests of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx). In this study, a total of 300 trees originating from three sites composed of trembling aspen and white spruce with varying compositions were investigated for wood quality traits: one site was composed mainly of aspen, one mainly of spruce and a third was a mixed site. Four wood quality traits were examined: wood density, microfibril angle (MFA), fibre characteristics, and cell wall chemistry. Social classes were also determined for each site in an attempt to provide a more in-depth comparison. Wood density showed little variation among sites for both species, with only significant differences occurring between social classes. The aspen site showed statistically lower MFAs than the aspen from the mixed site, however, no differences were observed when comparing spruce. Fibre characteristics were higher in the pure species sites for both species. There were no differences in carbohydrate contents across sites, while lignin content varied. Overall, the use of social classes did not refine the characterization of sites.

**Keywords:** wood quality; *Picea glauca*; *Populus tremuloides*; wood density; microfibril angle; cell wall chemistry; fibre traits; social classes

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## 1. Introduction

A large percentage of the Canadian boreal forests consists of mixed wood forests containing white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx). Following a disturbance these stands are initially dominated by aspen, and over time the extent of white spruce recruitment in the understory varies with spruce seed source and seedbed conditions [1]. Once established, the spruce will grow and dominate as the aging aspen declines.

A number of studies have attempted to understand the effects of single and mixed species stand dynamics of the boreal forest. However, most of these studies focused on identifying the effects of species composition on productivity (*i.e.*, yields in basal area), nutrient cycling, and rotation lengths [2–10]. In recent years, wood attributes have emerged as an added characteristic of interest. Initially, research focused on the white spruce wood quality, however, over time, aspen fibre has also become economically important due to recent advances in pulping and strand-board technology, adding incentives to examine the productivity of this mixed wood species [3]. In addition, aspen and the other *Populus spp*. have recently been identified as key potential tree crops for biofuel applications.

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 would be the most productive choice. The most common mixed species stands are mixtures composed of faster growing shade intolerant species above slower growing shade tolerant species [11]. 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 [6].

In a plantation setting, the reasons why monocultures are favored over mixed species stands are well understood and documented—mainly the ability to concentrate site resources on the growth of one species with the most desirable characteristics. However, the use of mixed species stands may produce long-term benefits. The goal of using mixed species is to strategically combine certain species to produce specific interactions that will increase stand-level productivity or individual tree growth rates. Other possible benefits of mixed species stands include shortening rotation lengths, increasing basal area, improving wood quality traits, as well as minimizing the expenses involving clear cutting, planting, and competition control [1,5,7,9].

Controversies exist about whether or not a mixed white spruce/trembling aspen stand would be more productive than a pure stand of either species. Kabzems and Senyk [12] reported higher annual wood increments for an 80-year old mixed aspen-spruce stand than a 90-year old spruce stand (1.33 $m^3$ $ha^{-1}$ *vs.* 1.05 $m^3$ $ha^{-1}$, respectively) [7]. When comparing aspen stands with and without a spruce understory, MacPherson *et al.* [4] found that the mixed plots contain approximately 10% more biomass than pure aspen stands. However, when comparing the productivity of the aspen alone, the pure aspen plots possessed 12.9% more biomass than the aspen in the mixed plots, concluding 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." [4]. Day and Bell [13] also showed 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 [13]. Additionally, in all cases, little attention was given to traits other than growth.

The objective of this study was to elucidate the effects of stand-level species composition and social position on wood quality traits of trembling aspen and white spruce. Although some wood quality characteristics are inherent to a particular species, the same traits are also influenced by tree growing conditions. Via an analysis of wood quality traits such as wood density, microfibril angle, fibre traits and cell wall chemistry, this study attempted to investigate what impact the presence or absence of one species has on the wood quality of the other.

## 2. Experimental Section

### *2.1. Sample Procurement*

Between July and August of 2009, a total of 100 increment cores were collected from each of the three different in the boreal mixedwood forests of central Alberta, Canada for a total of 300 samples. These sites were selected based on basal area and species distribution, allowing 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 90% 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. The sample sites are part of the Permanent Sample Plots (PSP) established in Alberta for long-term evaluation, located in the Central Mixedwood Natural sub region, inside the Boreal Forest Natural region of Alberta. All sites are classified as mesic on the moisture scale, and modal on the soil nutrient scale.

The aspen site (PSP 430) was located near Lac la Biche, AB (Long: 111.56 Lat: 54.86 Elevation: 643 m) and is classified as C19aw9sw1—C class density (51%–70% of above canopy light blocked by overstory) according to the Alberta Vegetation Inventory (AVI) system of overstory classification. On average, the tree height on the site was 19 m for the leading species (aspen), which occupied 90% of the total crown canopy, while spruce occupied 10%. The mixed site (PSP 434) was also located in the Lac la Biche, AB region (Long: 111.42 Lat: 54.87 Elevation: 672 m), and is classified as C20aw9sw1—C class density (51%–70% of above canopy light blocked by overstory). On average, the tree height of the leading species (aspen) was 20 m and occupied 90% of total crown canopy. The spruce site (PSP 379) was located near Athabasca, AB (Long: 113.44 Lat: 55.34 Elevation 664 m), and classified as 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), and 90% of total crown canopy occupied by spruce. 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.

Initially, trees were measured for height and diameter at breast height (DBH) inside the PSP, and candidate trees were identified based on DBH. Next, trees inside the buffer zone immediately adjacent to the PSP, which had DBH and height measurements similar to the desired trees from inside the PSP were identified. These trees were then selected as the candidate tree for that ampling group, and an 8 m radius around the candidate tree was created and all trees of the desired species inside this 8 m radius were then measured for DBH and height. Based on these estimates, the 10 trees with the DBH values closest to that of the candidate tree in the PSP were randomly selected for increment core sampling. These 10 trees were cored with a 10 mm increment core borer at breast height on the north profile of each tree. This process was repeated ten times for each site, for a total of approximately 300 cores. All DBH measurements were made using a diameter tape, while tree heights were recorded using a Vertek III and T3 Transponder. Subsequently, tree volume was estimated using the height and DBH information for each tree according to standard volume formula [14].

### *2.2. Wood Density*

All increment core samples were allowed to air dry on the bench. Once dry, each core was cut to 1.68 mm thickness using a twin blade pneumatic precision saw. The side slabs generated from the sawing operation were subsequently used for wood chemistry and fibre properties estimation. The density samples were then soxhlet extracted overnight with acetone at 70 °C. Each sample was scanned using X-ray densitometry at 0.254 nm resolution (Quintek Measurement Systems Inc. Knoxville, TN, USA) from bark to pith, and an average sample density for each sample was obtained.

### *2.3. Cellulose Microfibril Angle (MFA)*

The same precision cut specimens used for density determination were used to obtain microfibril angle measurements. 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 readily discernible to the naked eye. In an attempt to overcome MFA variations with tree age, 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 fit with an area array detector. The X-ray source was equipped with a 0.5 mm 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 average of the *T*-values from each of the two 200 diffraction arc peaks was used to calculate the MFA.

### *2.4. Fibre Traits*

One residual side slab, generated during increment core sawing processing, was manually cut into smaller pieces measuring approximately 10 mm × 3 mm × 3 mm using a sterile razor blade. These pieces were then digested in Franklin solution (1:1, Glacial Acetic acid:30% hydrogen peroxide) at 70 °C for 48 h. After digestion, the remaining fibrous material was thoroughly rinsed with tap water and placed into a Waring blender with water and gently stirred for approximately 15 min to disrupt the fibrous materials into individual fibres. The material was then assessed for fibre length and width on a Fibre Quality Analyzer (OpTest Equipment Inc., Hawkesbury, Ontario, Canada). Subsequently, a fraction of each sample was precision weighed (1.2–2.4 mg for aspen and 3.2–5.8 mg for spruce), and then assessed for coarseness on the same Fibre Quality Analyzer.

### *2.5. Cell Wall Chemistry*

Thirty representative samples from each site were randomly selected for cell wall chemistry analysis (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). The woody material used for these analyses was derived from the second residual slab generated during the sawing operation. First, samples were ground in a Wiley

Mill to pass through a 0.40 mm mesh (40 mesh). The samples were then Soxhlet extracted overnight in 70 °C acetone. A modified Klason technique was used to determine the lignin and carbohydrate content of each sample [15]. Initially, 200 mg of each sample were hydrolyzed using 72% $H_2SO_4$ for two hours, being mixed every ten minutes. This solution was then transferred into serum bottles, to which 112 mL 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. The hydrolyzate was then filtered through a 4 mm Chromspec syringe filter (nylon; 0.45 µm) and the carbohydrate content of each sample were 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).

### *2.6. Social Classes*

Initially, samples were to be divided 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 3rd quartile of the whole stand were classified as co-dominant. Individuals whose DBH surpassed the 3rd 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.

### *2.7. Statistical Analysis*

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

The null hypothesis was that wood density, microfibril angle, fibre characteristics, carbohydrate content and lignin content would be the same for all trees of the same species, regardless of the site of origin. The $\alpha$ level was set at 0.05 for all tests (95% confidence level). A folded *F*-tests was first conducted to test for equality of variance, and depending on the outcome either a pooled or Statterthwaite *T*-test was conducted to test for significance of the means for each trait on the pair sites. The same tests were executed to compare the social classes across sites. All statistical analyses were completed in SAS (version 9.2).

## 3. Results and Discussion

Studies evaluating forest ecosystems are difficult to undertake due to the fact that the ideal scenario should consist of stands of even-age, mixed and single species grown under the same biogeoclimatic conditions (e.g., soil conditions, nutrients, climatic patterns, water regime, *etc*.). Moreover, such sites would need to include the appropriate variables that warrant investigation, for example forest type and species makeup. Alternatively, surrogate sites can be used, and often existing stands with common variables, which offers a means to compare pure stands of species with their mixtures [5,16]. In this project, we used the PSP for such an investigation; although not ideal, they are naturally regenerated stands in the boreal forest that are reserve sites and not available for forestry activities.

### *3.1. Wood Density*

Wood density is the single most important physical property influencing wood quality. It is an excellent predictor of strength, stiffness and hardness, and can be related to pulp quantity and quality [17–20]. Aubry *et al.* [18] identified wood density as a major contributor to the whole tree dollar value along with branch angle and volume. Wood density results from three interacting components: earlywood density, latewood density and the proportion of latewood [20,21]. Earlywood is produced early in the growing season until shoot elongation terminates, then latewood is deposited until cambial activity ceases in late summer [20].

Figure 1 shows the mean density for the aspen trees grown on the pure and mixed sites, as well as the densities of each social class. The aspen wood density ranged from 338 kg·m$^{-3}$ to 581 kg·m$^{-3}$ with a mean value of 457 kg·m$^{-3}$ for all trees. These findings are consistent with previously published values for aspen [22–25].

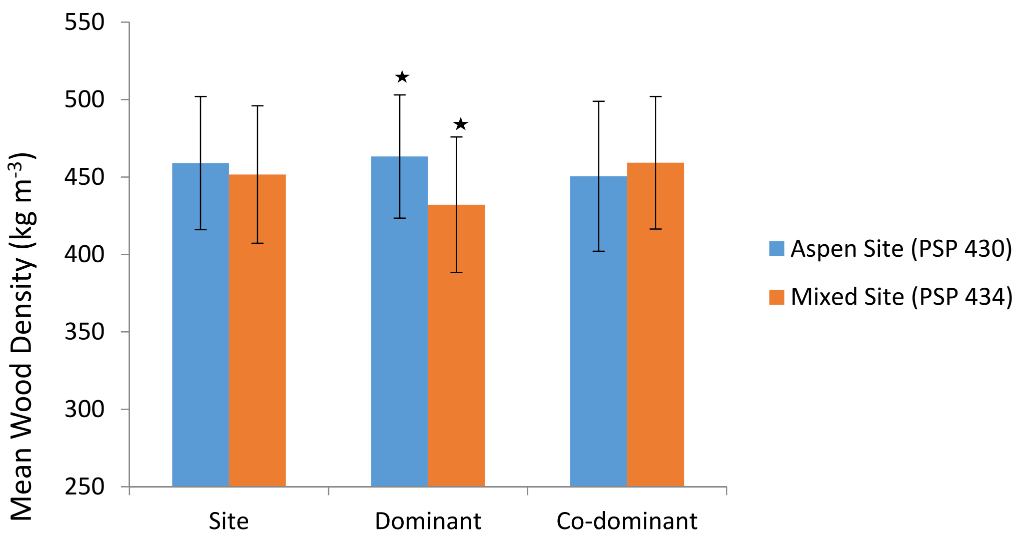


**Figure 1.** Mean wood density (kg·m$^{-3}$) for trembling aspen trees originating from an aspen site (PSP 430) and mixed site (PSP 434) by site and social classes. Error bars indicate standard deviation. Asterisk indicate significant differences (α = 5%). *n* = 100 on the aspen site, while *n* = 50 on the mixed site.

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 little effect on the overall wood density of trembling aspen. However, this is not the case when comparing trees by social class between sites. The dominant trees originating from the aspen site had a significantly higher mean density than those from the mixed site (463 kg·m$^{-3}$ *vs.* 438 kg·m$^{-3}$, respectively). This suggests 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 originating from the aspen site have only the co-dominant aspen trees with which to compete, and as such have 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 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 resource availability, and thus does not impact the wood trait in these trees.

Similarly, Figure 2 shows the mean density values for white spruce trees originating from both the spruce and the mixed site, as well as the spruce density values for each site as a function of social class.

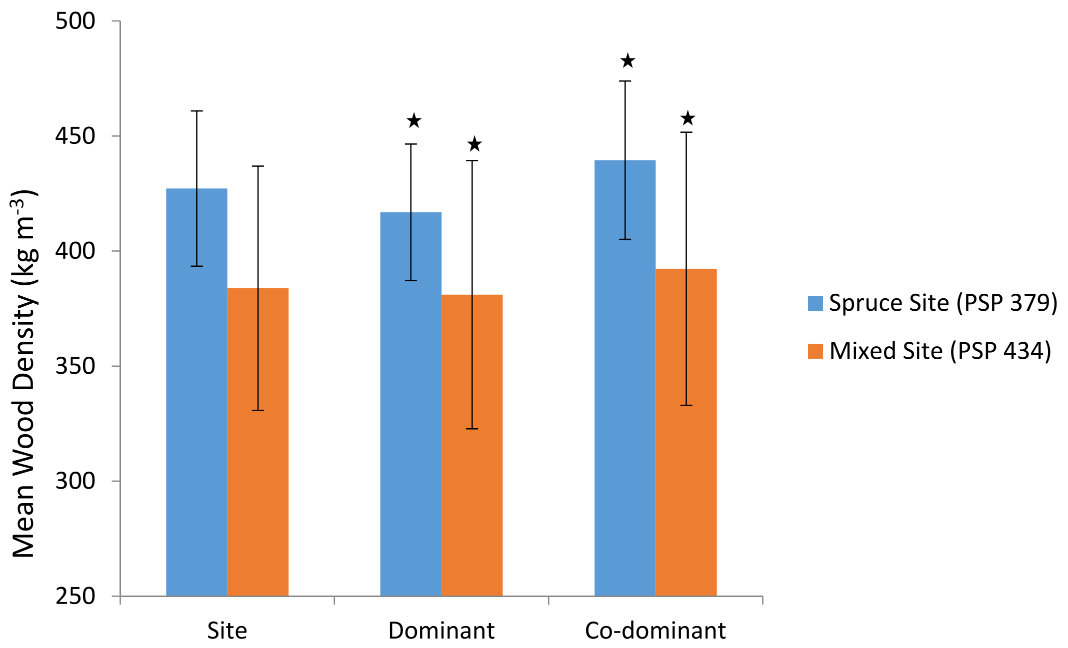


**Figure 2.** Mean wood density (kg·m$^{-3}$) for white spruce trees originating from a spruce site (PSP 379) and mixed site (PSP 434) by site and social classes. Error bars indicate standard deviation. Asterisk indicate significant differences ($\alpha = 5\%$). $n = 100$ on the spruce site, while $n = 50$ on the mixed site.

The density of the white spruce samples varied from 326 kg·m$^{-3}$ to 519 kg·m$^{-3}$, with a mean density of 412 kg·m$^{-3}$. These results are in accordance with previously published values for white spruce [26–28]. 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 (384 kg·m$^{-3}$ *vs.* 427 kg·m$^{-3}$, respectively). As previously discussed, the trees from the pure spruce site are older than those from the mixed site, and this difference likely explains 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 the comparison of trees originating from the spruce and mixed sites showed no difference in wood density, 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 class. 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 suggests that the presence of aspen in the mixed site had no significant apparent effect on the differences in wood density between social classes.

Given the importance of wood density [22,29,30], it is understandable that any difference in wood density between the single species and mixed species site would be of industrial importance. Unfortunately, when comparing 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. 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 where significant differences occurred between sites for both dominant and co-dominant classes. Therefore, when forest managers make decisions 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 be a factor taken into consideration if the trees have not first been sub-divided into social classes.

### *3.2. Microfibril Angle (MFA)*

Microfibril angle is the dominant angle of cellulose microfibrils, primarily in the $S_2$ layer of the cell wall, measured against the long axis of fibre cells. It is an important determinant of wood strength and elasticity [31]. Microfibril angle has been shown to explain a large portion of the variation of longitudinal modulus of elasticity ($E_L$) in loblolly pine and *Eucalyptus delegatensis* R.T. Baker (Evans and Ilic 2001) [32,33]. Cramer *et al.* [32] reported that up to 75% of the variation in $E_L$ could be explained by microfibril angle and specific gravity when earlywood and latewood data are combined, while Evans and Ilic [33] report an $R^2$ of 0.956 relating $E_L$ to the ratio of microfibril angle and density. There has been an increase in the recognition of the importance of incorporating wood quality traits in tree improvement programs, however, until recently, microfibril angle has been largely ignored, probably due to the inherent challenges in measuring this trait [31]. There is little doubt that microfibril angle is an important contributor to wood strength, yet the genetic control and relationship with other traits are largely unexplored. Within individual tracheids, microfibril angle changes little from tip to tip, however, the trend is for decreasing angles from the first earlywood cell to the final latewood cell within a growth ring [34,35]. Microfibril angle decreases from pith to bark and with increasing tree height, and there is a strong relationship with the number of rings from the pith [36,37]. It is widely accepted that microfibril angle is related to fibre length (Barnett and Bonham 2004) with an $R^2$ of 88.4% for

Douglas-fir [36] and significant negative correlations reported by Ivkovich *et al.* [38] and Hannrup *et al.* [39] in spruce.

For the trembling aspen samples, measurements were taken every centimeter starting at the pith in order to better understand changes in MFA as a function of cambial age. As expected, a higher MFA was apparent near the pith, which decreased with age, and then eventually stabilized (Table 1).

**Table 1.** Mean microfibril angle (degrees) at given distances from pith for trembling aspen trees originating from the aspen site (PSP 430) and the mixed site (PSP 434). $n = 100$ for the aspen site, while $n = 50$ for the mixed site.

| Distance (cm) | Aspen Site | Mixed Site |
|---|---|---|
| 0 | 28.59 | 29.46 |
| 1 | 23.84 | 26.28 |
| 2 | 20.50 | 23.25 |
| 3 | 18.47 | 21.30 |
| 4 | 17.90 | 20.27 |
| 5 | 17.79 | 19.83 |
| 6 | 17.53 | 19.45 |
| 7 | 17.64 | 19.23 |
| 8 | 17.76 | 19.30 |
| 9 | 17.45 | 19.60 |
| 10 | - | 19.55 |
| 11 | - | 18.71 |
| 12 | - | 18.74 |
| 13 | - | 17.49 |

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. 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, it is feasible to compare the differences between sites for the first 10 cm from the pith. Using this approach, it was clear 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 MFA from the mixed and aspen sites, reaching a maximum difference of 2.83° at 3 cm from the pith. 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 analyzed using a t-student test, revealing significant differences ($\alpha = 5\%$) between sites; the mixed site exhibiting higher values for both mean MFA and final MFA (19.75° *vs.* 20.89°, and 18.01° *vs.* 18.94°, 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 (Figure 3). 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 demonstrated 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 social class categorization may not be efficient when the microfibril angle is being considered, since the results are similar to those obtained by site comparisons.

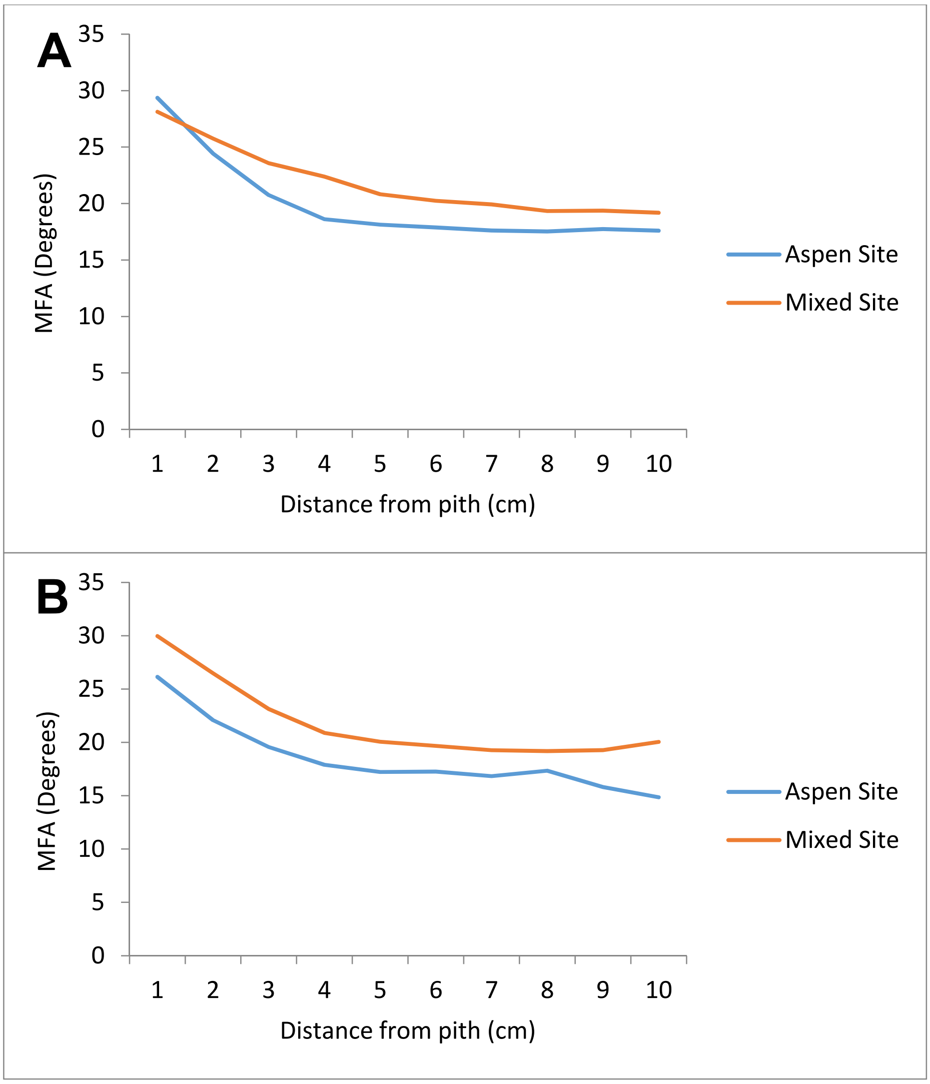


**Figure 3.** Mean microfibril angle (degrees) at given distances from pith for all dominant (**A**) and co-dominant (**B**) trembling aspen trees in aspen site (PSP 430) and mixed site (PSP 434). $n$ = 100 for the aspen site, while $n$ = 50 for the mixed site.

In contrast, since growth rings were easily discernible in the spruce samples, measurements of MFA were taken every five years of growth, starting from the pith. Generally, trees from both sites had similar MFAs in first ten years of growth (Table 2). As the trees aged, trees from the mixed site (PSP 434) showed a more rapid decline and consequently lower overall MFA estimated than those from the pure spruce site at similar ages. Trees originating from the mixed site also reach a plateau at a younger age than those from the spruce site. Unlike the trembling aspen, the MFA estimated for the white spruce trees 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. Thereafter, the MFA of the mixed site drops below that of the spruce site, reaching a maximum difference of 3.80° at age 25. After which, the difference between sites once again decreased, remaining at less than a degree different until age 50. When the mean MFA for the entire tree and the final MFA value for each tree were compared in an attempt to identify potential differences between sites, there were no significant differences between sites ($\alpha = 5\%$). 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).

**Table 2.** Mean microfibril angle (degrees) at given ages for white spruce trees originating from the spruce site (PSP 379) and the mixed site (PSP 434). $n = 100$ for the spruce site, while $n = 50$ for the mixed site.

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

The use of social classes to compare sites produced similar results (Figure 4). 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 not significant, for both site *vs.* site comparison, as well as social class comparisons.

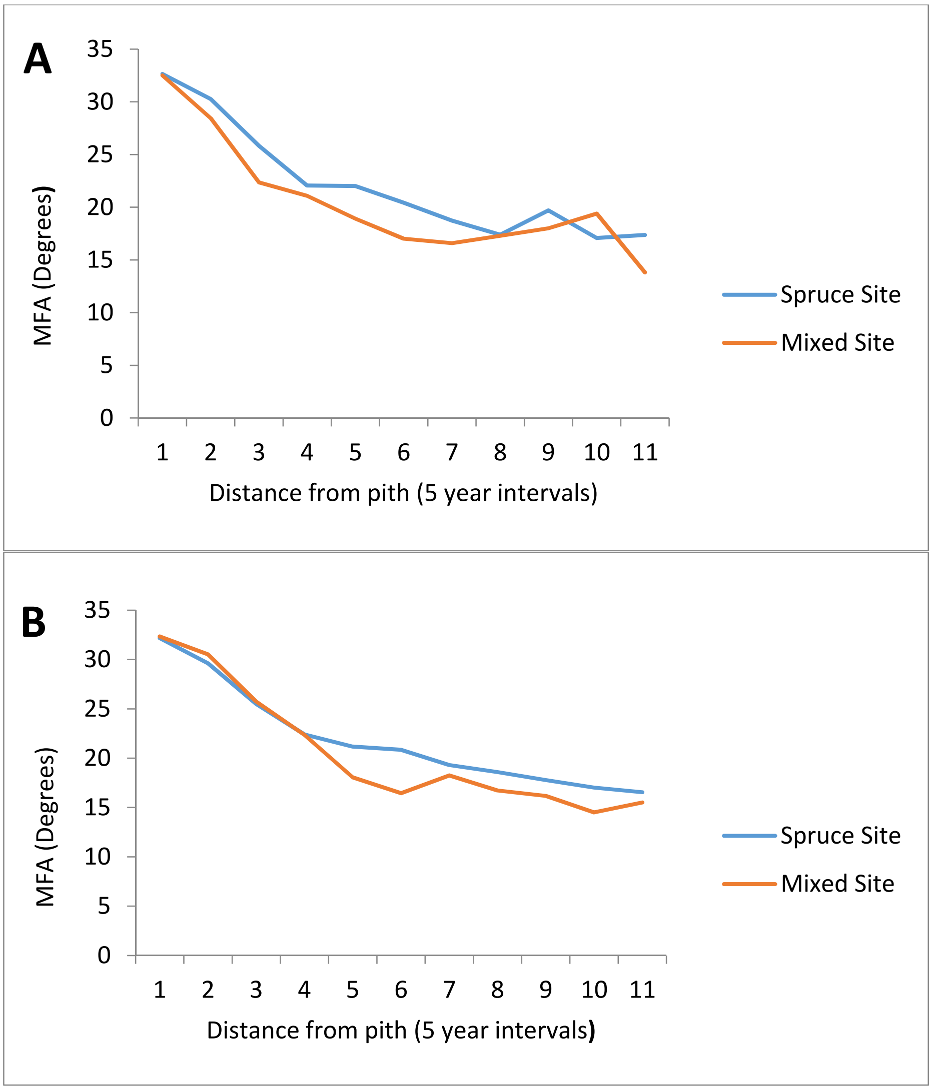


**Figure 4.** Mean microfibril angle (degrees) at given ages for all dominant (**A**) and co-dominant (**B**) white spruce trees originating from the spruce site (PSP 379) and mixed site (PSP 434). $n = 100$ for the spruce site, while $n = 50$ for the mixed site.

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 rendering the aspen wood from the pure aspen site a more attractive choice, especially for the lumber sector. 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 [33,40–42]. Evans and Ilic [33] 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 to compare aspen resources, since it could be used to infer differences in wood and fibre stiffness and shrinkage between the sites, as well as between social classes.

### *3.3. Fibre Traits*

Fibre length and coarseness are important wood fibre traits, which significantly influence paper quality, and thus have implications for the pulp and paper industry. Fibre morphology and cell wall structure directly influences fibre flexibility, plasticity and resistance to processing [43]. Coarseness is important to paper strength, which decreases with increasing coarseness [44]. It is also expected that improvements to growth and wood density through silvicultural and breeding activities will directly result in changes to fibre dimensions. For example, in an extreme case, the effect of increasing growth rate due to fertilizer application on fibre properties was measured in *Picea abies* (L.) Karst. [43]. Measurements were taken on trees involved in a long-term nutrient optimization experiment in northern Sweden. Trees from control plots were compared to trees from irrigation/fertilization plots. The authors found that in the presence of unlimited water and nutrients, growth rate increased resulting in a concurrent increase in lumen diameter and cell wall thickness, and a decrease in cell wall proportion and fibre length. This suggests that fibre morphology may be controlled by maturation and the number of cell divisions [43]. In Scots pine (*Pinus sylvestris* L.), Ericsson and Fries report a negative phenotypic correlation between fibre length and diameter [45]. However, strong positive phenotypic and genetic correlations were observed between fibre length, coarseness and height in maritime pine, and fibre length, height and diameter growth in Scots pine [19,46]. Furthermore, a strong relationship between wood density and coarseness and a weak relationship between wood density and fibre length have been documented [47].

All fibre traits showed significant differences when comparing sites regardless of social class, as seen on Table 3. Fibres from the pure aspen site were longer than those from the mixed site. Fibre coarseness also followed a similar trend. Fibre length for the trembling aspen had a mean value of 0.868 mm for all trees from both aspen and mixed aspen site combined, which were similar values to those previously published [25,48,49].

**Table 3.** Fibre and tracheid length (mm), width (μm) and coarseness (mg·m$^{-1}$) per site and social class. ($n$ = 100 samples per site).

| Site/Social Class | Length (mm) | Width (μm) | Coarseness (mg·m$^{-1}$) |
|---|---|---|---|
| Aspen Site (PSP 430) | 0.897 ± 0.102 * | 27.0 ± 1.4 * | 0.136 ± 0.028 * |
| Dominant | 0.893 ± 0.104 | 27.0 ± 1.5 † | 0.138 ± 0.029 |
| Co-Dominant | 0.909 ± 0.094 ‡ | 26.9 ± 1.2 ‡ | 0.132 ± 0.026 |
| Mixed Site (PSP 434) | 0.804 ± 0.071 * | 24.9 ± 1.2 * | 0.124 ± 0.024 * |
| Dominant | 0.847 ± 0.062 | 25.3 ± 1.3 † | 0.127 ± 0.018 |
| Co-dominant | 0.788 ± 0.068 ‡ | 24.7 ± 1.1 ‡ | 0.123 ± 0.026 |
| Spruce Site (PSP 379) | 2.154 ± 0.245 ** | 38.1 ± 1.7 ** | 0.164 ± 0.025 ** |
| Dominant | 2.155 ± 0.244 †† | 38.7 ± 1.5 | 0.165 ± 0.025 †† |
| Co-Dominant | 2.196 ± 0.239 ‡‡ | 37.7 ± 1.7 ‡‡ | 0.163 ± 0.026 ‡‡ |
| Mixed Site (PSP 434) | 1.931 ± 0.192 ** | 37.2 ± 2.2 ** | 0.130 ± 0.019 ** |
| Dominant | 1.983 ± 0.196 †† | 38.3 ± 1.8 | 0.133 ± 0.021 †† |
| Co-dominant | 1.875 ± 0.189 ‡‡ | 36.2 ± 2.1 ‡‡ | 0.128 ± 0.018 ‡‡ |

*, †, ‡, and **, †† and ‡‡ indicate significant differences (α = 5%) for aspen site comparisons and spruce site comparisons, respectively.

The trembling aspen trees from the aspen site had a significantly longer mean fibre length than the trees from the mixed site (0.897 mm *vs.* 0.804 mm). Similarly, 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$^{-1}$ *vs.* 0.124 mg·m$^{-1}$). 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. Fibre length had a higher mean value in trees from the aspen site when comparing co-dominant classes. Again, there was a significant difference in fibre coarseness between sites, and when the trees were divided into social classes no such difference emerge.

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 1.469 mm and 2.641 mm with a mean value of 2.08 mm for all white spruce trees, regardless of site. These values are consistent with estimates previously published [27,49]. Tracheids originating from the spruce site possessed a higher mean (2.15 mm) than those from the mixed site (1.93 mm). 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" [50]. 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 coarseness of all white spruce trees independent of site, varied from 0.102 to 0.258 mg·m$^{-1}$ with a mean value of 0.152 mg·m$^{-1}$. As expected, coarseness also showed a similar pattern, where tracheids from the pure spruce site possess a higher mean coarseness than those from the mixed site (0.164 mg·m$^{-1}$ *vs.* 0.130 mg·m$^{-1}$).

When grouping the samples by social classes in an attempt to eliminate the effect of age, clear trends became apparent. 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. On the pure spruce site however, tracheids from dominant trees had shorter mean length than those from the co-dominant trees. This was not the case in the trees originating from the mixed site, suggesting 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. Grouping the trees into social classes had no effect on white spruce coarseness.

It is imperative to determine what the final use for the wood from each site is in order to decide which of the two sites is the most efficient for each species. However, as a general rule, longer cells are of greater interest to the pulp and paper industry, as fibres possessing these characteristics generate higher quality paper products [51,52]. If indeed longer cells are desired, the aspen trees from the pure aspen site possess the desired properties, as they show significantly longer fibre length, and greater coarseness. In contrast, if spruce is the species of interest, then the trees originating from the pure spruce site have the highest quality fibres. 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. A lower coarseness will generate higher fibre collapse, producing a paper with improved density and optical properties, while fibres with high coarseness will generate paper with a high porosity [53]. 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 a mixed site.

When considering social classes in the trembling aspen, there is no strong indication that a particular social class will be better than its equivalent in the mixed or pure site. In white spruce, the trees from the spruce site possess significantly higher tracheid length and coarseness regardless of social class. Therefore, classification by social classes for both trembling aspen and white spruce is not beneficial, in terms of fibre traits.

### *3.4. Cell Wall Chemistry*

Wood chemical components ultimately contribute to the strength of wood and primarily affect pulping [19,54]. During the production of high quality paper, lignin is removed from the polysaccharide component of wood, which must be balanced with cellulose degradation [55]. Chantre *et al.* conducted a comprehensive study on the feasibility and relevance of selection for pulping potential in Douglas-fir. They report strong positive relationships between density traits and cellulose content, but negative relationships with lignin. They also report a strong positive relationship between modulus of elasticity (MOE), an indicator of lumber strength, and cellulose (0.606), but a negative relationship with lignin (−0.548) [56].

The results of cell wall composition analysis are summarized in Table 4. 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 [25,57].

**Table 4.** Xylem cell wall carbohydrate and lignin content (%) per site and social class ($n$ = 30 samples per site).

| Site/Social Class | % Carbohydrate | % Lignin |
|---|---|---|
| Aspen Site (PSP 430) | 74.12 ± 6.44 | 22.62 ± 1.92 * |
| Dominant | 75.17 ± 4.63 | 22.32 ± 1.62 † |
| Co-Dominant | 71.38 ±9.65 | 23.41 ± 2.50 ‡ |
| Mixed Site (PSP 434) | 77.60 ± 3.38 | 20.39 ± 1.63 * |
| Dominant | 78.54 ± 1.52 | 19.91 ± 1.92 † |
| Co-dominant | 76.79 ± 4.39 | 20.81 ± 1.31 ‡ |
| Spruce Site (PSP 379) | 70.89 ± 2.50 | 25.57 ± 0.99 ** |
| Dominant | 67.16 ± 4.19 | 25.10 ± 0.77 †† |
| Co-Dominant | 68.98 ± 5.20 | 25.22 ± 0.70 ‡‡ |
| Mixed Site (PSP 434) | 70.11 ± 4.08 | 26.88 ± 0.93 ** |
| Dominant | 70.12 ± 4.71 | 26.85 ± 1.02 †† |
| Co-dominant | 70.10 ± 1.93 | 26.95 ± 0.76 ‡‡ |

*, †, ‡, and **, †† and ‡‡ indicate significant differences (α = 5%), for aspen site comparisons and spruce site comparisons, respectively.

There were no significant differences in carbohydrate content of the aspen, regardless of site. However, there was a reduction in lignin content in the aspen trees from the mixed site (20.4% *vs.* 22.6%). 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. The lower lignin content apparent by social classes on the aspen site compared to the mixed site is 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.

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 similar to previously published cell wall chemistries in white spruce [58,59]. Following the same trend as 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 pulp and paper 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. As with the trembling aspen, dividing the sites by social classes showed no advantage.

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. 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. Conclusions

Comparing different wood traits for both species across the sites has produced some interesting results regarding wood quality traits. Wood density, considered by many the most important factor affecting wood quality, is a highly valued trait for both lumber, and pulp and paper industries, since higher wood densities are often highly correlated to better physical properties of solid wood and higher pulp yields. 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. Although there were differences between sites when social classes categorization was 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. The trembling aspen trees from the aspen site possess significantly lower MFAs than the trees from the mixed site, making them a better alternative for harvesting, in particular if aspen were to be manufactured into solid products, similar to the use of hybrid poplar in furniture components in China. 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.

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 indicates that the mixed site possesses trees with less desirable fibre traits, and as such could produce wood fibre of lower quality. However, one must keep in mind the differences in age of the trees, tree volume, and consequently, basal area of each site.

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. 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 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 originating from the mixed site show a significantly higher content.

In summary, for the trembling aspen, the mixed site shows lower quality fibre traits, a larger microfibril angle, and lower lignin content than the pure aspen stand. For white spruce, the mixed site has lower fibre quality traits, and higher lignin content. As an overall conclusion, one might consider the trees from the pure species stand generally have improved 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 for what industrial use the resource is intended. This study, however, only represents three sites, and it is recommended that follow up studies focus on the traits of interest in these species and examine several sites, to investigate the level of variability within these different site types.

## Acknowledgments

This project was supported by The For Value Network, a part of the National Sciences and Engineering Research Council of Canada (NSERC). We wish to thank Derek Sattler for his help in the field, as well as Tony Kozak for assistance with statistical analysis.

## Conflicts of Interest

The authors declare no conflicts of interest.

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