DETERMINING HYBRIDIZATION IN JACK PINE AND LODGEPOLE PINE FROM BRITISH COLUMBIA

Lisa J. Wood

PhD Candidate
Department of Geography
University of Victoria
Victoria, Canada
V8W 3R4

Ian D. Hartley†

Associate Professor
Ecosystem Science and Management Program
University of Northern British Columbia
Prince George, Canada
V2N 4Z9

Paul Watson[1]

Program Manager—Fibre Supply and Quality
Pulp and Paper Research Institute of Canada
Vancouver, Canada
V6S 2L9

(Received January 2009)

Abstract. This study was conducted to find wood quality evidence of hybridization between jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta* var. *latifolia*) in northeast British Columbia (BC). To determine if wood and fiber traits could be used as distinguishing features among jack pine, lodgepole pine, and their hybrids, differences in morphology and wood and fiber traits were related to the genetic identity of each sample. Thirty samples each of pure lodgepole pine, pure jack pine, and potential hybrids were collected from the Prince George area of BC, the Smoky Lake area of Alberta, and the Fort Nelson region of BC, respectively. Two 10-mm cores (bark to bark) were taken from each tree and analyzed for fiber length and coarseness, microfibril angle (MFA), basic density, earlywood:latewood ratios, and cell dimensions. Needle and cone morphology was used to distinguish among species groups in the field. Based on genetically identified samples, the fiber traits that best differentiated among pure jack pine, lodgepole pine, and hybrids were MFA and cell area.

Keywords: Hybridization, *Pinus contorta* var. *latifolia*, *Pinus banksiana*, wood properties, Fiber Quality Analysis, SilviScan

INTRODUCTION

Conifers can be classified by several distinguishing features. Morphological traits such as cones, needles, bark, height, and crown shape are most commonly used to identify pine species in their natural environment. These morphological characteristics can be used as evidence of hybridization between lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*Pinus banksiana*) (Critchfield 1985; Wheeler and Guries 1987). Hybridization is defined as the "...interbreeding of two populations or groups of populations, which are distinguishable on the basis of one or more characters..." (Woodruff 1973). Wheeler and Guries (1987) studied four putative hybrid populations surrounding Blue River, White Court, Grande Prairie, and Wapiti, Alberta, Canada, where hybrids were identified through cone and branch characteristics. Further

* Corresponding author: hartley@unbc.ca
† SWST Member
[1] Now with Canfor Pulp LP, Vancouver, V6S 2L9.

examples of pines found with mixed lodgepole–jack pine morphology were found between Yellowstone Lake, Wyoming, and Banff, Alberta; these trees displayed cone angles significantly smaller and more variable than lodgepole pine but not completely curved toward the branch as in jack pine (Wheeler and Guries 1987).

Although substantial morphological evidence exists to support hybridization, little evidence has been shown at the cellular level. Wood properties that might be useful for differentiation between pure pine populations and hybrids include fiber length, fiber coarseness (a measurement of fiber weight over length), microfibril angle (MFA), density, and earlywood:latewood (EW:LW) ratios. Wood cells and fibers vary with tree age, genetic influence of the parental trees, and environmental influences; differences in wood properties between species can be attributed to one of these factors or more probably from these factors in combination (Panshin and de Zeeuw 1980). Specific hybrids may possess wood quality characteristics highly desirable for end-use industries.

This study was conducted to find evidence of hybridization between jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta* var. *latifolia*) in the Fort Nelson region of northeast British Columbia (BC) using wood properties. Morphological evidence supporting hybridization in this area has been documented (Critchfield 1985; Wheeler and Guries 1987). Hybrid samples were collected for further investigation; samples genetically verified as hybrids (Wood 2006) were used for wood property analysis. Supportive evidence of hybridization in the Fort Nelson region of BC provides the scientific community with information about the variation in wood and fiber properties between hybrids and pure pine species. This research in hybrid wood quality also provides information for optimal forest use.

Specific objectives of this study were to compare pine species based on wood and fiber traits with correlation to genetic and morphological differences; to determine differences in morphology between species for proper identification in the field, providing visual evidence of hybridization so noted in the literature; and to determine if wood and fiber traits can be used as distinguishing features among jack pine, lodgepole pine, and their hybrids, which may be beneficial for industrial use.

METHODS

Sites and Sampling Design

Thirty samples of pure lodgepole pine were collected from the Prince George area of BC (53°51′05″ N. lat., 123°25′30″), 30 of pure jack pine were collected from Smoky Lake, Alberta (54°09′16″, 113°07′36″), and 30 potential hybrid samples were collected from the Fort Nelson region of BC (59°14′20″N. lat., 123°24′21″) (Fig 1). Twenty of the 30 samples collected from the Fort Nelson region were verified as hybrid lodgepole–jack pine trees (Wood 2006). Samples were gathered from nine sites within the three main forest stands. The first stand, located east of Smoky Lake, was composed of even-aged pure jack pine and was classified in the Bellis Lake and Bellis North natural areas of Alberta. The second stand used for sampling, composed of pure lodgepole pine, was within the SubBoreal Spruce biogeoclimatic

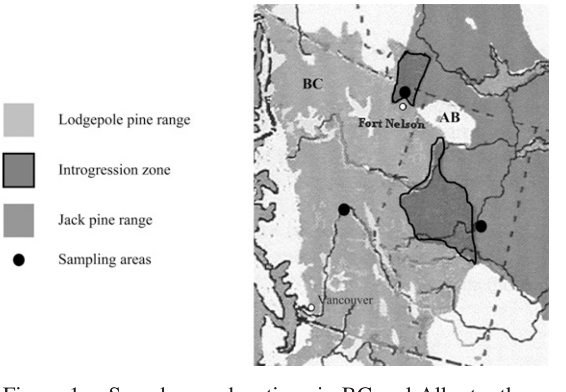

Figure 1. Sample area locations in BC and Alberta; three sites were located within each area. Original map taken from Wheeler and Guries (1987) with the extension of the northern introgression zone into BC.

zone, subzone moist–cool with a variant of 1 (SBSmk1) (Meidinger and Pojar 1991) and a site series of 03. The stand was an even-aged mature stand and subject to fairly heavy mountain pine beetle (*Dendroctonus ponderosae*) infestation; trees were selected that did not demonstrate symptoms of attack. The third study area was located north of Fort Nelson and was within the BWBSmw2, Boreal White, and Black Spruce biogeoclimatic zone, moist and warm subzone with a variant of 2. Site series for the areas sampled is 02, representing the lodgepole pine forest cover of the area (Delong et al 1990). This region was distinct because it was the only area found in BC where the species range of jack pine and lodgepole pine overlap. Composition was largely pine with some spruce (*Picea* spp.) and a small deciduous component.

Morphology

Cone length, orientation, and curvature as well as needle length and position were recorded. Data were analyzed by comparing characteristics to establish trends and interactions between variables. Pairwise comparisons were performed using SPSS software to compare each species group with respect to each characteristic. Cone length was measured from the tip of the cone to the base where the cone met the branch, not including any cone curvature. Measurements of cone height from the branch and length along the branch were also recorded to calculate the angle that the cone formed with the branch (Fig 2). Two cones per tree were measured depending on availability at time of sampling. In total, an average of 60 cones per sampling area was used to calculate cone dimensions. Hybrid cone dimensions were calculated with cones from those trees that were confirmed as genetic hybrids; a total of 38 hybrid cones were measured. Needle pair size, which is a ratio of width of needle "V" formation over needle length, was recorded (Fig 3). Five needle pairs per sample were measured to obtain average dimensions; 150 needles per sampling area were measured in total.

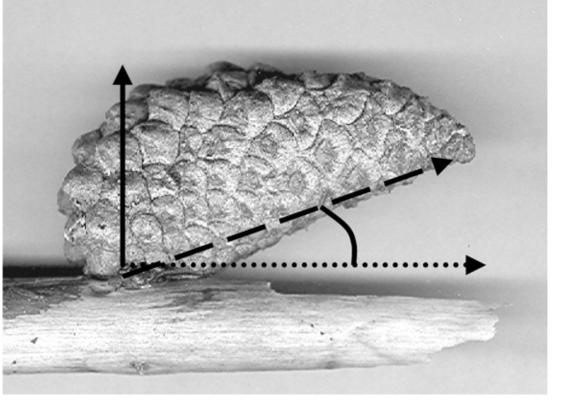

Figure 2. Cone measurements: Cone length was measured from the tip of the cone to the base where the cone met the branch, not including any cone curvature (dashed line). Measurements of cone height from the branch (solid line) and length along the branch (dotted line) were recorded to calculate the angle that the cone formed with the branch.

Wood and Fiber Traits

Two 10-mm cores (bark to bark) were taken from each tree sampled at breast height. Wood and fiber traits were measured through Fiber Quality Analysis (FQA) and SilviScan analysis. FQA was performed to obtain statistically correct measurements of fiber length and coarseness. Fibers for FQA were prepared using core segments from growth rings at age 20 – 40, 40 – 60, and 60 – 80. These were macerated using perchloric acid to produce a pulp, which was then dispersed to a low concentration in water (Franklin 1945).

Wood characteristics that were generally more difficult to assess such as microfibril angle and average cell dimensions were measured using SilviScan. This instrumentation combines X-ray densitometry, diffractometry, and image analysis to precisely evaluate cell properties. Fifteen samples for each site were randomly selected for this analysis.

RESULTS

Morphology

Jack pine needle pairs were characteristically much shorter and split in a wider "V" than

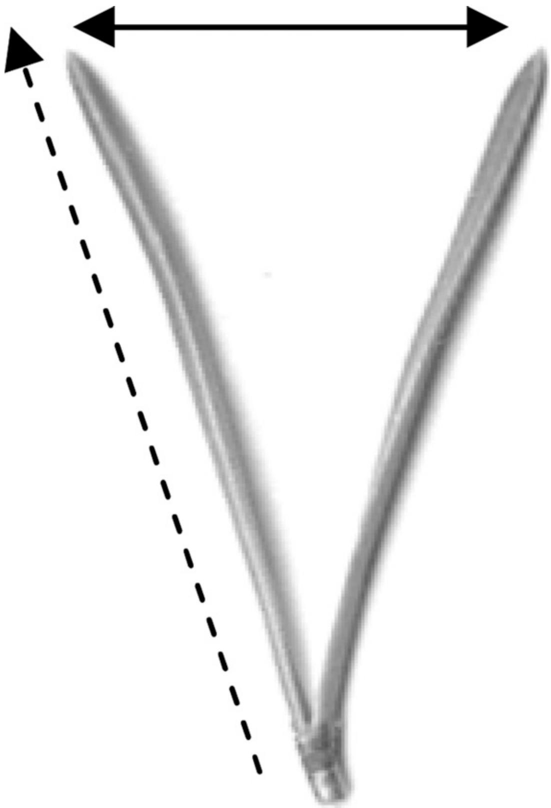

Figure 3. Needle measurements: A ratio of width of needle "V" formation (solid line) over needle length (dotted line) was used to compare samples; the width of the V is dependent on the length of the needles.

lodgepole pine needles, which were longer and oriented in a much tighter "V", yielding a significantly different formation (Fig 4). The hybrid pine needle measurements were found to be in between those of the other species and moderate in both length and "V" width. Species groups were statistically different ($\alpha = 0.05$) for needle pair sizes analyzed by pairwise comparison. Analysis of variance (ANOVA) indicates that there was a significant difference between needle–pair size ratios according to species group (Table 1). Therefore, this characteristic provides evidence of hybrid intermediacy within the regression zone and may indicate trait modification in the hybrids because of genetic recombination from pure pine parents that produced intermediate needle forms.

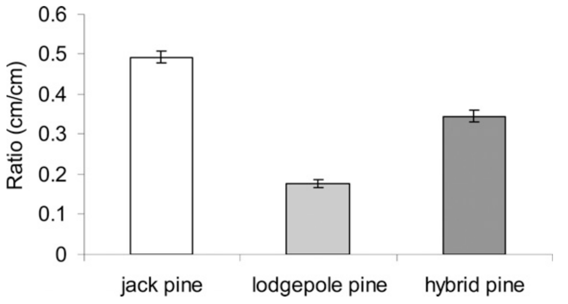

Figure 4. Average ratio of needle V width over needle length. Standard error bars present.

Mean cone angles of attachment to the branch were lowest in jack pine and highest in lodgepole pine (Fig 5), whereas hybrid pines showed intermediate cone angles. There were significant differences ($\alpha = 0.05$) between species groups. It was observed that generally the lower or more negative the cone angle value, the more curvature the cone displayed. Negative cone angles of attachment were indicative of the cone curving over the branch to the opposite side of which it began to grow. The pairwise comparison revealed that cone angles were significantly different among all three main species groups with a confidence interval of 95%. Further statistical analysis also revealed a strong significant relationship between cone angle of attachment and species group. ANOVA results were significant ($\alpha = 0.05$) and Pearson correlation coefficients displayed a strong correlation between cone angle and species type (Table 1). These results suggest that hybrid pine cone angles are a characteristic feature that may be genetically controlled and may have been influenced by both pure species, forming an intermediate, genetically recombined, characteristic cone angle. This finding parallels needle pair size, which also suggested a recombined intermediate characteristic.

Wood and Fiber Traits

Samples were categorized into age classes 0 – 20, 20 – 40, 40 – 60, and 60 – 80 to analyze fiber length and coarseness. Juvenile wood of northern pines is usually described as the first 20 – 25 yr

Table 1. *Statistical analysis of morphology and wood and fiber traits between species groups.*[a]

Characteristic	F statistic	*p* value	Pearson correlation coefficient
Fiber length segment age 60 – 80 (mm)	0.852	0.472	−0.137
Fiber length segment age 40 – 60 (mm)	4.371	0.004	−0.273
Fiber length segment age 20 – 40 (mm)	0.813	0.513	−0.327
Cell area (μm^2)	6.135	0.020	0.467
Microfibril angle (°)	11.298	0.002	−0.579
Fiber coarseness segment age 60 – 80 (mg/m)	4.628	0.006	−0.219
Fiber coarseness segment age 40 – 60 (mg/m)	6.362	0.000	−0.124
Fiber coarseness segment age 20 – 40 (mg/m)	0.922	0.462	0.306
Needle width/length ratio (cm/cm)	11.914	0.001	−0.352
Cone angle of attachment (°)	170.481	0.000	0.621
Cell wall thickness (μm)	6.985	0.007	−0.278
Earlywood:latewood ratios	2.073	0.162	0.417

[a] F-statistic and *p* value represent the analysis of variance results when determining the statistical difference between species groups for each trait. Pearson r-values represent the correlation between the trait and the species group.

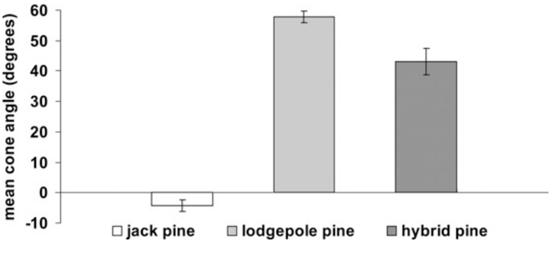

Figure 5. Mean cone angle for all species groups according to sampling area with standard error bars.

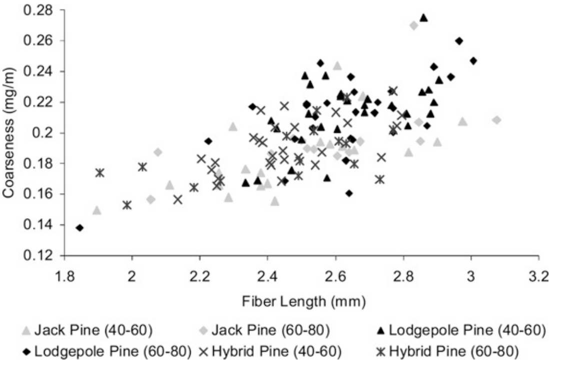

Figure 6. Fiber coarseness as a function of fiber length. Measurements by Fiber Quality Analysis.

of growth, and a gradual transition wood (a combination of juvenile and mature wood) is at times observed up until approximately Year 40 (Haygreen and Bowyer 1996; Koch 1996). The 40 – 60 and 60 – 80-yr core segments are described as the mature wood segments for this study. Each age class had a longer average fiber length than the prior age class, as expected, as a result of the transition from juvenile to mature wood (Hatton 1997). Throughout the age classes, lodgepole pine had the longest fibers on average, and hybrid fibers were the shortest. However, no significant explanatory power or correlation was found between fiber length and species group. The ANOVA ($\alpha = 0.05$) results indicate that species group was only significant to fiber length within wood segments aged 40 – 60 (Table 1).

The relationship between coarseness and fiber length for all samples in mature wood groups 40 – 60 and 60 – 80 yr is shown in Fig 6. Generally, jack pine samples were lower in coarseness and fiber length values than lodgepole pine samples. Hybrid samples seemed to be intermediate in both coarseness and fiber length according to this distribution. According to the statistical analysis performed, significant differences were found for species differentiation by fiber coarseness in the 40 – 60 and 60 – 80 age categories; however, correlations between species group and coarseness are low. Coarseness did not indicate intermediacy in hybrids but did demonstrate variation from pure species according to the pairwise comparison performed. Lodgepole pine samples had coarser fibers and were denser; hybrid fibers were the finest and samples were not as dense. This is indicative of an environmentally controlled characteristic. Fiber length and coarseness do not seem to demonstrate strong genetic variation at this level of genetic recombination. Therefore, it may be assumed that the physiological controls in the selected hybrid trees were responding to environmental factors such as temperature and precipitation and that these factors may play a more influential role in the formation of fiber coarseness and length than genetic variability.

Jack pine samples showed higher MFA than both lodgepole pine and hybrids throughout the entire core for most samples. Lodgepole pine had the lowest overall MFA, whereas MFA for hybrid samples showed more variability but was more similar to lodgepole pine than jack pine. These relationships were reflected almost continuously over the entire profile of the sample cores. Hybrids displayed clear intermediacy for this trait (Fig 7). Based on the statistical analysis, MFA could be considered one of the best distinguishing features among the species studied. The Pearson correlation coefficient shows a relatively significant negative correlation, –0.579, and ANOVA was significant ($\alpha = 0.05$; Table 1). Among the samples collected for this study, hybrid EW: LW ratios did not demonstrate intermediacy between pure species. Therefore, the more specific trait, cell wall thickness, was investigated in its relationship to EW:LW content. Measurements of cell wall thickness provide insight into the ratio of earlywood to latewood in a pith to bark profile because of the extreme thickness of the latewood material in comparison with the thin cell walls of the earlywood (Panshin and de Zeeuw 1980). Using SilviScan measurements, cell wall thickness is calculated as a function of the measured density and radial vs tangential cell diameter dimensions:

$$W = P/8 - 1/2(P/16 - C/d)1/2 \qquad (1)$$

where

$$P = 2(R + T) \qquad (2)$$

and R and T are the radial and tangential tracheid diameters, respectively, C is the tracheid coarseness, and d is the density (Jones et al 2005). The pairwise comparisons of each species group showed that the overall average cell wall thickness was significantly different ($\alpha = 0.05$) between jack pine and lodgepole pine and between lodgepole pine and hybrid pine, but not between jack pine and hybrids, suggesting that hybrid average cell wall thickness is more like that of jack pine. Cell wall thickness can therefore be used to distinguish between some samples, but not others, and cannot be used as an indicator of intermediacy in hybrids unless further analysis is performed.

Cell dimensions varied between species as represented by the average cell diameters shown in Fig 8. Lodgepole pine cells are, on average, larger in the tangential direction than the other species groups and smaller in the radial direction. Hybrid cells have intermediate average measurements in both directions. This may be a function of the species genetic ability to photosynthesize, a species-specific rate or amount of auxin produced, or a species ability to carry

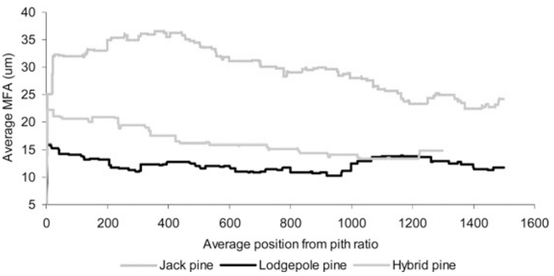

Figure 7. Microfibril angle average from pith to bark in each species group. Pith to bark position was divided by the diameter growth rate for each sample to directly compare samples.

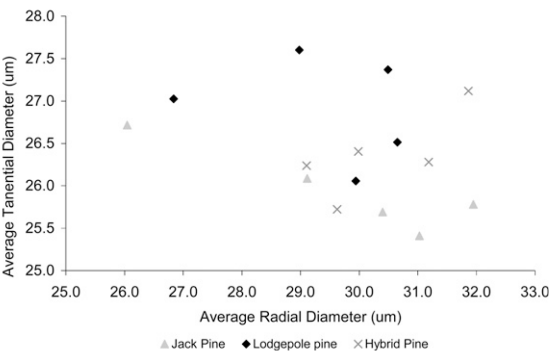

Figure 8. Average cell dimensions by species from SilviScan analysis.

out cell enlargement phases of development (Kozlowski 1979). For statistical analysis of cell proportions, the product of tangential and radial directions was calculated to yield an average cell area for each sample (mature wood only). The Pearson correlation coefficient for cell area was calculated as 0.467, which reveals a moderate positive relationship between cell area and species. ANOVA results indicate a significant difference among jack pine, lodgepole pine, and hybrids ($\alpha = 0.05$; Table 1). It should be noted that greater significance exists for these samples because of the difference in tangential direction measurements over radial direction measurements. Cell dimensions can therefore be used to distinguish among lodgepole pine, jack pine, and their hybrids for this study. Cell dimensions provide a moderate determination between species groups as represented in Fig 8; taking into consideration the environmental factors at play when investigating tree growth allows appreciation for this contribution as a definite factor in cell development. A degree of intermediacy can be seen in Fig 8 with respect to growth in the tangential direction; however, intermediacy is not clearly demonstrated in the radial direction. Cell area demonstrates significant differences between species groups (Table 1).

DISCUSSION

Morphology

Needle length, cone curvature, angle of cone attachment, and cone length were identified in a study by Wheeler and Guries (1987) as traits that had significant ability to distinguish between species. Each of these traits allowed for supportive species identification and, when observed in combination, allowed for accurate assessment of species type. The information provided by Lubischew's coefficient of determination (Christensen and Dar 2003) for the characteristics analyzed by Wheeler and Guries (1987) indicated that cone angle of attachment and needle length, among others, are very useful for discriminating between hybrids and pure pine species. This provides support for the use of these characteristics in this study and supports findings that revealed there is a large distinction between pine species based on their morphology. It was evident that jack pine samples possessed shorter, wider spread needle pairs when compared with lodgepole pine, along with a very different cone angle, and degree of cone curvature. According to Wheeler and Guries (1987), the coefficient of determination for angle of cone attachment is one of the most discriminating factors between jack pine and lodgepole pine, which supports the results in this study. Each of these characteristics played a key role in distinguishing jack pine from lodgepole pine and provides evidence of intermediate characteristics found in hybrid pines.

Wood and Fiber Traits

Natural hybrids can provide seed sources with already evolved genetic material (Savolainen and Kärkkäinen 2004). The lodgepole pine × jack pine hybrids that exist in the northeast corner of BC exhibit characteristics varying from the parental species and may therefore offer increased value to some products, depending on what traits are being sought. Wood quality needs vary depending on what is being produced. Low microfibril angles are important for solid wood axial stiffness and prevention of timber warping resulting from longitudinal shrinkage. Long fibers are important for solid wood strength and tearing strength in writing paper. Thin-walled cells as well as large lumens are important for production of tissue paper (Barnett and Jeronimidis 2003; Zobel 2004).

In this study, jack pine cells were larger in radial diameter than lodgepole pine cells. This could potentially be related to lower density values, which would indicate that jack pine wood is more suitable for products that do not require high density. It follows that the hybrid wood in this area would also be suited for similar products as a result of its comparable cell size.

Microfibril angle is also an important indicator of wood strength. Because MFA in hybrids was identified as an intermediate trait between lodgepole and jack pine, it can be assumed that wood produced from these hybrids would on average yield a moderate strength. This means that hybrid wood may be useful for low-grade wood products, composites, or paper.

Wood quality is said to be strongly inherited (van Buijtenen 2004) and therefore genetically improved tree stock, which can be the outcome of hybridization, has potential to greatly improve wood uniformity as well as other wood characteristics (Savolainen and Kärkkäinen 2004). Learning from naturally hybridized forest stands such as the jack pine × lodgepole pine stands investigated in this study will enable the scientific community to better understand what these populations have to offer the forest industry and how they should be managed for various purposes. Because these natural populations have been growing and evolving over a long period of time, they lend insight into effects that hybridization may have on environments and wood quality that are not obvious from newly formed plantation-based progeny.

Wood characteristics under genetic control, as confirmed to date, include latewood percentage, cell dimensions, chemical properties, and microfibril angle (van Buijtenen 2004). Other traits are being investigated for their genetic applicability. Latewood percentage ranges in heritability depending on the population in question; however, little more is known about EW:LW genetic relationships partially because of the difficulty in controlling very influential environmental conditions. The percentage of EW:LW in any given sample is heavily influenced by climate and other environmental factors (Kozlowski 1979). However, this variation can also be partially the result of genetic inheritance. If factors such as age of samples and site conditions were perfectly controlled, it may be possible to support interspecies variation based on EW:LW ratios. In a study by Ivkovich et al (2002), LW percentage in spruce was observed to have high heritability in both East Kootenay and Prince George study sites. This observation suggests that EW:LW ratios could be used as a species or population identifier. However, the pairwise comparison conducted in this study did not reveal any significant differences between the species groups. This characteristic may be more valuable for distinguishing between spruce populations as indicated in Ivkovich et al's (2002) study as a result of the slower transition between earlywood and latewood in spruce as opposed to the abrupt transition in pines (Panshin and de Zeeuw 1980).

Tracheid length, diameter, and cell wall thickness are all strongly inherited; variation in populations has been noted in lodgepole pine (van Buijtenen 2004), although not observed in this study. Chemical properties have been studied in relation to genetic inheritance since the 1970s, and genetic improvements in these areas have been accomplished. Lignin content has been studied most extensively because of its applications in the paper-making process, whereas less is known about genetic improvements to cellulose content. Lastly, very little is known about MFA heritability and this trait is still under investigation (van Buijtenen 2004). MFA could be a wood property with substantial potential for genetic variation. Fiber angle formation is not as directly affected by environmental factors as other wood properties, meaning that the genetic influence is not as masked by site conditions. Although environmental variation is always present to some extent, MFA varies only slightly with certain aspects of site such as slope and factors affecting formation of reaction wood (Panshin and de Zeeuw 1980). Further study is required on the intricacies of MFA and its formation based on environment and genetics to be more definite regarding the role of MFA in the differentiation of hybrids. For this study, MFA provides a statistical distinction between species.

Wood and fiber traits are related in many ways. Microfibril angle as well as fiber length are both a reflection of wood maturity (Barbour 2004), and fiber coarseness is directly correlated to cell wall thickness and therefore EW:LW ratio (Potter et al 2001). Awareness of these relationships is essential to the assessment of the wood quality of an individual or population for production purposes. Because the characteristics mentioned possess the ability to distinguish between species groups, it is possible to use them as predictive tools for hybridization. If a certain characteristic is measured, and falls within the measurement range that is characteristic for a hybrid as opposed to a pure jack pine or lodgepole pine, then assumptions can be derived that the species may be a hybrid without having to conduct a more invasive and time-consuming genetic analysis.

Managers or manufacturers can use this information to alter their practices to best suit the material with which they are working. Managers may adjust growing conditions to account for trees with faster or slower growth rates, and manufacturers may alter production to account for varying latewood content in raw wood. Wood that is being used for pulp products may be sorted according to variation in fiber coarseness to be processed more accurately.

CONCLUSIONS

Results indicate that genetic pine hybrids are in existence in the Fort Nelson area where lodgepole pine and jack pine ranges overlap. It was found that MFA, cell area, needle width-to-length ratio, and cone angle of attachment are the most distinctive traits for differentiation of jack pine × lodgepole pine hybrids in this region of BC. For field identification, needle width-to-length ratio and cone angle of attachment are the most useful characteristics for differentiating between all species groups (including the distinction of hybrids) while also demonstrating intermediacy in hybrids. Although relationships exist between the wood and fiber characteristics investigated, some provide a strong differentiation between species and some do not. Some traits revealed clear intermediacy between pure species and hybrids, whereas others were insignificant. Wood and fiber quality traits that were useful in identifying species groups were MFA and cell area; these traits also support the theory of intermediacy in hybrids. In addition to these characteristics, fiber length and coarseness can be used to differentiate among lodgepole pine, jack pine, and hybrids, however, no significant explanatory power exists for species contribution to the observed difference. Cell wall thickness can be used to distinguish between lodgepole pine and jack pine but was ineffective for distinguishing the subtle differences that exist in hybrids.

Possible sources of error that may have skewed results include variation in stand aspect and slope, wood types such as reaction wood that may have be present in the stems, and any undiagnosed disease or pest attack. These variables were controlled as well as possible, slope was minimized, stems were relatively uniform, and factors such as growth rate and site index taken into consideration; however, natural environments always yield some variation. To better support the conclusions drawn from the wood analysis portion of this study, alternate characteristics could be looked at to achieve greater confidence in the variability between species. It was suggested in a study by Christensen and Dar (2003) that number of resin ducts can be distinctive of species. This could be further investigated and related to percentage of EW and LW in this study to draw more conclusive evidence of differentiation between species groups and intermediacy of hybrids.

This study adds to the knowledge of genetically controlled wood characteristics. The significant influence that population groups had on MFA and cell dimensions in this study indicates that some wood properties are under significant genetic control. Knowledge of natural hybridization could potentially lead to management for select traits to obtain the best wood quality output for certain products and for optimal processing and manufacturing. This could potentially improve wood quality for end users, reduce waste wood, increase yield, and permit more cost-effective production.

ACKNOWLEDGMENTS

The authors acknowledge support through Evalutree (partnership among FPInnovations–

Paprican Division, University of Northern British Columbia and University of Victoria). Support was also provided by Dr. Hartley's NSERC Discovery Grant.

REFERENCES

Barbour J (2004) Wood quality. Pages 1840 – 1847 *in* J Evans, J Burley, J Youngquist, eds, Encyclopedia of forest sciences. Elsevier Major Reference Works, Oxford, UK.

Barnett JR, Jeronimidis G (2003) Wood quality and its biological basis. CRC Press LLC, Boca Raton, FL. 226 pp.

Christensen KI, Dar GH (2003) A morphometric study of hybridization between *Pinus mugo* and *P. sylvestris* (*Pinaceae*). Intern Soc Hortical Sci Acta Hort 615:211 – 221.

Critchfield WB (1985) The late quaternary history of lodgepole and jack pines. Can J Res 15:749 – 772.

Delong C, MacKinnon A, Jang L (1990) A field guide for identification and interpretation of ecosystems of the northeast portion of the Prince George forest region. BC Ministry of Forests. Pages 9 – 11, 21, 35.

Franklin GL (1945) Preparation of thin sections of synthetic resins and wood–resin composites, and a new macerating method for wood. Nature 155:51.

Hatton JV (1997) Pulping and papermaking properties of managed second growth softwoods. TAPPI J 80(1):178 – 184.

Haygreen JG, Bowyer JL (1996) Forest products and wood science. Iowa State University Press, Ames, IA. 484 pp.

Ivkovich M, Namkoong G, Koshy M (2002) Genetic variation in wood properties of interior spruce 2. Tracheid characteristics. Can J Res 32:2128 – 2139.

Jones PD, Schimleck LR, Peter GF, Daniels RF, Clark AI II (2005) Non-destructive estimation of *Pinus taeda* L tracheid morphological characteristics for samples from a wide range of sites in Georgia. Wood Sci Technol 39:529 – 545.

Koch P (1996) Lodgepole pine in North America, Vol. 1 – 3. Forest Products Society, Madison, WI. 1096 pp.

Kozlowski TT (1979) Tree growth and environmental stresses. The University of Washington Press, Seattle, WA. 192 pp.

Meidinger D, Pojar J (1991). Ecosystems of British Columbia. BC Ministry of Forests, Victoria, BC, Canada. 330 pp.

Panshin AJ, de Zeeuw C (1980) Textbook of wood technology, 4th ed. McGraw-Hill Inc. Toronto, Ontario, Canada. 722 pp.

Potter S, Hanemaayer V, Pitts S, Watson P (2001) Fiber quality prediction in BC spruce with DNA based methods. Pulp and Paper Research Institute of Canada, PPR 1528, Vancouver, BC.

Savolainen O, Kärkkäinen K (2004) Breeding and genetic resources of scots pine. Pages 1517 – 1520 *in* J Evans, J Burley, J Youngquist, eds, Encyclopedia of forest sciences. Elsevier Major Reference Works, Oxford, UK.

van Buijtenen JP (2004) Genetics and improvement of wood properties. Pages 1466 – 1472 *in* J Evans, J Burley, J Youngquist, eds, Encyclopedia of forest sciences. Elsevier Major Reference Works, Oxford, UK.

Wheeler NC, Guries RP (1987) A quantitative measure of introgression between lodgepole and jack pines. Can J Bot 65:1876 – 1885.

Wood LJ (2006) An investigation of the natural hybridization between jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta* var. *latifolia*) in Northern British Columbia. MSc thesis, University of Northern British Columbia, Prince George, BC, Canada. 251 pp.

Woodruff D (1973) Natural hybridization and hybrid zones. Syst Zool 22:213 – 218.

Zobel B (2004) Biological improvement of wood properties. Pages 1458 – 1466 *in* J Evans, J Burley, J Youngquist, eds, Encyclopedia of forest sciences. Elsevier Major Reference Works, Oxford, UK.